# On the wings of change
# Species' responses in fragmented landscapes under climate change

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## ABSTRACT

Climate change influences nature. In North-West Europe species respond to climate change – increasing temperatures and weather variability – by moving northward and by showing increased population fluctuations. It is however not only important that species can move and recover from fluctuations, but also that they can do that in time, considering the current fragmentation of nature areas. This study was carried out to (1) increase our understanding of the influence of weather and climate change on demographic processes (dispersal, reproduction, survival) in faunal populations, and (2) to disentangle the interaction between the influence of weather and climate change on the one hand, and habitat fragmentation on the other hand, on demographic processes in populations. I took birds and butterflies as study species. Considering species characteristics, I showed that dispersal capacity, migration strategy, and diet type correlate to responses of species to changing weather conditions. These responses can be positive – climate change may diminish the effects of fragmentation by enhancing flight behaviour and dispersal of butterflies – or negative – advanced spring timing may lead to mismatches in food supply of passerine birds. I showed that both positive and negative responses at the individual level can lead to parallel responses at the (meta)population level. At these higher organization levels, (meta)population viability is also affected by the landscape pattern. I showed that increasing spatial cohesion, patch size, and amount of suitable habitat can enhance (meta)population viability and recovery under climate change. Such measures are already known to counteract effects of habitat fragmentation, but this study shows their additive usefulness in adapting to effects of climate change.

# 1
# Introduction

Once upon a time, somewhere in the ninth century, there was an Emperor living in Kyoto, at that time the capital of Japan. The Emperor decided to give a party under the flowering cherry trees of his estate, when the trees were in full bloom. From then on, the parties under the flowering cherry blossoms became a tradition, which was prolonged by the next Emperors in Kyoto. The timing of the parties, and thus the timing of the flowering has been registered since then. Hence, to date, a record of phenological data on cherry blooming dates exists. The blooming dates give a fairly accurate record of spring warmth in the vicinity of Kyoto since the ninth century (Arakawa 1956). Such records make clear that currently the global climate is drastically changing (e.g. Roy & Sparks 2000; Menzel et al. 2006). About 11 centuries since the first party under the Emperor's cherry blossoms in Kyoto, during a conference in the same city a protocol was drawn up to reduce the human impact on climate change.

The Intergovernmental Panel on Climate Change (IPCC) expects that global climate change will influence our environment for the coming decades and centuries (IPCC 2001). Already nowadays, a change in weather patterns can be observed in the Netherlands, and these are expected to be persistent (MNP 2005, see Table 1). Means in temperature and precipitation will rise, and more frequently extreme weather events will occur.

Climate is the driving force beyond many ecological processes (e.g. IPCC 2001). Hence, climate change sorts a noticeable effect on species and ecosystems (Fig. 1.1). Humans perceive this impact from their direct environment by the timing of natural processes in the life cycle of species, such as flowering, fruiting, and the starting dates of reproduction (McCleery & Perrins 1998; Visser et al. 1998). Temperature rise affects the phenology of natural processes, as became clear from the story about the Japanese emperor. Crick et al. (1997) show for instance that many bird species in the United Kingdom have advanced their date of egg laying by almost 9 days on average over few previous decades. Moreover, a rising temperature, next to the increased atmospheric greenhouse gas concentration, leads to a direct enforcement of physiological processes, such as photosynthesis, growth, and decomposition. Hughes (2000) showed that for plants, the growth rate has been increased by the increased atmospheric $CO_2$ concentration since 1850 AD. On a longer time-scale, even evolutionary impacts are likely: species may adapt themselves genetically to the new climatic conditions (Hughes 2000).

**Table 1.1**

Climatic development for the Netherlands (MNP 2005)

| weather variable | | present situation | future expectations (ca. 2040 and later) |
|---|---|---|---|
| temperature | - average | + 1˚C (esp. since 1975) | + 1˚C to + 6˚C (2100) |
| | - extreme heat | 3 times as much warm days (since 1990) | extra increase in extremes |
| | - extreme cold | 0.5 times as much cold days (since 1990) | little decrease in extremes |
| precipitation | - average | ca. 20% more (since 1990) | probably decrease in; most probably increase in winter |
| | - extreme intensity | > 50% more days with > 15, 20, or 25 mm | uncertain chance of more intense rain showers |
| | - extreme drought | probably more dry years | probably more and longer dry periods |
| summer evapo-transpiration | | proportional to temperature rise | + 4% to + 16%  (2100) |
| wind | | most probably decrease in number of storms (since 1962) | uncertain chance of extreme storms |

Since climatic conditions determine the potentially suitable habitats for species, climate change – increasing temperatures – can also lead to shifts in the habitat distribution of species. Hence, climate change interacts with the landscape pattern. For species, it is important that their habitats are located within areas where the climatic conditions required for survival occur. Such shifts in habitat distribu-

tions are noticed for many species (Parmesan 1996; Parmesan et al. 1999; Hughes 2000; Parmesan & Yohe 2003). For most of these species, the range margins on the warm edges retreat in the direction of colder conditions. At the other sides of the ranges, new habitat areas evolve. Parmesan & Yohe (2003) show in a literature review, which considers the ranges of 460 species of divergent taxa, that 81% of these species has shifted their ranges in the direction of the (predicted) climate change. Species shifting their ranges due to climate change is an ongoing process that is expected to continue in the coming centuries (Hughes 2000).
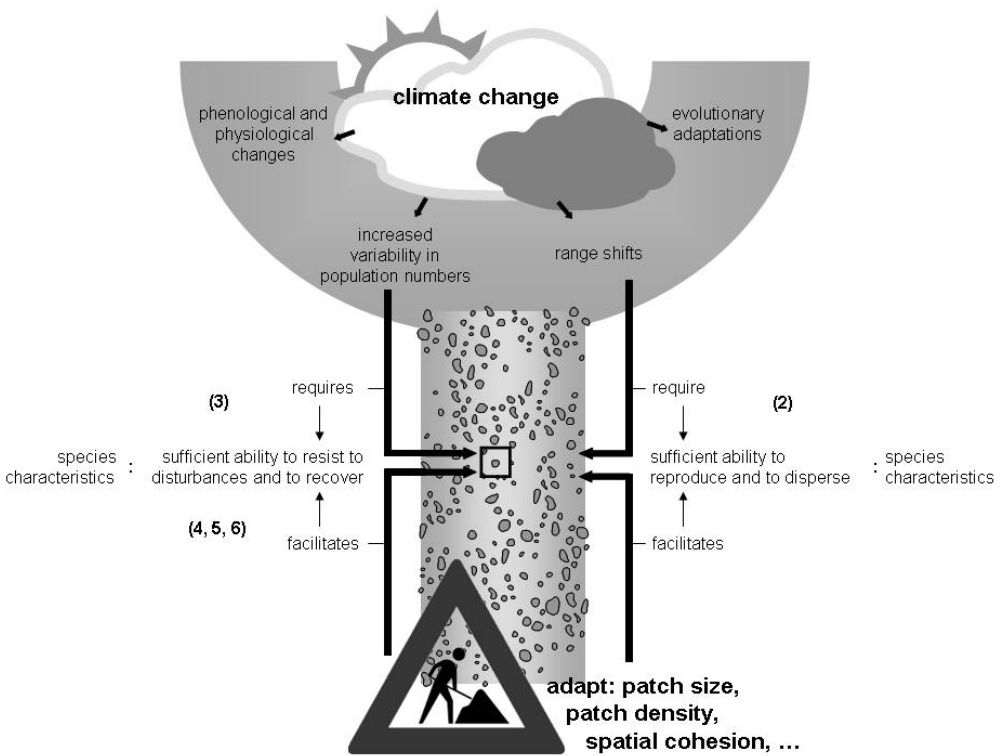


**Figure 1.1**

Effects of climate change, species characteristics, and facilitations by spatial adaptation measures at (meta)population to range level; (2)-(6): chapter number. This thesis elaborates demographic processes in a spatial context.

The settlement rates of species to their newly evolved habitats depend on the reproduction rates and the dispersal capacities (Clobert et al. 2004). By now, various mobile species, originally occurring up to the southern Netherlands, also appear in the rest of the country. Such a northward shift within two decades was shown for the distribution pattern of the Comma butterfly (*Polygonia c-album*); a mobile species that can traverse large distances over unsuitable terrain and therefore is able to respond rapidly to changing environmental conditions (Van Swaay 2004). Less mobile species require longer periods to shift to emerging suitable areas in the expanding part of their geographical range, and whether these species will ever reach these locations depends on the extent of habitat fragmentation and the level to which the species are controlled by this.

Another manifestation of climate change is the increased weather variability, with consequences on demographic processes (Drake 2005). Population numbers may oscillate more strongly due to extreme weather events. The consequences of large-scale extreme weather events on metapopulations, affecting the constituting local populations assembled in the spatially scattered metapopulation simultaneously, is largely missing from literature (Hanski 2001). Smaller densities and a lower percentage of habitat occupation decrease the resilience of metapopulations to increased environmental disturbance, compared to large continuous populations (Akçakaya & Baur 1996; McCarthy & Lindenmayer 2000; Piessens et al. 2009). After an extreme weather event, metapopulation recovery time is extended compared to large continuous populations, since extinction and colonization processes cause a less effective distribution over habitat, and because dispersal mortality is high (Opdam & Wascher 2004). The configurations of patches in a network may affect the recovery time of a metapopulation after a catastrophic weather event. Large patches (e.g. key patches) can serve as sources for recolonization of smaller patches (sinks) in the network after environmental disturbance (Verboom et al. 2001). Besides, an increased patch size and exchange of individuals can enhance the stability of source patches, considering a larger resilience after a catastrophe (Foppen et al. 2000). However, in networks with a weak spatial cohesion, effects of large-scale disturbances are stronger, causing local (temporary) extinction of populations (Richter-Dyn & Goel 1972; Pimm et al. 1988). Hence, as with range shifts due to temperature rise, weather and population variability interferes with the landscape pattern (Piha et al. 2007).

The extent of declines in population numbers after extreme weather events, as well as the duration of recovery depends on the growth rates of the species populations. Growth rates are species specific, and so is recovery time. Since large-scale climatic disturbances can reduce growth rates, recovery times can be extended (Foppen et al. 1999).

Responding to a rising temperature requires that species can disperse to and build up populations in newly emerging habitat sites, while responding to increased weather fluctuations requires either resistance to disturbances or a fast recovery rate (Fig. 1.1). Species' demographic processes – reproduction, survival, and dispersal - are therefore even more crucial when climate change interacts with the spatial pattern (Keith et al. 2008; Thuiller et al. 2008). The balance between these processes in determining species dynamics is species specific, and depends on their life-history traits or characteristics. Hence, while changing weather conditions affect processes at the level of individuals (Keddy 1992; Díaz et al. 1998), the sum of all these individual responses is expressed at the level of metapopulations (Jiguet et al. 2006), while the sum of responses of a large set of metapopulations is expressed as a range shift at the biogeographic level (Warren et al. 2001). Therefore, understanding the response of species to the combined effect of climate change and habitat fragmentation starts at the individual level. However, adaptation measures are targeted at the level of metapopulations, which eventually affect range dynamics.

When (meta)populations of a species respond to changing weather conditions by a decrease in number, landscape characteristics could alleviate this effect (Fig. 1.1): in networks with for instance a large spatial cohesion, species can move to escape hostile weather conditions, or recovery rates could be increased (Foppen et al. 1999). However, where spatial conditions are insufficient, we can adapt the landscape pattern. Offensive spatial adaptation measures can contribute to the development of sustainable ecological networks (Opdam et al. 2003). To identify the most effective spatial adaptation measure, it is necessary to find out how landscape characteristics affect population growth and expansion – and hence (meta)population viability – under climate change.

## 1.1 AIMS AND QUESTIONS

This study is carried out (1) to increase our understanding of the influence of weather and climate change on demographic processes (dispersal, reproduction, survival) in faunal populations, and (2) to study to what extent landscape characteristics determine responses on demographic processes in populations to changing weather conditions. The main question relating to the first aim that needs to be answered is:

*What species characteristics considering dispersal capacity, reproduction, and survival correlate to responses to changing weather conditions?*

The following question needs to be answered in relation to the second aim:

*How can landscape characteristics (patch size and density, spatial cohesion) affect local population growth, dispersal, and extinction risks, and subsequently (meta) population viability under climate change?*

Answering these main questions will help to discuss how measures can facilitate in adapting fragmented landscapes to effects of climate change and how they offer perspectives for nature conservation to mitigate the impacts of climate change.

## 1.2 STRUCTURE OF THE THESIS

To answer the questions, several methodological techniques have been applied. Time series of both census data for species and weather records have been used, as well as field surveys and modelling approaches. All techniques complement each other in building a bridge to spatial planning and design. In my thesis I connect characteristics of individuals and processes at the individual level to dynamics of metapopulations in climate-affected habitat configurations. The study was carried out using data collected in the Netherlands. Of all faunal species studied in the Netherlands, birds and butterflies are investigated most extensively, and over the longest time span. For this study, several bird and butterfly species have been selected to investigate their responses to climate change. Butterflies are ectothermic species, and their behaviour is controlled by temperature. For the next century, the spatial scale of their shifts in habitat distribution is likely to resemble the extent of the Netherlands. For birds, on the spatial scale of the Neth-

erlands, the rising trend in temperatures is expected to show minimal effects on the persistence of the species for the coming decades. Yet, on this scale increased weather variability may be translated into species' demography.

For – ectothermic – butterfly species, dispersal capacities are expected to be influenced by climate change. In a field study (Chapter 2), individual butterflies were captured and released, and subsequently tracked to study the flight behaviour and mobility of the individuals. Tendencies to start and stop flying, and time spent flying have been recorded, as well as the short-distance dispersal routes. The spatial and temporal analyses of the track records in relation to weather measurements have provided data on climatic effects on dispersal parameters, that were subsequently used in the models described in Chapters 5 and 6, and could be compared to monitoring data on colonization frequencies, obtained from standardized transect counts.

Dispersal propensity, reproduction, migration strategy, and diet type are life-history traits that make species sensitive to or benefit from specific weather events. In Chapter 3, I investigated how breeding bird species can be grouped, based on their life-history traits and according to weather-correlated variation in their abundances. Extrapolating these correlations to the future, it is possible to point out bird species that are expected to show most significant responses to changing weather conditions under climate change.

Density distribution patterns of a specific bird species, Great bittern (*Botaurus stellaris*) have been compared to weather data, collected during the last decades in the Netherlands. With this correlative study (Chapter 4), I investigate the contribution of landscape characteristics patch size and spatial cohesion to population growth and recovery rates.

Mechanistic models incorporating processes such as reproduction, mortality, and dispersal can be used to disentangle the mechanisms underlying metapopulation dynamics. Such a model has been developed for a univoltine butterfly species, of which all processes are affected by daily weather (Chapter 5). With this model, I study the effect of patch size and amount of suitable habitat on population viability under climate change.

In chapter 5 I assumed a stable state of the habitat network. However, climate change can affect habitat quality and suitability, and thereby the spatial configu-

ration of the habitat network. To investigate this effect, I brought the model used in Chapter 5 a step further and extended them with soil and plant development models; this allowed me to study the indirect impact of climate change on habitat quality to the univoltine butterfly species on top of the direct effect on demographic processes. In this way, the model can be used as an assessment model in landscape planning at the regional scale that incorporates complex effects of climate change. In the case study described in Chapter 6, the positions of potential weak spots in an ecological network became apparent. As in Chapters 4 and 5, I suggest spatial adaptation measures to compensate for the pressure of a changing climate in a fragmented landscape.

# 2

# Effect of local weather on butterfly flight behaviour, movement, and colonization: significance for dispersal under climate change

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ABSTRACT

Recent climate change is recognized as a main cause of shifts in geographical distributions of species. The impacts of climate change may be aggravated by habitat fragmentation, causing regional or large scale extinctions. However, we propose that climate change also may diminish the effects of fragmentation by enhancing flight behaviour and dispersal of ectothermic species like butterflies. We show that under weather conditions associated with anticipated climate change, behavioural components of dispersal of butterflies are enhanced, and colonization frequencies increase. In a field study, we recorded flight behaviour and mobility of four butterfly species: two habitat generalists (*Coenonympha pamphilus*; *Maniola jurtina*) and two specialists (*Melitaea athalia*; *Plebejus argus*), under different weather conditions. Flying bout duration generally increased with temperature and decreased with cloudiness. Proportion of time spent flying decreased with cloudiness. Net displacement generally increased with temperature. When butterflies fly longer, start flying more readily and fly over longer distances, we expect dispersal propensity to increase. Monitoring data showed that colonization frequencies moreover increased with temperature and radiation and decreased with cloudiness. Increased dispersal propensity at local scale might therefore lower the impact of habitat fragmentation on the distribution at a regional scale. Synergetic effects of climate change and habitat fragmentation on population dynamics and species distributions might therefore appear to be more complex than previously assumed.

## 2.1 INTRODUCTION

Climate change causes shifts in geographical distributions of species (Parmesan & Yohe 2003; Root et al. 2003). Such shifts are considered to be the result of (meta)population extinction at the equatorial range boundary, and poleward colonization in regions where climatic conditions have newly become suitable (Opdam & Wascher 2004). Parmesan & Yohe (2003) reported shifts in the direction of the predicted climate change for 81% of 460 species of diverse taxa. Warren et al. (2001) expected butterfly species approaching their northern climatic range margins in Britain to respond positively to climate warming over the past decennia. Yet, only a quarter of these species increased their area of geographical distribution, supposedly because positive responses to climate warming were outweighed by negative effects of habitat fragmentation, especially for less mobile specialists (Travis 2003). Other empirical studies (Schwartz et al. 2001; Devictor et al. 2008; Anderson et al. 2009) confirm for other species groups that a response to climate change may be hampered by habitat fragmentation.

Habitat availability and spatial cohesion of habitat patterns play a crucial role in the persistence of species under global temperature rise: below a critical threshold the expansion of ranges will be blocked and species can rapidly become extinct (Travis 2003; Opdam & Wascher 2004). Increased frequency of extreme weather events will moreover cause overall range contraction, especially with relatively low spatial cohesion (Opdam & Wascher 2004).

However, these statements on detrimental effects of climate change in fragmented habitat assume that habitat availability, habitat use and interpatch movement do not vary under the expected climate change regime. Thomas et al. (2001) show that such assumptions may not be realistic, as they found a significant broadening of the range of habitats used by Silver-spotted skipper, *Hesperia comma*, spreading into north-facing hill slope habitats that were previously climatically not suitable. We suggest that for butterflies, interpatch movement can be facilitated if dispersal propensity will be enhanced by climate change. Butterfly behaviour responds to weather conditions, as is shown by previous studies (Clench 1966; Brown 1970; Douwes 1976; Shreeve 1984; Brattstrom et al. 2008). These studies, however, focus on single weather parameters, species or types of behaviour, and do no elucidate the link between weather, behaviour, and dispersal.

In practice, butterfly dispersal is difficult to measure. Butterflies are not robust enough to carry biotelemetry transmitters (Van Dyck & Baguette 2005). In this paper we therefore use a proxy for dispersal, and assume that dispersal propensity will increase as individuals of species fly over longer bout durations, increase their tendency to start flying, spend more time flying, and fly over longer distances (cf. Morales & Ellner 2002; Van Dyck & Baguette 2005; Nathan et al. 2008). We recorded flight behaviour and mobility of four butterfly species under variable weather conditions. Because dispersal differs widely between species, we consider two habitat generalist and two specialist species. Next, we tested whether dispersal propensities and patch colonization probability are indeed enhanced by the favourable weather conditions emerging from the field study. To this effect we correlated data on annual colonization frequencies from monitoring transects counts to weather conditions.

## 2.2   METHODS

### 2.2.1 Study area

The fieldwork was carried out in National Park 'De Hoge Veluwe' in the centre of the Netherlands (Fig. 2.1 ; 52°02'-52°07' N; 5°47'-5°52' E; elevation about 40m asl.) during the summers of 2006 and 2007. The total area of the park is 5,500 hectares, including 2,500 hectares of heathland and inland dunes.

### 2.2.2 Studied species

Four butterfly species were studied: the habitat generalists Small heath, *Coenonympha pamphilus* and Meadow brown, *Maniola jurtina*, and specialists Heath fritillary, *Melitaea athalia* and Silver-studded blue, *Plebejus argus*.

*C. pamphilus* is a common resident in the Netherlands (Bos et al. 2006). It lives in open mosaic habitats such as grasslands, dunes, roadside verges, and gardens (Van Swaay 2003). The species is bivoltine (first flight period from May 20 – July 20, and July 29 – September 5 for the second generation, on average) and not very
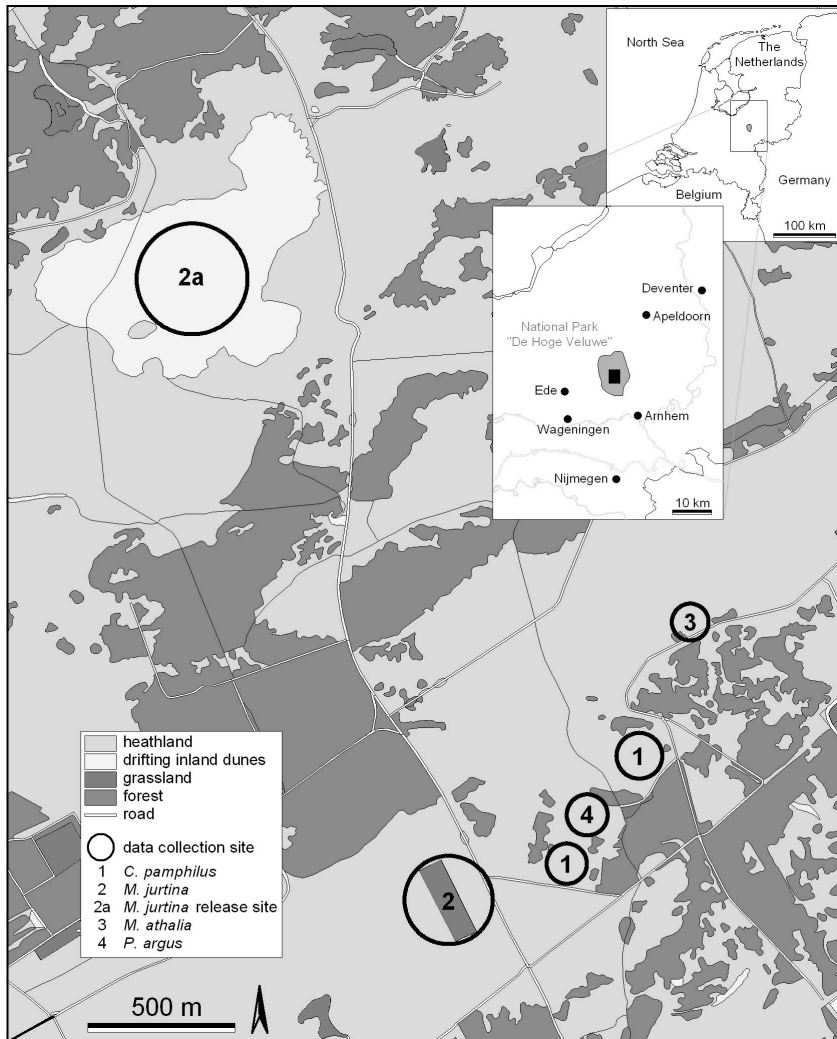
**Figure 2.1**

Study area within National Park 'De Hoge Veluwe' indicating location of data collection sites per species. Inset shows location of the National Park in the Netherlands

mobile. Only minor range shifts are expected in response to climate change for *C. pamphilus* (Settele et al. 2008).

*M. jurtina* is a common resident in the Netherlands. It lives in a variety of rough grasslands and open woodlands. The butterfly is univoltine (average flight period: June 26 – August 15) and quite mobile. In response to climate change, only minor range shifts are anticipated for *M. jurtina* (Settele et al. 2008).

*M. athalia* has become a very rare resident in the Netherlands, nowadays restricted to the Veluwe area. Suitable habitats are sunny, open places in forests such as woodland edges, newly felled woodlands and clearings in coppice. The species is univoltine (average flight period: June 16 – July 15) and sedentary. Still, in response to climate change, *M. athalia* is expected to show northward range expansion (Hill et al. 2002; Berry et al. 2007).

*P. argus* is a scarce resident in the Netherlands, classified as vulnerable on the Dutch Red List. *P. argus* lives both in dry and wet heathlands with sparse vegetation and patches of bare ground. It is a univoltine species (average flight period: June 26 – August 5) and rather sedentary. In response to climate change, *P. argus* is expected to show northward range expansion (Hill et al. 2002; Berry et al. 2007). We studied mostly male individuals of *P. argus*, because the inconspicuously coloured females were more difficult to track.

### 2.2.3 Measured weather variables

Climate is often defined as meteorological conditions (wind, humidity, temperature, cloudiness, precipitation, etc) over long periods, usually 30 to 50 years (Barry & Chorley 2003). Effects of climate or climate change should therefore be studied with data gathered over long time spans. Weather is the short-term manifestation of meteorological conditions and changes can therefore be observed within the time frame of a field study. We considered four weather variables that influence activity and dispersal (Clench 1966; Douwes 1976; Shreeve 1984; Mitikka et al. 2008): ambient temperature (measured with mercury thermometer placed in the shade; in Celsius (°C)), cloudiness (observer's estimation in percentage cover), wind speed (observer's estimation or measured with anemometer; in Beaufort (Bft)), and a proxy for solar radiation. The solar radiation proxy was determined by placing a black and white surface in the sun, and measuring the surface temperatures using a portable infrared thermometer. The difference in temperature between the surfaces is a measure of temperature gain by solar radiation (Van Dyck & Matthysen 1998).

*2.2.4 Data collection*

The fieldwork was conducted in 2006 and 2007 from mid June until mid August. Observations took place between 10.00-17.00 hours. A total of 207 tracks (114 in 2007), were recorded for the four species: *C. pamphilus* 106 tracks (73 in 2007); *M. jurtina* 55 (22); *M. athalia* 23 (12); and *P. argus* 23 (7). For each track, a butterfly was caught in a net and its sex was determined. The butterfly was coded with permanent marker on the underside of both hindwings. After release from the net, we allowed the butterfly to calm down before behavioural observations started. We followed the butterfly at a distance of 2-5 metres. To each activity, we assigned one of the potential behaviour types: flying, nectaring, resting (with wings closed), basking (with wings opened perpendicular to the sun), testing (the abdominal and antennal exploration of a host plant associated with ovipositing, (Root & Kareiva 1984)), or ovipositing. The time spent in each of the activities was recorded. Each individual was followed for 30 minutes, or until lost from sight. We used a GPS device (2006: Garmin eTrexVenture™; 2007: HP iPAQ hw6500) to record the track locations. The four studied species of butterflies were tracked within their habitat (see Fig. 2.1). In addition, in 2007 we conducted release experiments for *M. jurtina* in an area of drifting inland dunes, that we considered as non-habitat to this species. In this hostile environment, we tracked the behaviour and mobility of 8 individuals as if they were moving between habitat patches. The release site was located at a distance of approximately 2000m from the catching site, which is much further than the perceptual range of individuals (100-150 m according to Conradt et al. (2001)). We used only *M. jurtina* for the release experiments, because it was most abundant, not endangered, and easiest to track in an open, windy environment. Each individual was tracked only once.

At the beginning of each track, we measured temperature, wind speed and cloud cover. At the end of the observation we re-measured temperature, wind speed, and determined the temperature difference between the black and white surfaces (further referred to as radiation; Table 2.1). In the Netherlands, the summer of 2006 was hot and dry in June and July (July was on average the hottest month since the beginning of the records by the Royal Netherlands Meteorological Institute in 1706), while August was relatively chilly and rainy. After a very mild spring, the weather during the summer of 2007 was changeable and rainy.

**Table 2.1**

Means (standard deviation) of temperature, radiation, cloudiness, and wind speed during the field-work in 2006 and 2007

| year | temperature (˚C) | radiation (˚C) | cloudiness (%) | wind speed (Bft) |
|------|------------------|----------------|----------------|------------------|
| 2006 | 26.5 (4.7)       | 17.6 (8.3)     | 47.0 (39.5)    | 3.3 (1.7)        |
| 2007 | 19.5 (3.4)       | 16.3 (9.1)     | 52.4 (28.0)    | 3.6 (2.3)        |

*2.2.5 Survival analysis*

The field data of 2006 and 2007 together were used to assess the influence of the measured weather variables on the observed duration of flying bouts (i.e. the time of uninterrupted flight behaviour (Haccou & Meelis 1992)) and non-flying bouts (i.e. nectaring, resting, basking, testing, or ovipositing) per species. We summed the durations of all consecutive non-flight behaviour as a single non-flying bout. The nature of the data (i.e. 'time-to-event' data with censors) required the application of survival analysis (Kleinbaum & Klein 2005). Censoring occurred when the observation time elapsed or when the butterfly was lost from sight. Cox's proportional hazards model was used to analyze which weather variables affected the tendency of a butterfly to terminate a bout. It was assumed that butterflies have a basic tendency to stop a specific behaviour (baseline hazard). Therefore, the observed hazard rate (the observed tendency to stop a specific behaviour) is the product of the baseline hazard and a factor that gives the joint effect of all covariates (here, weather variables). The general form of the model is (Haccou & Hemerik 1985; Kalbfleisch & Prentice 2002):

$$h(t; x_i, ..., x_p) = h_0(t) \cdot \exp\left(\sum_{i=1}^{p} \beta_i x_i\right) \qquad \text{[in probability per time unit]}$$

where $h(t; x_i, ..., x_p)$ represents the observed hazard rate at time $t$ with $p$ fixed covariates having values $x_i, ..., x_p$; $h_0(t)$ is the baseline hazard; $t$ is the time since the last bout termination; and $x_i$ is the vector of covariates. The baseline hazard is multiplied by an exponential function that expresses the multiplicative effect of the 1 to $p$ covariates, multiplied by the corresponding regression parameters $\beta_i$. If a particular covariate $x_i$ does not influence the observed hazard rate, then $\beta_i$ does

not differ significantly from 0. The estimates for the regression coefficients are used to compute a hazard ratio (HR), which describes the effect of the covariate (Kalbfleisch & Prentice 2002). Its significance is assessed with a Z score. Covariates used in the analysis were coded as categorical since the measurements were unevenly spread over the ranges: temperature (°C; $T$), radiation (°C; $R$), cloudiness (% cloud cover; $C$), wind speed (m/s; $W$), gender ($G$; male versus baseline female), and year ($Y$; 2007 versus baseline 2006; representing unmeasured factors changing between years, e.g. food supply). Weather variables were clustered into 'low', 'intermediate', and 'high' categories to distinguish optimum or unidirectional effects of weather variables on the duration of bouts (Table 2.2). We based the clustering of covariates on Kaplan-Meier plots. A Kaplan-Meier survival curve is a step function that decreases from 1 (all individuals are still flying at time $t$) toward a minimum value >0 due to termination of flying bouts. Kaplan-Meier survival curves should be parallel for all covariate categories, i.e. should not cross (Kalbfleisch & Prentice 2002), in order to be able to assume proportionality estimating the effect size in Cox model(s). We plotted Kaplan-Meier survival curves for flying bouts for all covariate values separately, to see under what values curves do not cross (for an example see Appendix 2.1). Clustering was subsequently based on best Kaplan-Meier plot appearance. Next, we tested for pairwise differences in behavioural response under low, intermediate and high weather categories. The effects of single weather variables were estimated simultaneously with other weather variables. We used R 2.7.0 software (Ihaka & Gentleman 1996) to perform the survival analysis. For *P. argus*, temperature, cloudiness, and wind speed were highly correlated, and differed strongly between years (see Appendix 2.2). Therefore, only radiation was used in the analysis, together with gender and year.

### 2.2.6 Time budget analysis

For each tracked individual, we calculated the proportion of time devoted to a certain behaviour. We tested for differences between weather categories in proportion of time spent flying as opposed to non-flight behaviour, using Wilcoxon rank sum test (W) in R 2.7.0. Ten individuals devoting their total tracked time to flight behaviour, were excluded from the analysis, because these individuals were lost from sight within the first recorded bout. Time budget analysis (Miron et al.

1992) is complementary to survival analysis, since possible changes in bout duration are compensated by changes in occurrence of these bouts.

**Table 2.2**

Clustering of weather variables into 'low', 'intermediate', and 'high' categories per species, resulting from Kaplan-Meier survival curves for flying bouts

| weather variable | category | C. pamphilus | M. jurtina | M. athalia | P. argus |
|---|---|---|---|---|---|
| temperature ($T$; in $°C$) | low | $T{\le}19.5$ | $T{\le}20$ | $T{\le}14$ | $T{\le}22$ |
| | intermediate | $19.5{<}T{\le}25.5$ | $20{<}T{\le}31$ | $14{<}T{\le}25$ | $22{<}T{\le}28$ |
| | high | $T{>}25.5$ | $T{>}31$ | $T{>}25$ | $T{>}28$ |
| radiation ($R$; in $°C$) | low | $R{\le}12$ | $R{\le}10$ | $R{\le}14$ | $R{\le}17$ |
| | intermediate | $12{<}R{\le}28$ | $10{<}R{\le}20$ | $14{<}R{\le}31$ | $17{<}R{\le}20$ |
| | high | $R{>}28$ | $R{>}20$ | $R{>}31$ | $R{>}20$ |
| cloudiness ($C$; in %) | low | $C{\le}15$ | $C{\le}15$ | $C{\le}25$ | $C{=}0$ |
| | intermediate | $15{<}C{\le}60$ | $15{<}C{\le}70$ | $25{<}C{\le}70$ | $0{<}C{\le}20$ |
| | high | $C{>}60$ | $C{>}70$ | $C{>}70$ | $C{>}20$ |
| wind speed ($W$; in $Bft$) | low | $W{\le}1$ | $W{\le}2$ | $W{\le}3$ | $W{\le}2$ |
| | intermediate | $1{<}W{\le}2$ | $2{<}W{\le}4$ | $3{<}W{\le}4$ | $2{<}W{\le}3$ |
| | high | $W{>}2$ | $W{>}4$ | $W{>}4$ | $W{>}3$ |

*2.2.7 Spatial analysis*

Spatial coordinates were recorded at a constant time interval (2006: 10 seconds; 2007: 1 second) by the GPS device. Coordinates derived from the Garmin eTrexVenture™ were transformed into .shp files using GPS2Shape software (Jochem 2006). Successive points were connected with straight lines and are further referred to as steps. For each individual, we analysed the total pathway, determining tortuosity as the standard deviation in turning angle in proportion to a full circle (in radians divided by $2\pi$) and the net displacement of the pathway (i.e. the distance between the track starting and ending points; in metres). The effects of weather variables on tortuosity and net displacement were tested using regression analysis with generalized linear models in R 2.7.0.

In addition, we compared the tortuosity and net displacement of the pathways of released individuals of *M. jurtina* with pathway characteristics of individuals tracked within their habitat using Wilcoxon rank sum test (W) in R 2.7.0. The effects of weather variables and presence of habitat on tortuosity and net displacement were tested using regression analysis with generalized linear models in R 2.7.0 and Akaike's information criterion for model selection (Burnham & Anderson 2002).

*2.2.8 Colonization frequency*

Data on colonization frequency were obtained from the Dutch Butterfly Monitoring Scheme monitoring (Van Swaay et al. 2008), with standardized transect counts over the period 1990-2008. The total number of transects where the study species were sighted strongly differed between species: 452 for *C. pamphilus*, 737 for *M. jurtina*, 22 for *M. athalia*, and 155 for *P. argus*. Because of the small sample size, we excluded *M. athalia* from this analysis. A colonization event for a particular species was defined as a sighting of at least one individual after two years of absence. Absences were only counted as such when sufficient counts were carried out during the flight period. Relative colonization frequencies were then calculated on an annual basis between 1992 and 2008 as the number of transects with colonizations relative to the total number of actively counted transects where the species might be expected, i.e. where it had been sighted in the period 1990-2008. Data on daily temperature (mean and maximum; in ˚C), radiation (in $J/cm^2$, converted to temperature differences in ˚C), cloudiness (in octants, converted to %), and wind speed (in m/s, converted to Bft) were obtained from the Royal Netherlands Meteorological Institute (www.knmi.nl) for the flight periods of the three species. For each year, we averaged the weather variables over the flight periods. The effects of average weather variables on colonization frequencies were tested using regression analysis with generalized linear models in R 2.7.0. We corrected for possible effects of density dependence by taking national population numbers (as indices) into consideration. The effect of both the current and the previous year's weather was included (see also Roy et al. 2001). The current year's weather is assumed to affect dispersal propensity of individuals that will subsequently be sighted on a transect, newly colonized due to their dispersal. The previous year's weather is assumed to affect dispersal propensity of individuals that will subse-

quently reproduce on a transect, newly colonized after their dispersal; their offspring will be sighted in the following year.

## 2.3  RESULTS

### 2.3.1 Survival analysis

Results of the survival analysis are on tendencies to stop flying (behaviour type: flying; Table 2.3) or to start flying (behaviour type non-flying; Table 2.4). A greater tendency to stop flying implies shorter flight duration. The duration of flying bouts extended with high temperatures (*C. pamphilus*, P=0.01; *M. jurtina*, P=0.013). Intermediate and high radiation extended duration of flying bouts for *P. argus* (P=0.011, P=0.002 resp.), but high radiation showed negative effects on the duration of flying bouts for *C. pamphilus* (P=0.01). Intermediate and high cloudiness reduced the duration of flying bouts (*M. athalia*, P=0.002, P=0.001 resp.; *C. pamphilus*, P=0.017 for high cloudiness only). Intermediate and high wind speed also showed negative effects on the duration of flying bouts (*C. pamphilus*, P=0.006, P=0.0004 resp.) In general, males exhibited longer flights than females (*C. pamphilus*, P=0.014) and in 2007, flight durations were longer (*M. jurtina*, P=0.005; *M. athalia*, P=0.025).

The tendency to start flying was enhanced at intermediate and high temperatures (*M. jurtina*, P=0.018, P=0.039 resp.), and at intermediate and high radiation (*C. pamphilus*, P=0.004; *M. athalia*, P=0.004, P=0.002 resp.). Intermediate and high cloudiness showed negative effects on this tendency for *C. pamphilus* (P=0.026; P<0.0001 resp.) and *M. athalia* (P=0.038 for intermediate cloudiness only), while it was enhanced at intermediate cloudiness for *M. jurtina* (P=0.015). The tendency to start flying was not affected by wind speed, while in general it was enhanced for males (*C. pamphilus*, P=0.026; *P. argus*, P=0.045).

The influence of measured wind speed on observed duration of flying and non-flying bouts for *C. pamphilus* is summarized in the scheme in Appendix 2.3, based on both Tables 2.3 and 2.4. The width of the bars shows the duration of flying and non-flying bouts relative to the baseline situation (wind speed ≤ 1Bft).

**Table 2.3**

Results survival analysis for flight behaviour based on multivariate Cox's proportional hazards model

| species: | *C. pamphilus* (n=853) | | | *M. jurtina* (n=420) | | |
|---|---|---|---|---|---|---|
| covariate | coef | P | l:i:h | coef | P | l:i:h |
| gender (male) | -0.241 | 0.014 | | -0.101 | 0.53 | |
| year (2007) | -0.018 | 0.87 | | -0.896 | 0.005 | |
| low:intermediate temperature | 0.032 | 0.74 | | -0.328 | 0.28 | |
| low:high temperature | -0.487 | 0.01 | a:a:b | -0.795 | 0.013 | a:a:b |
| intermediate:high temperature | -0.519 | 0.002 | | -0.467 | 0.008 | |
| low:intermediate radiation | 0.09 | 0.39 | | -0.031 | 0.83 | |
| low:high radiation | 0.321 | 0.01 | a:a:b | -0.076 | 0.67 | a:a:a |
| intermediate:high radiation | 0.231 | 0.046 | | -0.045 | 0.79 | |
| low:intermediate cloudiness | 0.147 | 0.15 | | -0.376 | 0.05 | |
| low:high cloudiness | 0.285 | 0.017 | a:ab:b | -0.296 | 0.12 | a:a:a |
| intermediate:high cloudiness | 0.138 | 0.152 | | 0.080 | 0.58 | |
| low:intermediate wind speed | 0.277 | 0.006 | | -0.092 | 0.46 | |
| low:high wind speed | 0.414 | 0.0004 | a:b:b | 0.483 | 0.17 | a:a:a |
| intermediate:high wind speed | 0.137 | 0.17 | | 0.575 | 0.10 | |

| species: | *M. athalia* (n=174) | | | *P. argus* (n=141) | | |
|---|---|---|---|---|---|---|
| covariate | coef | P | l:i:h | coef | P | l:i:h |
| gender (male) | -0.011 | 0.96 | | -0.599 | 0.12 | |
| year (2007) | -1.008 | 0.025 | | 0.334 | 0.14 | |
| low:intermediate temperature | -0.99 | 0.19 | | | | |
| low:high temperature | 0.467 | 0.66 | ab:a:b | | | |
| intermediate:high temperature | 1.456 | 0.0495 | | | | |
| low:intermediate radiation | 1.129 | 0.12 | | -0.574 | 0.011 | |
| low:high radiation | -0.2 | 0.82 | ab:a:b | -0.795 | 0.002 | a:b:b |
| intermediate:high radiation | -1.329 | 0.008 | | -0.221 | 0.36 | |

Table 2.3 (continued)

| species: | *M. athalia* (n=174) | | | *P. argus* (n=141) | | |
|---|---|---|---|---|---|---|
| covariate | coef | P | l:i:h | coef | P | l:i:h |
| low:intermediate cloudiness | 2.893 | 0.002 | | | | |
| low:high cloudiness | 3.791 | 0.001 | a:b:b | | | |
| intermediate:high cloudiness | 0.898 | 0.17 | | | | |
| low:intermediate wind speed | -0.145 | 0.58 | | | | |
| low:high wind speed | NA | NA | a:a:a | | | |
| intermediate:high wind speed | 0.145 | 0.58 | | | | |

n is number of bouts; l:i:h is category abbreviations: low:intermediate:high; NA could not be tested due to lack of data; effects are on tendencies to stop flying; P values based on Z score; categories sharing the same letter (a,b,c) are not significantly different (P>0.05).

### 2.3.2 Time budget analysis

The proportion of time spent flying was not affected by temperature (Fig. 2.2). This proportion was less for low radiation, compared with intermediate and high radiation (*C. pamphilus*, $W_{low:intermediate}$=715.5, P=0.029; $W_{low:high}$=161.5, P=0.042). The proportion of time spent flying was affected by cloudiness in various ways, depending on the species. It decreased from low to intermediate to high cloudiness for *C. pamphilus* ($W_{low:intermediate}$=584, P=0.029; $W_{low:high}$=513, P=0.001; $W_{intermediate:high}$=1124, P=0.019), it showed an optimum at intermediate cloudiness for *M. jurtina* (less time was devoted to flight behaviour under low and high cloudiness in respect to intermediate cloudiness; $W_{low:intermediate}$=10, P=0.009; $W_{intermediate:high}$=208, P=0.026), and it showed a minimum for intermediate cloudiness for *M. athalia* (more time was devoted to flight behaviour under low and high cloudiness in respect to intermediate cloudiness; $W_{low:intermediate}$=53, P=0.028; $W_{intermediate:high}$=8, P=0.043). The proportion of time spent flying was less at low wind speed than at intermediate and high wind speed (*C. pamphilus,* $W_{low:intermediate}$=705, P=0.036; $W_{low:high}$=444, P=0.014).

**Table 2.4**

Results survival analysis for non-flight behaviour based on multivariate Cox's proportional hazards model

| species: | *C. pamphilus* (n=870) | | | *M. jurtina* (n=406) | | |
|---|---|---|---|---|---|---|
| covariate | coef | P | l:i:h | coef | P | l:i:h |
| gender (male) | 0.324 | 0.0003 | | 0.039 | 0.82 | |
| year (2007) | 0.169 | 0.082 | | 0.6124 | 0.078 | |
| low:intermediate temperature | -0.112 | 0.2 | | 0.779 | 0.018 | |
| low:high temperature | NA | NA | a:a:NA | 0.716 | 0.039 | a:b:b |
| intermediate:high temperature | NA | NA | | -0.063 | 0.72 | |
| low:intermediate radiation | 0.282 | 0.004 | | -0.004 | 0.98 | |
| low:high radiation | 0.32 | 0.004 | a:b:b | -0.222 | 0.21 | a:a:a |
| intermediate:high radiation | 0.038 | 0.68 | | -0.218 | 0.18 | |
| low:intermediate cloudiness | -0.23 | 0.026 | | 0.457 | 0.015 | |
| low:high cloudiness | -0.651 | 0.0000 | a:b:c | 0.109 | 0.55 | ac:b:c |
| intermediate:high cloudiness | -0.422 | 0.002 | | -0.348 | 0.017 | |
| low:intermediate wind speed | -0.071 | 0.41 | | -0.113 | 0.39 | |
| low:high wind speed | NA | NA | a:a:NA | -0.343 | 0.36 | a:a:a |
| intermediate:high wind speed | NA | NA | | -0.230 | 0.52 | |

| species: | *M. athalia* (n=182) | | | *P. argus* (n=146) | | |
|---|---|---|---|---|---|---|
| covariate | coef | P | l:i:h | coef | P | l:i:h |
| gender (male) | -0.086 | 0.65 | | 0.695 | 0.045 | |
| year (2007) | 1.004 | 0.028 | | -0.72 | 0.002 | |
| low:intermediate temperature | 0.248 | 0.68 | | | | |
| low:high temperature | -1.053 | 0.22 | ab:a:b | | | |
| intermediate:high temperature | -1.301 | 0.038 | | | | |
| low:intermediate radiation | 1.467 | 0.004 | | 0.217 | 0.33 | |
| low:high radiation | 2.14 | 0.002 | a:b:b | -0.373 | 0.12 | ab:a:b |
| intermediate:high radiation | 0.673 | 0.109 | | -0.591 | 0.01 | |

Table 2.4 (continued)

| species: | M. athalia (n=182) | | | P. argus (n=146) | | |
|---|---|---|---|---|---|---|
| covariate | coef | P | l:i:h | coef | P | l:i:h |
| low:intermediate cloudiness | -1.463 | 0.038 | | | | |
| low:high cloudiness | -0.065 | 0.94 | a:b:a | | | |
| intermediate:high cloudiness | 1.399 | 0.049 | | | | |
| low:intermediate wind speed | -0.196 | 0.49 | | | | |
| low:high wind speed | NA | NA | a:a:a | | | |
| intermediate:high wind speed | -0.196 | 0.49 | | | | |

n is number of bouts; l:i:h is category abbreviations: low:intermediate:high; NA could not be tested due to lack of data; effects are on tendencies to start flying; P values based on Z score; categories sharing the same letter (a,b,c) are not significantly different (P>0.05).



(a)                                        (b)
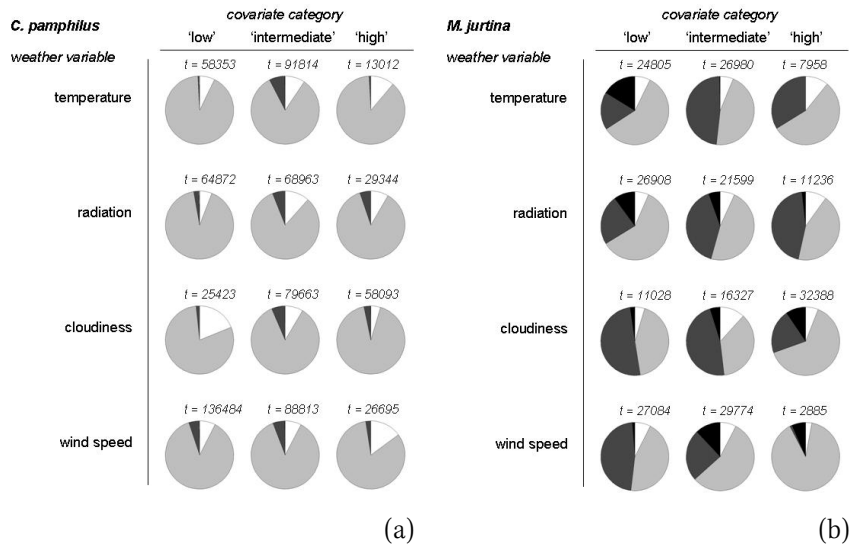
Figure 2.2

Proportion of time devoted to certain behaviour is shown per weather variable and covariate category. White slices represent flight behaviour; darker tones indicate non-flight behaviour; t = recorded time per covariate category in seconds
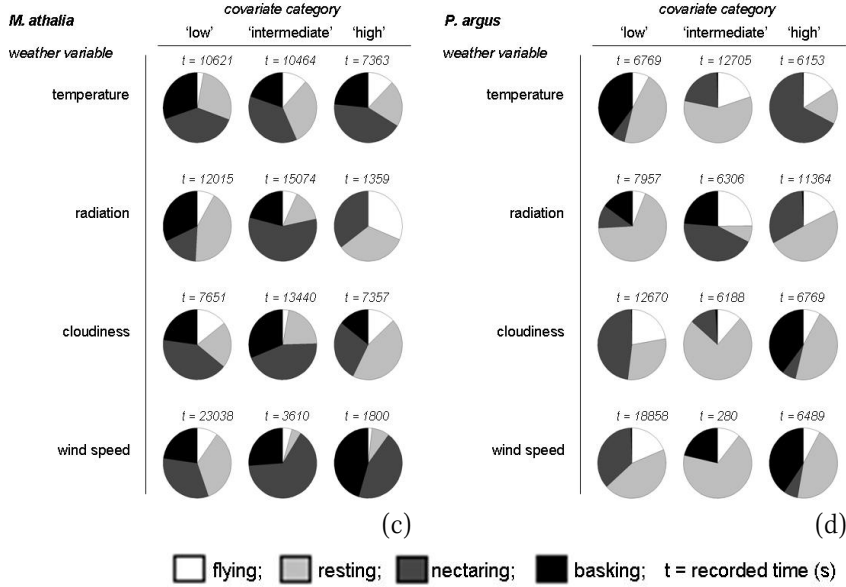
Figure 2.2 (continued)

### 2.3.3 Spatial analysis

The tortuosity of pathways of none of the species was affected by the weather variables (Table 2.5). Net displacements were greater at higher temperatures (*C. pamphilus*, P=0.003; *M. athalia*, P=0.034). However, *M. jurtina* showed increased net displacements at lower temperatures (P=0.001) and at higher radiation (P=0.004) and *M. athalia* showed greater displacements at higher wind speed (P=0.0283).

Pathway tortuosity of *M. jurtina* in non-habitat was smaller than within its habitat (Fig. 2.3; W=319, P=0.002). Net displacements of pathways of *M. jurtina* were greater in non-habitat (W=33, P<0.0001).

### 2.3.4 Colonization frequency

For *C. pamphilus*, colonization frequencies decreased with average cloudiness, experienced during the flight periods of the previous year, and with average wind speed during the flight periods of the current year (Table 2.6; best model). Cloudiness showed as well negative effects on flight propensity and proportion, and

**Table 2.5**

Effects of weather variables on tortuosity and net displacements of pathways for best models, based on AIC; '-' not included in best model

| species: | C. pamphilus | M. jurtina | M. athalia | P. argus |
|---|---|---|---|---|
| *tortuosity* | AIC | | | |
| best model: | | | | |
|    temperature | **-182.88** | **-99.75** | -10.30 | -24.73 |
|    temperature+radiation | -181.15 | -97.90 | **-12.47** | -23.07 |
|    radiation | -181.80 | -99.36 | -10.07 | **-24.97** |
| full model: | -179.37 | -95.96 | -9.94 | -19.60 |
| null model: | -182.55 | -101.28 | -11.58 | -26.66 |
| | estimates best models | | | |
| intercept | 0.300 | 0.255 | 0.916 | 0.214 |
| temperature | -0.004 | -0.001 | -0.033 | - |
| radiation | - | - | -0.010 | 0.001 |
| cloudiness | - | - | - | - |
| wind speed | - | - | - | - |
| *net displacement* | AIC | | | |
| best model: | | | | |
|    temperature | **731.82** | 436.00 | 120.93 | |
|    temperature+radiation | 733.72 | **428.97** | 122.79 | |
|    temperature+radiation+wind | 733.46 | 430.50 | **116.72** | |
|    radiation | 738.74 | 438.82 | 123.06 | **81.42** [a] |
| full model: | 733.53 | 432.48 | 117.04 | |
| null model: | 739.12 | 441.93 | 124.03 | 81.38 |
| | estimates best models | | | |
| intercept | -44.988 | 40.544 | -338.712 | 17.519 |
| temperature | 3.902 | -1.619 | 14.806 | - |
| radiation | - | 1.2961 | -3.935 | 0.784 |
| cloudiness | - | - | - | - |
| wind speed | - | - | 76.085 | - |

[a] only radiation used in analysis
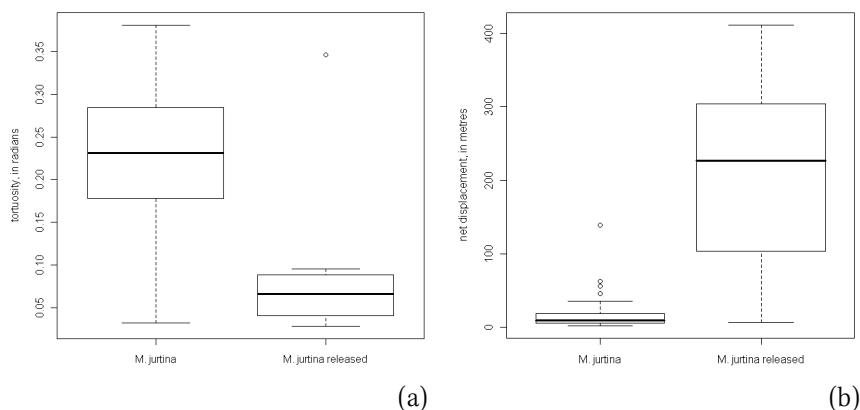
**Figure 2.3**

Differences in tortuosity (A; W=319, P=0.002) and net displacements (B; W=33, P=3.552e-05) of pathways of released and non-released individuals of *M. jurtina*

wind speed showed a negative effect on net displacement in the field study. For *M. jurtina*, colonization frequencies increased with average radiation during the flight period of the current year. Radiation showed as well a positive effect on net displacement in the field study. Models incorporating average temperature, maximum temperature, or cloudiness performed also well, due to high correlations between weather variables. For *P. argus*, colonization frequencies increased with average temperature during the flight period of the current year and average wind speed during the flight period of the previous year. In the field study, neither weather variables significantly affected the flight behaviour of *P. argus*.

## 2.4   DISCUSSION

We have shown that duration of flying bouts and net displacement of butterflies generally increased with temperature; duration of flying bouts and proportion of time spent flying decreased with cloudiness. When butterflies fly longer bouts, start flying more readily, spend more time flying, and fly over longer distances, we expect dispersal propensity to increase. Furthermore, the higher the flight activity

Table 2.6

Effects of average weather variables on colonization frequencies, measured over flight periods during 1991-2008; for best models, based on AIC; '-' not included in best model

| species: | C. pamphilus [b] | M. jurtina | P. argus |
|---|---|---|---|
| | AIC | | |
| best model: | | | |
|   cloudiness *t-1* + wind speed *t* [a] | **68.50** | 60.05 | 95.52 |
|   radiation *t* | 81.35 | **54.19** | 89.91 |
|   temperature *t* + wind speed *t-1* | 74.42 | 56.09 | **83.25** |
| full model: | 66.25 | 62.11 | 92.66 |
| null model: | 79.47 | 57.04 | 93.99 |
| | estimates best models | | |
| intercept | 29.408 | -3.783 | -35.527 |
| temperature *t* | - | - | 0.115 |
| radiation *t* | - | 0.003 | - |
| cloudiness *t-1* | -2.950 | - | - |
| wind speed *t* | -0.377 | - | - |
| wind speed *t-1* | - | - | 0.642 |

[a] colonization frequencies correlated to population indices and weather conditions experienced during the flight period of the same year (t) or the previous year (t-1)

[b] weather conditions during flight periods first and second generation of C. pamphilus taken together

the higher the probability to leave a patch. We have shown that colonization frequencies increased with temperature and radiation and decreased with cloudiness. We conclude that these results suggest that patches of habitat in a fragmented landscape are more readily colonized in periods with weather conditions favourable for dispersal. Therefore, we argue that climate change not only aggravates the impacts of habitat fragmentation on populations (Warren et al. 2001; Travis 2003; Opdam & Wascher 2004), but also may diminish these impacts by enhancing dispersal and colonization. This is indeed shown in the successful northwards range expansion of mobile generalist species (Warren et al. 2001). Further evidence supporting this view was found by Møller et al. (2006), who

found increased dispersal tendencies in a coastal seabird, the Arctic tern, in relation with long-term climate change. Moreover, increased dispersal tendencies in bush crickets in response to improving environmental conditions at their range margins have been reported by Thomas et al. (2001) and Simmons and Thomas (2004). Our study shows that increased dispersal under climate change may also apply to moderately mobile species.

The tendency to start flying was enhanced by increasing radiation (*C. pamphilus, M. athalia*), as expected. Males of *C. pamphilus* exhibited longer flights and flew off more readily than females. This was also found by Wickman (1985), and can be related to mate-locating and territorial behaviour (Shreeve 1984; Van Dyck & Matthysen 1998 for *Pararge aegeria*; cf. Fischer & Fiedler 2001 for *Lycaena hippothoe*; and Merckx et al. 2006).

The proportion of time spent flying was less at low solar radiation for *C. pamphilus*. For the other species this effect also seemed apparent (see Fig. 2.2), but effects were not significant. This may be due to two reasons: first, for the time budget analyses (in contrast to the survival analyses), only the effects of single weather variables were tested, without correction for other weather variables that acted simultaneously. Therefore, the effect of radiation can be masked by effects of other weather parameters. Second, in the field, each individual was tracked only once, under a particular set of weather conditions. Between individuals, the proportion of time spent flying differed greatly (see Appendix 2.4), so that differences in flight behaviour as a function of weather could not be demonstrated. The results of the survival analyses may also have been affected by differences between individuals. Unfortunately, tracking individuals more than once and under different weather conditions, was not practically feasible, because the weather did not change drastically within an individual's lifespan.

We expected an increase in cloudiness to shorten flying bouts, reduce the tendency to start flying, and decrease the proportion of time spent flying (after Dennis & Sparks 2006). We can recognize these effects in the behaviour of *C. pamphilus* (Tables 2.3&2.4 and Fig. 2.2A). For *M. jurtina*, however, the proportion of time spent flying showed an optimum at intermediate cloudiness (between 15 and 70%; Fig. 2.2B). Also, the tendency to start flying was enhanced by intermediate cloudiness (Table 2.4). We observed the opposite response for *M. athalia* (Fig.

2.2C). This result is difficult to explain and may be due to the small number of observations for *M. athalia*.

The weather variables did not show any effects on tortuosity. Net displacement, however, increased with higher temperature (*C. pamphilus* and *M. athalia*), radiation (*M. jurtina*), and wind speed (*M. athalia*). Individuals flying with increased net displacement but without altering tortuosity, will explore larger parts of their environment. In doing so, explorative individuals may increase the probability to encounter suitable habitat.

Released individuals of *M. jurtina* showed flight patterns resembling those found by Conradt et al. (2000): the butterflies either followed a more or less linear route or flew in large petal-like loops around the release site. Both types of flight pattern are significantly less tortuous than the patterns shown by individuals of *M. jurtina* flying within their habitat. Moreover, all but one of the individuals crossed longer distances outside their habitat than within. These findings confirm the statement by Van Dyck and Baguette (2005) that movement behaviour of animals outside their habitat differs considerably in speed and tortuosity from the routine explorative movements for local resource-use purposes. Flying straight over large distances in non-habitat is an efficient way to find new suitable habitat (Zollner & Lima 1999). Individuals of *M. jurtina* indeed explore the landscape efficiently, which is shown by the rapid colonization of the Dutch polder Flevoland after reclamation (Bos et al. 2006), over distances of 20 km within two decades after the first sightings.

We propose that climate change may diminish the effects of fragmentation by enhancing flight behaviour and dispersal of butterflies, and presumably also other ectothermic species. However, the probability to encounter suitable conditions for flight activity during dispersal might prevent this higher activity to lead to higher dispersal. If this probability is low, dispersal is expected to be less successful as dispersing individuals will take longer to reach a next patch of suitable habitat. These individuals will therefore have to remain longer in a hostile environment with reduced chances of survival. We propose that adding more suitable habitat should thus lead to more efficient and more successful dispersal at an increased survival rate. In butterflies, adopting straight movements for dispersal reduces its costs in fragmented landscapes (Schtickzelle et al. 2007). Butterflies

might therefore prefer continuous, line-shaped connections or corridors (cf. Noordijk et al. 2008).

A colonization event for a particular species was defined as a sighting of at least one individual after two years of absence. The observation of a single individual can be considered as a conservative estimate of a colonization event. The transect data are taken from optimal habitat and necessarily constitute samples from a population. Therefore, it is quite likely that the observation of only a single individual on a given transect in a particular year is rather representing a low population density of the sampled population rather than a vagrant individual. In any case, our results are not affected by applying a threshold of more than 1 individual. The majority (62%) of the identified colonizations concerned multiple individuals and the correlation between the total number of colonizations in different years with and without the threshold was very high (r=0.93).

### 2.4.1 Implications of future climate

Due to climate change, weather conditions in the Netherlands are predicted to change significantly during summer (Van den Hurk et al. 2007). Depending on the climate scenario, average annual temperature rise is predicted 1 to 2 °C until 2050. More hot (and dry) periods are predicted to occur as a result of more frequent easterly winds. Our results suggest that especially habitat generalists such as *C. pamphilus* and *M. jurtina* will respond by flying in longer bouts (Table 2.7). Net displacement of the habitat specialist *M. athalia* is expected to increase with more frequent easterly winds bringing clearer skies and higher solar radiation (Fig. 2.4). Especially *C. pamphilus* and *M. athalia* may then be expected to fly more readily and over longer periods, which might enhance dispersal.

The possibility to reach new habitats is a prerequisite under changing climatic conditions (Vos et al. 2008). Individuals must be able to cross distances over unsuitable environments. This study indicates that climate change may increase dispersal propensity in butterflies, as ectothermic species with generally poor mobility. Incorporation of these insights in metapopulation models is necessary to improve predictions on the effects of climate change on shifting ranges.

Table 2.7

Response on climate change regarding flight behaviour and mobility; + increase; - decrease; = neutral

| type of flight behaviour/ mobility per species | C. pamphilus | M. jurtina | M. athalia | P. argus |
|---|---|---|---|---|
| duration of flying bouts | + | + | + | + |
| tendency to start flying | + | + | + | = |
| proportion of time spent flying | + | - | + | = |
| tortuosity | = | = | = | = |
| net displacement | + | - | + | = |

## ACKNOWLEDGMENTS

APPENDIX



**Appendix 2.1**

Kaplan-Meier survival curve for flying bouts of *M. athalia* with temperature as single covariate. Under low temperature (solid line; less or equal to 14˚C), butterflies terminate flying bouts sooner than under intermediate temperature (between 14 and 25˚C; dashed line; P = 2.9E-08) and high temperature (more than 25˚C; dotted line; P = 1.1E-09)

**Appendix 2.2**

Correlations between covariates from field study

|  | G | Y | T | R | C | W |
|---|---|---|---|---|---|---|
| species: *C. pamphilus* | | | | | | |
| gender (G) | 1 | | | | | |
| year (Y) | 0.30 | 1 | | | | |
| temperature (T) | 0.03 | -0.42 | 1 | | | |
| radiation (R) | -0.05 | -0.23 | 0.44 | 1 | | |
| cloudiness (C) | -0.09 | 0.31 | -0.67 | -0.30 | 1 | |
| wind speed (W) | -0.06 | -0.07 | 0.05 | 0.33 | -0.13 | 1 |
| species: *M. jurtina* | | | | | | |
| gender (G) | 1 | | | | | |
| year (Y) | 0.33 | 1 | | | | |
| temperature (T) | -0.21 | -0.84 | 1 | | | |
| radiation (R) | 0.15 | 0.20 | -0.08 | 1 | | |
| cloudiness (C) | 0.20 | -0.20 | 0.09 | -0.31 | 1 | |
| wind speed (W) | 0.19 | 0.01 | 0.09 | 0.16 | 0.37 | 1 |
| species: *M. athalia* | | | | | | |
| gender (G) | 1 | | | | | |
| year (Y) | 0.38 | 1 | | | | |
| temperature (T) | -0.35 | -0.92 | 1 | | | |
| radiation (R) | -0.08 | -0.16 | 0.18 | 1 | | |
| cloudiness (C) | 0.10 | 0.67 | -0.79 | -0.30 | 1 | |
| wind speed (W) | -0.07 | 0.11 | -0.09 | 0.44 | 0.06 | 1 |
| species: *P. argus* | | | | | | |
| gender (G) | 1 | | | | | |
| year (Y) | 0.18 | 1 | | | | |
| temperature (T) | 0.01 | -0.84 | 1 | | | |
| radiation (R) | 0.00 | -0.32 | 0.06 | 1 | | |
| cloudiness (C) | 0.07 | 0.87 | -0.65 | -0.55 | 1 | |
| wind speed (W) | 0.18 | 0.99 | -0.83 | -0.30 | 0.86 | 1 |
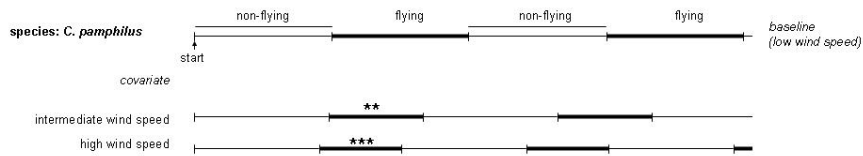
## Appendix 2.3

Effect of wind speed on observed duration of flying and non-flying bouts for *C. pamphilus*, based on survival analysis. Width of bars shows duration of behaviour type relative to baseline situation (low wind speed), where non-flight behaviour can consist of more than one behaviour type; P values from Z score test: ** $P < 0.01$; *** $P < 0.005$; number of flying bouts: 853; number of non-flying bouts: 870

## Appendix 2.4

Number of individuals, and mean and standard deviation in proportion of time spent flying per individual.

| species | statistic | low T | interme-diate T | high T | low R | interme-diate R | high R |
|---|---|---|---|---|---|---|---|
| *C. pamphilus* | n | 37 | 57 | 8 | 40 | 49 | 13 |
| | mean | 11.09 | 13.35 | 14.94 | 7.77 | 15.97 | 15.21 |
| | stdev | 16.20 | 18.45 | 23.96 | 12.35 | 20.85 | 18.93 |
| *M. jurtina* | n | 15 | 21 | 5 | 18 | 15 | 8 |
| | mean | 15.70 | 22.05 | 11.00 | 19.16 | 8.37 | 26.17 |
| | stdev | 24.18 | 25.09 | 11.58 | 24.95 | 9.25 | 25.50 |
| *M. athalia* | n | 6 | 9 | 7 | 9 | 11 | 2 |
| | mean | 3.07 | 19.13 | 22.81 | 10.80 | 14.83 | 44.99 |
| | stdev | 2.63 | 23.77 | 23.30 | 12.20 | 23.35 | 25.41 |
| *P. argus* | n | 6 | 10 | 6 | 8 | 5 | 9 |
| | mean | 9.87 | 20.84 | 24.05 | 11.30 | 25.03 | 21.81 |
| | stdev | 6.98 | 23.76 | 25.58 | 10.49 | 22.52 | 26.83 |

**Appendix 2.4 (continued)**

| species | statistic | low C | interme-diate C | high C | low W | interme-diate W | high W |
|---|---|---|---|---|---|---|---|
| *C. pamphilus* | n | 18 | 48 | 36 | 21 | 51 | 30 |
| | mean | 26.84 | 12.24 | 6.12 | 22.95 | 10.36 | 9.35 |
| | stdev | 29.26 | 14.86 | 8.62 | 26.54 | 13.28 | 15.50 |
| *M. jurtina* | n | 6 | 13 | 22 | 19 | 20 | 2 |
| | mean | 4.52 | 31.54 | 14.38 | 17.05 | 21.14 | 3.44 |
| | stdev | 3.37 | 25.81 | 22.01 | 25.87 | 22.12 | 2.99 |
| *M. athalia* | n | 8 | 8 | 6 | 19 | 2 | 1 |
| | mean | 29.29 | 2.90 | 15.46 | 17.92 | 4.03 | 1.83 |
| | stdev | 28.30 | 2.43 | 12.57 | 21.94 | 1.37 | - |
| *P. argus* | n | 11 | 5 | 6 | 16 | 1 | 5 |
| | mean | 23.63 | 18.54 | 9.87 | 22.04 | 10.71 | 9.71 |
| | stdev | 25.89 | 20.01 | 6.98 | 23.65 | - | 7.79 |

# 3

# Using life-history traits to explain bird population responses to increasing weather variability

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ABSTRACT

It is expected that bird population dynamics will change in response to increased weather variability, an expression of climate change. The extent to which species are sensitive to effects of weather on survival and reproduction depends on their life-history traits. We investigated how breeding bird species can be grouped, based on their life-history traits and according to weather-correlated population dynamics. We developed and applied the linear trait-environment method (LTE) which is a modified version of the fourth-corner method. Despite our focus on single traits, two strategies - combinations of several traits - stand out. As expected, breeding populations of waterfowl species that often breed at ground or water level, feed on plant material, are precocial, and are generally short-distance or partial migrants are negatively impacted by severe winters directly preceding territory monitoring, probably due to increased adult mortality. Furthermore, a decline in population growth rates of insectivorous long-distance migrants due to mild winters and warm springs in the year before territory monitoring was found, which may be caused by reduced reproduction due to trophic mismatches. If we extrapolate these correlations to the future, we are able to point out species that are expected to show most significant responses to changing weather variability - assuming that our conclusions are based on causal relationships, and that the way species, weather variables, and the nature of habitat types interact will not alter. As species traits play an important role in constructing functional groups that are relevant to the provisioning of ecosystem services, our study allows to incorporate the vulnerability of ecosystems to climate change into such functional approaches.

## 3.1  INTRODUCTION

Climate change is likely to be manifested by changes in the variance of weather with an increased frequency of extreme weather (IPCC 2001; IPCC 2007). Population dynamics of many bird species are changing in response to increased weather variability (Bolger et al. 2005; Jiguet et al. 2006; Robinson et al. 2007), presumably through impacts of weather on variation in adult survival and reproduction success (including first year survival, Robinson et al. 2007). The extent to which species are sensitive to effects of weather on survival and reproduction has been shown to depend on life-history traits (Van Turnhout et al. 2010). Considering resident birds, in several recent studies, relationships were found between adult survival and (extreme) weather circumstances during the preceding non-breeding season (temperature and snowfall, e.g. Brown & Brown 1998; Sæther et al. 2000; Both & Visser 2001; Sparks et al. 2002; Jones et al. 2003; Robinson et al. 2007). Mild winters and early, warm springs were on the other hand found to have negative effects on reproduction of insectivorous migrants, because of increased probability of mismatches between the timing of reproduction and the main food supply, i.e. organisms at lower levels in the food chain (Brown & Brown 1998; Both & Visser 2001; Both & Visser 2005; Both et al. 2006; Both et al. 2009). This is especially pronounced in habitats with a seasonal food peak, such as forests (Both et al. 2010). Furthermore, population growth rates of altricial ground nesting species have been shown to be negatively impacted by a dry heat wave (Jiguet et al. 2006), while Sæther et al. (2004) reported negative effects of extreme rainfall and wind events year-round on adult survival and reproduction success of altricial species. Most of the cited studies are focused on only one or a few species and traits, and responses in population dynamics to (extreme) weather vary amongst the species, habitats, and geographical locations considered in the different studies. However, Van Turnhout et al. (2010) found that population trends of 170 Dutch breeding bird species in 1990-2005 were strongly correlated with amongst others migration strategy, and that declines were associated with late arrival on the breeding grounds in migratory birds (see also Møller et al. 2008), suggesting climate change to be an important driver of population changes.

Impacts of enhanced weather variability on population dynamics may interfere with aims set in nature conservation programmes, which are often described in terms of the presence and abundance of target species in protected areas. In re-

sponse to the emerging understanding of the impacts of climate change, re-searchers and policy makers (e.g. EU 2009 White paper Adapting to climate change) have called for adaptive measures to mitigate the effects of climate change on population dynamics. Therefore, there is a need for more insight into the impacts of weather variability on a broad spectrum of species. Because nature conservation is generally not based on species-specific measures, such adaptive measures demand a generalized view on responses of species (Dolédec et al. 1999). An approach that allows for the generalization and extrapolation of predictions on future performance of species (Keddy 1992), is to investigate which specific combination of life-history traits makes species sensitive to specific weather events (c.f. Dolédec et al. 1999). In this paper, we aim to investigate this by examining how breeding bird species can be grouped, based on their life-history traits and according to weather-correlated population dynamics.

The interaction between weather and life-history traits could be influenced by habitat characteristics (Karlsson & Wiklund 2005) due to the way weather affects specific habitats. The same species may therefore show different responses in different ecosystem types (Karlsson & Van Dyck 2005; Both et al. 2010). Therefore, we analyze possible differences between habitat types by comparing growth rate data of a broad selection of specialist and generalist species breeding in two eco-system types in the Netherlands: marshlands (i.e. a mosaic of open water, reed marshes and marshland shrubs) and deciduous forests. These ecosystem types are important from a nature conservation point of view. About 16% of the Netherlands has been classified as international key marshland area (Wolff 1993), and this area is of importance for marshland species in Europe. Moreover, we expect marshlands and forests to differ in the way weather affects these systems. Water levels in marshlands can highly fluctuate with precipitation amount, and can freeze over during severe winters, whereas forests are relatively buffered against extreme weather (Stoutjesdijk & Barkman 1992). On the other hand, forests show a more pronounced seasonal food peak, especially to insectivorous species, than marshlands, due to simultaneous leaf unfolding over the whole habitat area during spring (Both et al. 2010). This might result in higher sensitivity to mismatches in the food chain.

In exploring the relationship between population dynamics and weather, we studied changes in abundances after the occurrence of specific weather circumstances. We tested the relationships between typical nest location, diet, offspring de-

velopment, and migration strategy of selected bird species – traits that were shown to correlate with weather conditions in other studies – and weather variables. Further argumentations for using these specific traits are indicated in more detail in Table 3.1. We analyzed data on annual changes in bird abundances, above mentioned traits, and values of weather variables simultaneously. As the analyzed species experienced the same weather conditions, we hypothesize that differences in their response could be attributed to different trait combinations. Instead of looking at linear population trends (cf. Both et al. 2010; Van Turnhout et al. 2010), we analyzed year-to-year changes in abundances in response to weather conditions. We developed and applied the linear trait-environment method (LTE) which is a modified version of the fourth-corner method (Legendre et al. 1997; Dray & Legendre 2008). Subsequently, we compared changes in the occurrence of the significant weather variables between the present climate and several climate change scenarios. This comparison gives an indication which combination of traits and corresponding species might benefit or suffer from future weather circumstances in terms of population growth.

## 3.2 METHODS

### 3.2.1 Deriving yearly population indices

We selected 77 species that annually breed in the Netherlands, of which 43 species breed in marshland areas and 53 species breed in forest areas; from these 77 species, 19 breed in both marshland and forest areas (Appendix 3.1). Since 1984, monitoring of breeding birds in the Netherlands, organized by SOVON Dutch Centre for Field Ornithology and Statistics Netherlands, is based on the method of territory mapping in fixed study plots (Bibby et al. 1997; Van Turnhout et al. 2010). Between March and July study plots (10-500 hectares each) are visited 5-10 times. Size of study plots, as well as number, timing and duration of visits depend on habitat type and species selection. All birds with behaviour indicative of a territory (e.g. song, pair bond, display, alarm, nests) are recorded on field maps. Species-specific interpretation criteria are used to determine the number of territories at the end of the season.

**Table 3.1**

Traits, used for analysis in **Z** matrix

| trait (source) | abbr. | explanation (classification) | reasoning |
|---|---|---|---|
| nest location (Cramp and Simmons (1977-1994)) | lownest | Nest location at water table, along water banks or in holes in the ground (1; low elevations), in contrast to nest locations higher in elevation (0) | Low precipitation in non- and pre-breeding season leads to low water tables, which is most negative for species breeding on or just above water and ground level, because of low nest site availability and high predation pressure (Newton 1998). Extreme wind may destroy nests located higher in elevation (trees and reed vegetation) (Wunderle et al. 1992). A dry heat wave might negatively impact ground nesting species (Jiguet et al. 2006). |
| main diet type (Cramp and Simmons (1977-1994)) | fdpl | Main food during breeding season: plants (vegetative and generative parts) (1; herbivorous), in contrast to other diets (0) | When temperature drops below 5˚C, plant growth stops leading to reduced food availability for herbivores. Temperatures below 0˚C are negative for piscivorous species (frozen water bodies) (Morgan & Glue 1977; Besbeas et al. 2002), as well as for insectivorous species (Newton 1998). Snow cover is negative for ground feeders (insectivorous species and herbivores) (Peach et al. 1995). Both low water tables during non-breeding and breeding seasons are negative to piscivorous species (Den Held 1981). Warmth in spring and summer is |
| | fdinvert | Main food during breeding season: insects (1; insectivorous), in contrast to other diets (0) | |
| | fdpisci | Main food during breeding season: fish (1; piscivorous), in contrast to other diets (0) – trait occurs only for marshland species | |

Table 3.1 (continued)

| trait (source) | abbr. | explanation (classification) | reasoning |
|---|---|---|---|
| main diet type | fdmeat | Main food during breeding season: small mammals (1; raptors), in contrast to other diets (0) | positive for insectivorous species, because of high insect abundance (Birch 1953). But in combination with drought, warmth is expected to negatively affect herbivorous species through food shortages (Newton 1998). |
| offspring development (Cramp and Simmons (1977-1994)) | altr | Altricial species (1) that are nidicolous and hatched without feathers, in contrast to precocial species (0) that are nidifugous and hatched with feathers | Extreme rainfall and wind events during the breeding season is most negative for precocial species that often lack shelter of a nest, in contrast to altricial species (Sæther et al. 2004). A dry heat wave might negatively impact altricial species (Jiguet et al. 2006). |
| migration strategy (Speek and Speek (1984), Wernham et al. (2002)) | resid | Migration strategy: resident (1) during winter time, in contrast to other migration strategies (0) | Mild winters are most beneficial for sedentary birds, because of high winter survival. For long-distant migrants mild winters will have either neutral effect, because they are away on the wintering grounds, or even negative due to the competition with residents for the resources and occurrence of mismatches (Newton 1998). Early warm spring temperatures are negative to (long-distance) migrants due to the increased probability for a food mismatches (Both & Visser 2001; Both & Visser 2005; Both et al. 2006). |
| | pmigr | Migration strategy: partial migrant/short-distance migrant (1) during winter time, in contrast to other migration strategies (0) | |
| | migr | Migration strategy: long distance migrant (1) during winter time, in contrast to other migration strategies (0) | |

Fieldwork and interpretation methods are standardized and are described in detail in manuals (Van Dijk 2004; Van Dijk et al. 2004). For the selected species, abundances per habitat type are presented as yearly indices; for each of the 19

species that breed in both marshland and forest areas, 2 indices are available. Indices are calculated using TRIM-software (Pannekoek & Van Strien 2005), based on loglinear Poisson regression. Indices are presented using 1990 as a base year (index=100). Logratios of subsequent yearly values of indices ($\ln[\text{index}_{\text{species\_i, year\_t}}/\text{index}_{\text{species\_i, year\_t-1}}]$) are used in our analyses and correspond to yearly population growth rates of the species on log scale. Since weather influences population growth via reproduction and mortality rates, population growth rate is a proper index to describe population dynamics. We used index values from 1984-2005.

### 3.2.2 Deriving weather variables

The Royal Netherlands Meteorological Institute (KNMI) acquires weather data according to the global standards of the World Meteorological Organization. The KNMI administers ca. 35 weather stations and 54 wind stations evenly distributed over the Netherlands, of which the station in De Bilt is located in the centre of the country. Weather data acquired from this station are representative for the mean climate conditions in the Netherlands (Van Oldenborgh & Van Ulden 2003), except for wind speeds that differ too much spatially (generally higher wind speeds along the North Sea coast). We obtained data on mean daily temperatures and wind speeds, as well as total daily precipitation, precipitation duration, snowfall, and occurrence of thunderstorms from KNMI for the period 1984-2005. From these we calculated 12 weather variables, that describe the weather in the breeding season and in the non-breeding season (Table 3.2). For wind speeds, values were derived from data from all meteorological stations in the Netherlands; remaining weather variable values were derived from the De Bilt meteorological station.

Weather variables that impact population dynamics due to adult mortality will change numbers of territories immediately. Changes in population dynamics due to a weather event affecting recruitment rates (reflecting reproductive success and first winter survival) will become noticeable in territory numbers one year after the occurrence of the weather event, especially for species that are able to reproduce one year since their hatching. Therefore, we derived values for weather variables that occurred during the non-breeding or winter season ('NB'; from October to March) and the breeding season ('B'; from April to August); see Appendix 3.2. We related weather variable values of current years ('t') and previous

Table 3.2

Weather variables, used for analysis in **X** matrix

| abbreviation | explanation (units) |
|---|---|
| | weather variables during the non-breeding season ('NB') |
| NB_IJnsen | IJnsen value (IJnsen 1981) ranging from 0 to 60 (-), expressing winter severity; the higher the value, the more severe the winter. Calculation: ( $v^2$/363) + (2 y/3) + (10 z/9), where v, y and z stand for the number of 24 h periods with a minimum temperature below 0°C, with a maximum temperature below 0°C and with a maximum temperature below - 10°C, respectively, during the period November-March. |
| NB_tempcoldmonth | Mean temperature of the coldest month (°C). For each year, the mean temperature of each month from October to March was calculated and the coldest monthly average was taken. |
| NB_frostdays | Longest duration of consecutive days (-) with daily mean temperature below 0°C. |
| NB_rain | Total precipitation sum over non-breeding season (mm) |
| NB_snowdays | Longest duration of consecutive days (-) with snow cover more than or equal to 2 cm |
| | weather variables during the breeding season ('B') |
| B_temp | Mean temperature (°C) |
| B_tempaprmay | Mean temperature (°C) from 16 April to 15 May |
| B_rain | Total precipitation sum over breeding season (mm) |
| B_heavyraindays | Longest duration of consecutive days (-) with daily average precipitation sum exceeding 3mm |
| B_drydays | Longest duration of consecutive days (-) with daily precipitation sum less than 1mm (Robinson et al. 2007) |
| B_squall | Total number of squalls (-) (wind speed exceeding 22 knots (11.31m/s) and lasting for at least one minute (MANMAR). |

Table 3.2 (continued)

| abbreviation | explanation (units) |
|---|---|
| B_heatwave | Number of days comprising a heat wave (-). For the Netherlands, a heat wave is defined as a period of at least 5 consecutive days in which the maximum temperature at De Bilt exceeds 25°C, provided that on at least 3 days in this period the maximum temperature at De Bilt exceeds 30°C (Meehl & Tebaldi 2004). |

NB: non-breeding season; B: breeding season. For B_squall, values were derived from data from all meteorological stations in the Netherlands; remaining weather variable values were derived from the De Bilt meteorological station. All weather variable values were log transformed (ln(x+1), and ln(x+5) for NB_tempcoldmonth), except values for B_temp and B_tempaprmay

years ('t-1'; one year before territory monitoring) to population growth rates (Fig. 3.1). Weather in the non-breeding season of the previous year ('NBt-1') can affect species condition and eventually the reproduction success (carry-over effects, Norris & Taylor 2006). Reproduction success in the breeding season of the previous year (Bt-1) will lead to altered population numbers in the breeding season of the current year (Bt). Adult mortality in the non-breeding and breeding season of the current year (NBt and Bt) will also lead to altered population numbers in the breeding season of the current year (Bt).

Weather variables indicating winter severity (IJnsen, mean temperature of the coldest month, longest duration of consecutive frost days) are strongly correlated (see Appendix 3.3). Mild winters are often rainy – relatively high winter temperatures and precipitation are supplied by west winds from the North Sea (Van Oldenborgh & Van Ulden 2003) - and are frequently followed by a warm spring and breeding season (Vandendool & Nap 1981). Moreover, in the period 1984-2005 warm breeding seasons were often followed by mild winters, and a rainy winter was frequently followed by another rainy (but not necessarily a mild) winter. The number of days comprising a heat wave is positively correlated to the mean temperature of the breeding season. Correlations between weather variables will not affect the analysis because each weather variable is tested separately. However, it may affect the interpretation of the results and hamper inferences (see Discussion).
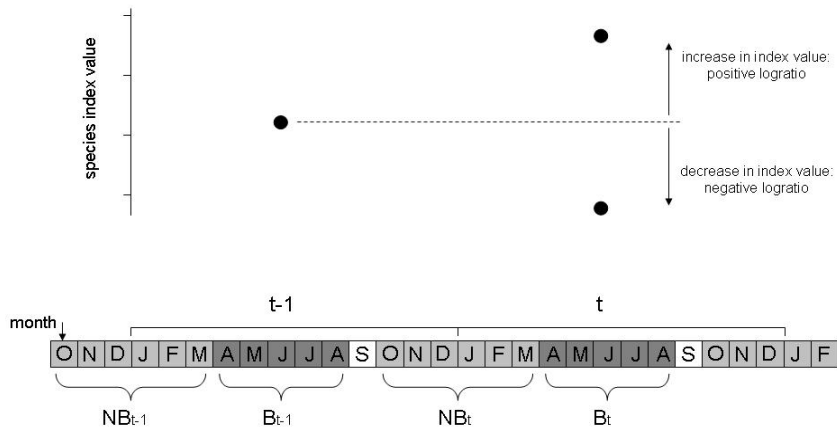
**Figure 3.1**

Timing of territory monitoring (•) and periods of occurrence of weather variables in two subsequent years, t-1 and t. Increase in index value between t-1 and t results in positive population growth rate, and vice versa. NB: non-breeding season, from October to March; B: breeding season, from April to August

### 3.2.3 Selecting traits

We selected 4 traits that have been demonstrated to correlate with population dynamics in response to weather circumstances in literature. For each species, the following categorical traits are considered: (1) nest location (at water table, along water banks or in holes in the ground (low elevations) vs. higher elevations), (2) main diet type (food during breeding season consists of plant material vs. insects vs. fish vs. mammals), (3) offspring development (altricial vs. precocial), and (4) migration strategy (resident vs. partial migrant vs. long-distance migrant). These traits are used in the analysis with the LTE method (see below). Data sources for trait values, classifications, and references are indicated in Table 3.1.

### 3.2.4 The linear trait-environment method (LTE)

LTE relates a species trait ($z$) to an environmental variable ($x$) via data on (change in) abundance of the set of species in a set of sites. Here, sites are years, the environmental variable is an annual weather variable, and year-to-year change in abundance or growth rate is derived for the selection of Dutch breeding birds. To

Chapter 3

introduce LTE we start with a two-step analysis. In the first step regressions per species of the growth rate values to each weather variable give a species specific regression coefficient $b_k$. In the second step, these regression coefficients are correlated to each trait. LTE integrates both steps in a single model (see Fig. 3.2 for a schematic overview). LTE, described in detail in Appendix 3.4, achieves this integration on the basis of a linear model with main effects for the weather variable and the trait and their interaction. The interaction between trait and weather variable in this model captures the trait-weather relationship, in particular the trait-dependent effect of weather on the population growth rate. We tested the significance of this interaction by a permutation test. In Appendix 3.4 we
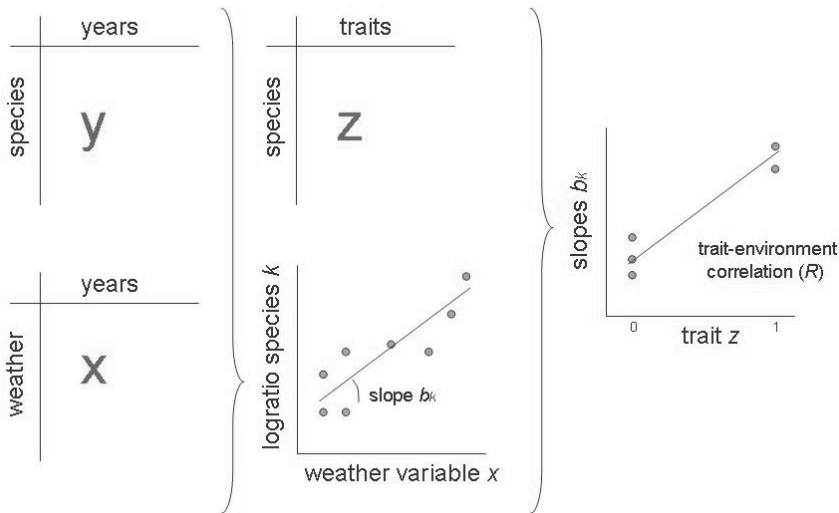


**Figure 3.2**

Schematic overview of LTE analysis procedure. Species-specific regression coefficients ($b_k$) are obtained from regressions per species of the population growth rate values (**Y** matrix) on to each weather variable (**X** matrix). Subsequently, the species-specific regression coefficients are correlated to each trait $z$ (**Z** matrix). $R$ is the Pearson correlation between the trait $z$ and the species-specific regression coefficients $b_k$, with $R^2$ being the fraction of the environmentally structured variation that can be explained by the trait. When both regressions (regression population growth rates – weather variable and regression $b_k$'s – trait) are significant, we report a trait-environment relationship.

compare LTE and permutation test with fourth-corner analysis (Legendre et al. 1997; Dray & Legendre 2008) which is a method of trait-environment analysis designed primarily for presence-absence data. We performed separate analyses for marshland birds and for forest birds and we report correlation coefficients $R$, statistics on the $b_k$, and the results of the significance tests, obtained from the LTE function that we wrote in R 2.9.0 software (Ihaka & Gentleman 1996).

To obtain first insight into the clustering of species against their traits, we performed a separate ordination of the traits ($Z$ matrix) next to the LTE analyses. This principal component analysis (PCA) was conducted with CANOCO (Ter Braak & Šmilauer 2002), providing an optimal ordination of species and traits.

## 3.3    RESULTS

The PCA and LTE analyses show that in marshland birds one distinct group of species, that share a specific combination of traits, stands out: waterfowl species that often breed at ground or water level, feed on plant material, are precocial and do generally not migrate over long distances. These traits are correlated (see Fig. 3.3a and Appendix 3.5a). As expected, these waterfowl are negatively impacted by severe winters directly preceding territory monitoring during the breeding season, and benefit from mild, rainy winters (see Table 3.3a for results marshland birds). Moreover, the analyses show a decline in population growth rates of altricial marshland species that do not breed at ground level and feed on other sources than plant material (especially insects) that is correlated with warm springs in the year preceding territory monitoring. Our results do not indicate a relationship between growth rates of altricial species and heat waves or rain storm events. Beside our expectations, we found a few other correlations between life-history traits and weather-correlated variation in growth rate. Migratory marshland species that do not breed at ground level and are often altricial benefit from severe winters. Waterfowl species are negatively impacted by long snow cover duration in the year preceding territory monitoring. Furthermore, waterfowl species benefit from a warm spring in the year before territory monitoring (April-May), while residential marshland species benefit from a warm breeding season.
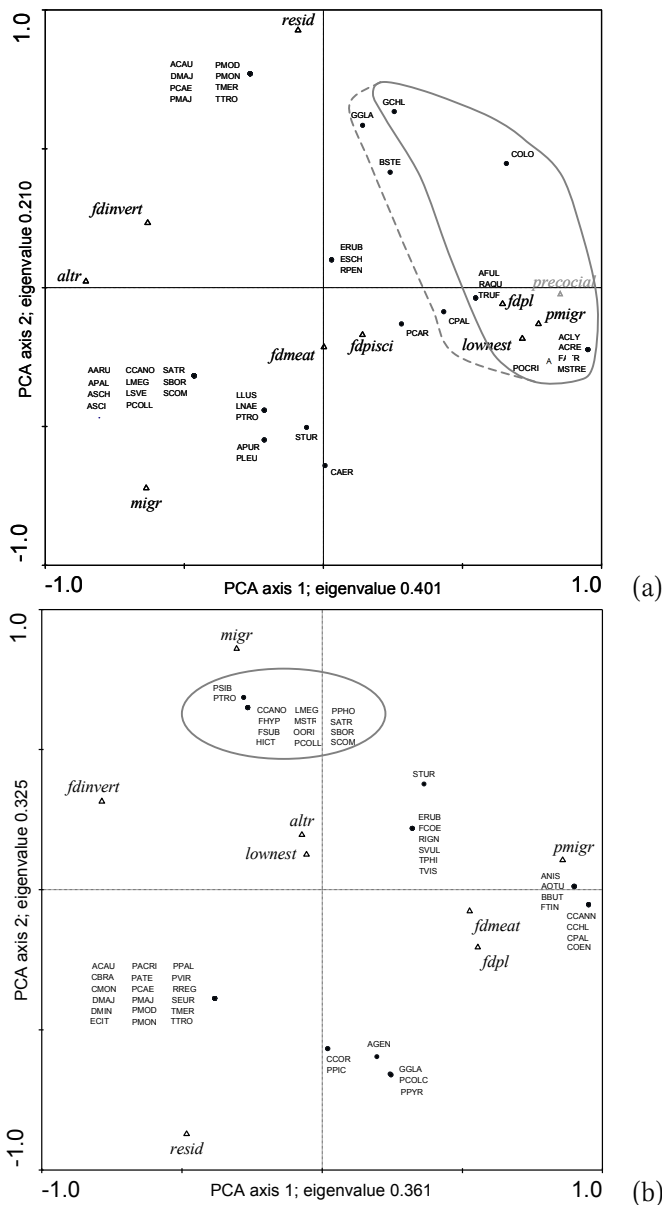
**Figure 3.3**

Ordination of marshland (a) and forest (b) species and traits, resulting from PCA. Encircled are waterfowl s.s. (dashed: s.l.; Jay, Bittern and Wood pigeon can strictly not be classified as waterfowl, but share most traits and responses) (a) and insectivorous long-distance migrants (b). For abbreviations of species names, see Appendix 3.1; for abbreviations of traits, see Table 3.1.

## Table 3.3

Relations between traits and weather variables expressed by significance (P), traits-weather correlation (R) and mean species-specific regression coefficients $b_k$ resulting from the LTE analysis for different trait categories.

a: marshland species

| trait | abbreviation (n trait 0; n trait 1) | weather variable | P | R | $b_k$ mean (trait=0) | $b_k$ 25-75% (trait=0) | $b_k$ mean (trait=1) | $b_k$ 25-75% (trait=1) |
|---|---|---|---|---|---|---|---|---|
| nest location | lownest (28;15) | NB_IJnsen | 0.042 | -0.348 | 0.019 | -0.016 - 0.071 | -0.036 | -0.083 - 0.014 |
| | | NB_tempcoldmonth | 0.013 | 0.407 | -0.035 | -0.085 - 0.02 | 0.065 | -0.019 - 0.136 |
| | | NB_frostdays | 0.043 | -0.384 | 0.017 | -0.007 - 0.057 | -0.032 | -0.082 - 0.012 |
| | | NB_rain | 0.023 | 0.335 | -0.066 | -0.173 - -0.01 | 0.123 | -0.041 - 0.21 |
| | | NB_snowdays *t-1* | 0.011 | -0.628 | 0.023 | 0.002 - 0.052 | -0.043 | -0.088 - -0.005 |
| | | B_tempaprmay *t-1* | 0.005 | 0.628 | -0.012 | -0.026 - -0.001 | 0.023 | 0.005 - 0.042 |
| main diet type | fdpl (35;8) | NB_snowdays *t-1* | 0.035 | -0.421 | 0.010 | -0.011 - 0.039 | -0.045 | -0.096 - 0.008 |
| | | B_tempaprmay *t-1* | 0.044 | 0.392 | -0.005 | -0.018 - 0.009 | 0.022 | 0 - 0.054 |
| offspring development | altr (10;33) | NB_IJnsen | 0.035 | 0.380 | -0.052 | -0.085 - 0.005 | 0.016 | -0.027 - 0.059 |
| | | NB_tempcoldmonth | 0.010 | -0.447 | 0.094 | -0.01 - 0.165 | -0.029 | -0.079 - 0.027 |
| | | NB_frostdays | 0.047 | 0.430 | -0.048 | -0.085 - 0 | 0.014 | -0.013 - 0.055 |
| | | NB_rain | 0.040 | -0.305 | 0.149 | -0.009 - 0.212 | -0.045 | -0.164 - 0.022 |
| | | NB_snowdays *t-1* | 0.009 | 0.683 | -0.063 | -0.098 - -0.026 | 0.019 | 0 - 0.046 |
| | | B_tempaprmay *t-1* | 0.010 | -0.678 | 0.033 | 0.017 - 0.052 | -0.010 | -0.019 - 0.004 |
| migration strategy | resid (31;12) | B_temp *t-1* | 0.037 | 0.373 | -0.016 | -0.035 - 0.015 | 0.042 | 0.022 - 0.082 |
| | | B_tempaprmay | 0.040 | 0.308 | -0.007 | -0.017 - 0.004 | 0.018 | -0.001 - 0.037 |
| | migr (25;18) | NB_tempcoldmonth | 0.026 | -0.351 | 0.035 | -0.036 - 0.108 | -0.048 | -0.089 - -0.002 |
| | | NB_frostdays | 0.044 | 0.366 | -0.019 | -0.07 - 0.02 | 0.026 | -0.004 - 0.056 |

b: forest species

| trait | abbreviation (n trait 0; n trait 1) | weather variable | P | R | $b_k$ mean (trait=0) | $b_k$ 25-75% (trait=0) | $b_k$ mean (trait=1) | $b_k$ 25-75% (trait=1) |
|---|---|---|---|---|---|---|---|---|
| main diet type | fdinvert (15;38) | NB_IJnsen *t-1* | 0.014 | 0.380 | -0.029 | -0.054 - 0.009 | 0.011 | -0.022 - 0.046 |
| | | NB_tempcoldmonth *t-1* | 0.027 | -0.369 | 0.038 | 0.009 - 0.06 | -0.015 | -0.042 - 0.032 |
| | | NB_frostdays *t-1* | 0.030 | 0.379 | -0.023 | -0.053 - 0 | 0.009 | -0.014 - 0.033 |
| | | B_rain | 0.016 | 0.359 | -0.088 | -0.138 - 0 | 0.035 | -0.051 - 0.113 |
| | fdmeat (48;5) | NB_IJnsen *t-1* | 0.006 | -0.557 | 0.009 | -0.022 - 0.038 | -0.082 | -0.078 - -0.058 |
| | | NB_frostdays *t-1* | 0.015 | -0.591 | 0.007 | -0.014 - 0.033 | -0.070 | -0.073 - -0.059 |
| | | NB_rain *t-1* | 0.017 | 0.511 | -0.022 | -0.082 - 0.038 | 0.211 | 0.086 - 0.37 |
| | | B_rain | 0.008 | -0.539 | 0.027 | -0.057 - 0.089 | -0.257 | -0.366 - -0.157 |
| migration strategy | resid (29;24) | NB_IJnsen *t-1* | 0.019 | -0.332 | 0.014 | 0.005 - 0.047 | -0.017 | -0.032 - 0.001 |
| | | NB_tempcoldmonth *t-1* | 0.027 | 0.331 | -0.020 | -0.054 - 0.021 | 0.024 | 0.008 - 0.049 |
| | | NB_frostdays *t-1* | 0.019 | -0.348 | 0.012 | -0.005 - 0.047 | -0.015 | -0.031 - 0.005 |
| | pmigr (39;14) | NB_IJnsen | 0.007 | -0.403 | 0.015 | -0.002 - 0.05 | -0.041 | -0.088 - 0.011 |
| | | NB_tempcoldmonth | 0.003 | 0.412 | -0.022 | -0.068 - 0.012 | 0.061 | -0.011 - 0.114 |
| | | NB_frostdays | 0.012 | -0.344 | 0.011 | -0.009 - 0.044 | -0.032 | -0.066 - 0.009 |
| | | B_rain *t-1* | 0.032 | 0.328 | -0.031 | -0.107 - 0.024 | 0.088 | -0.034 - 0.186 |
| | | B_rain | 0.042 | -0.323 | 0.030 | -0.061 - 0.121 | -0.083 | -0.067 - 0.011 |
| | migr (38;15) | NB_IJnsen *t-1* | 0.001 | 0.579 | -0.017 | -0.033 - 0.008 | 0.044 | 0.023 - 0.058 |
| | | NB_tempcoldmonth *t-1* | 0.003 | -0.524 | 0.022 | -0.008 - 0.042 | -0.055 | -0.089 - -0.011 |
| | | NB_frostdays *t-1* | 0.001 | 0.611 | -0.015 | -0.028 - 0.007 | 0.037 | 0.03 - 0.052 |
| | | NB_rain *t-1* | 0.018 | -0.412 | 0.034 | -0.03 - 0.058 | -0.087 | -0.149 - -0.036 |
| | | B_tempaprmay *t-1* | 0.040 | -0.358 | 0.005 | -0.002 - 0.013 | -0.013 | -0.024 - 0.007 |
| | | B_rain | 0.005 | 0.462 | -0.045 | -0.104 - 0.025 | 0.113 | 0.013 - 0.205 |

Significant relationships are shown; n: number of species; P: statistical significance for trait-environment relationship; R: Pearson correlation between the trait $z$ and the species-specific regression coefficients $b_k$, obtained from regressions per species of population growth rate values on indicated weather variables; $b_k$ mean: mean of $b_k$ values of species that do not hold the trait (trait 0) or hold the trait (1); $b_k$ 25-75%: $25^{th}$ and $75^{th}$ percentile of $b_k$ values of species that do not hold the trait (trait 0) or hold the trait (1)

In forest birds, also one distinct group of species stands out: long-distance migrants that are often insectivorous, or feed insects to their juveniles (see Fig. 3.3b and Appendix 3.5b for results forest birds). These insectivorous migrants show an increase in population growth rates following severe winters and cold springs (April-May), and a decline in population growth rates following mild winters and warm springs in the year before territory monitoring (Table 3.3b). Our results do not indicate a negative impact of cold and snowy winters. Neither can we distinguish a negative impact of heat waves or rainstorm events on growth rates of altricial (low nesting) species. However, also for forest species we found a few other correlations between life-history traits and weather-correlated variation in growth rates. Carnivorous and residential species show a decline in population growth rates that is correlated with severe, dry winters in the year before territory monitoring. Partial or short-distance migrants are negatively impacted by severe winters directly preceding territory monitoring and by high precipitation sums over the breeding season when territories are counted. Partial migrants profit from rainy breeding seasons in the year before territory monitoring, while carnivorous and other non-insectivorous species are negatively impacted by high precipitation sums over the breeding seasons. Migrants, however, profit from these weather circumstances.

## 3.4   DISCUSSION

We investigated how bird species can be grouped according to weather-correlated population dynamics, based on their life-history traits. Despite our focus on single traits, two strategies (traits that jointly appear in bird species) stand out. We have shown that waterfowl that often breed at ground or water level, feed on plant material, are precocial, and do not migrate over long distances in general, are negatively impacted by severe winters directly preceding territory monitoring. This is probably due to increased adult mortality (e.g. Bibby 1981). Furthermore, a decline in population growth rates of insectivorous long-distance migrants due to mild winters and warm springs in the year before territory monitoring may be caused by a reduced reproduction success. When these species arrive relatively late from the wintering grounds after mild winters, mismatches can occur between the timing of reproduction and the food supply to the juve-

niles. Competition with residents who survived the mild winter in high numbers could be another cause for reduced reproductive success of migrants.

As we interpret our data, juvenile survival in year t-1 and adult survival in year t of residential marshland and waterfowl species increase due to a warm spring and breeding season. This can probably be explained by increased food availability during a warm spring. However, increased chance for juveniles to survive their first year until the next breeding season – the moment of territory monitoring -, can also be caused by a mild winter, often following a warm breeding season (Morgan & Glue 1977; Besbeas et al. 2002).

We see remarkable differences as well as similarities in comparing the results between marshland and forest species (Tables 3.3a and b). Both marshland and forest species respond to winter severity. Nest location and offspring development are important traits for marshland species in this respect, but not for forest species. This is probably caused by the fact that almost all forest species breed in trees and are altricial. Hence, the variation amongst traits nest location and offspring development is relatively low (see also Fig. 3.3b), and these traits do not affect the sensitivity to winter severity in forest birds.

Marshland and forest long-distance migrants differ in their response to winter severity and spring temperature considering timing (t and t-1, respectively). Our findings on long-distance migrants in forests that are negatively impacted by mild winters and warm springs in the year before territory monitoring are in agreement with the findings of Both and Visser (2001; 2005) and Both et al. (2006; 2010). Both et al. (2010) show mismatches between timing of food requirements and food availability for long-distance migrants, but only in habitats with a seasonal food peak, like forests. The correlations Both et al. used were based on linear trends over a 20-year time span. We analyzed population trend data in a different way, looking at year-to-year variation, using the (positive or negative) population growth rate between subsequent years. In addition to the long-term trend analyses of Both et al. we showed that the impact on population dynamics of long-distance migrants is not immediate but delayed by one year. This indicates clearly, as hypothesized by Both et al., that early springs result in a low breeding success, consequently followed by a lower population size one year later. This is in further support of the mismatch hypothesis. It is remarkable that, in contrast to Both et al., we also found an effect of winter severity, which is strongly correlated

to spring temperatures, on long-distance migrants in marshland habitat. This is difficult to interpret however. Winter conditions are correlated with population size in the following breeding season, suggesting an immediate response. This indicates effects on survival, e.g. lower survival rates for long-distance migrants after mild winters. But this seems quite unlikely, since these migrants are in their distant winter quarters. One can only speculate about the true causal relationship. It might result from impact on food resources or interspecific competition pressures. After a severe winter, the population size of sedentary species is low thus allowing a higher population size of migrants to settle (Lemoine et al. 2007). Clearly this needs further study. In contrast with the forest bird community in which most of the migrants are passerines and insectivores, the migrant marshland bird community is more diverse. This and the year-to-year approach could explain the difference with the findings of Both et al. that are based on long-term trend estimates and deals with a restricted species set (only passerines).

For long-distance migrants, there might be other constraints en route or on the wintering grounds that could additionally impact population fluctuations (Newton 2004; Sanderson et al. 2006), which are not taken into account by considering only Dutch weather variables. Especially species wintering in the Sahel have shown strong declines in breeding population numbers during severe droughts there in the 1970s and 1980s (Foppen et al. 1999; Zwarts et al. 2009). However, most likely these effects do not change our results considering responses to weather on the breeding grounds. Conditions during the breeding season in the Netherlands - which the Dutch populations of long-distance migrants share - correlate unambiguously to population fluctuations of most of these species and their responses adequately match the expectations we formulated in Table 3.1 on basis of recent literature.

Marshland species respond to snow cover duration, while forest species do not. This difference can be attributed to the fact that marshland systems are open and can become totally covered with snow. Especially in combination with temperatures below the freezing point, long-lasting snow cover can be detrimental to waterfowl species, foraging on terrestrial plant material (e.g. agricultural managed grasslands) which is then covered with snow (see also Fig. 3.3a; waterfowl clustered near trait main diet type of plants).

Neither marshland nor forest species respond to heat waves and dry periods. This is in contrast to the results of Jiguet et al. (2006), who found a response in population growth rates to the 2003 French heat wave, a 6-month exceptionally hot and dry period. In the Netherlands, only 9 heat waves occurred over the period 1984-2005, with an average duration of 9 days. Probably, these heat waves were not experienced as harmful by the species. Moreover, the longest duration of dry days during the breeding season over the period 1984-2005 was 28 days, which occurred in both 1995 and 2003. Again, these dry periods were probably not experienced as exceptionally long by the species. Furthermore, events such as droughts, heavy rain, and squalls often occur at a local scale, and effects of these events on population dynamics can be leveled off in national population trends.

The main assumption in our study is that species differ in their responses to weather, and that these responses could be attributed to different trait combinations. We used a dataset on a large number of species counted in the same (biogeographical) region over the same set of years. Population changes may be correlated to other causal factors operating in the same years and region, that are not covered by our explanatory variables. However, we expect that on such temporal and spatial scales, weather will be an important explanatory factor in year-to-year population changes, taking into account the numerous studies that found evidence for the impact of weather on bird vital rates (e.g. Sæther et al. 2004; Both et al. 2006).

We chose not to explicitly take account of differences in accuracy in the index values (derived from TRIM), except by taking logarithms and by excluding rare species, of which the indices are likely to be more error prone. By trying to take account of differences in accuracy, the simplicity of the method would be lost. We believe the permutation approach to be quite robust to any differences. Moreover, if the errors associated with the LTE model are large compared those in the (log) indices, not taking account of differences in accuracy is close to optimal.

Autocorrelation in time series may lead to spurious cross-correlations and a standard cure is pre-whitening. We diminished the autocorrelation in yearly indices by analysing the logratio of subsequent values. The resulting lag-1 autocorrelations are mostly slightly negative (in absolute value 75% is smaller than 0.3 and the maximum is 0.55). The lag-1 autocorrelations in the weather variables are even smaller in size. The values are too small to invalidate our analysis and the

series are too short to account in a more elaborate way for autocorrelation. Ranta et al. (2000) warn that it can be very hard to detect environmental forcing of population dynamics if the dynamics is not stable. However, they argue that slowly growing species such as birds show mostly stable dynamics and "are likely to respond to climatic variability in a straightforward way". By consequence, the method of our paper works for birds, as we showed, but may fail to detect environmental forcing for rapidly multiplying organisms.

### 3.4.1 Implications of future weather conditions

We extrapolated the observed correlations to future weather conditions predicted by climate change models. By doing so, we assume that these correlations are based on causal relationships, and that the way species, weather variables, and the nature of habitat types interact will not alter in the future. This enables us to point out species that are expected to show most outspoken responses to weather circumstances under climate change. From KNMI data on future daily temperatures and precipitation sums (http://climexp.knmi.nl/Scenarios_monthly/), we could calculate future values for weather variables affecting species population dynamics (Fig. 3.4). We used KNMI scenarios W and W[+], which implies for both scenarios an average global temperature rise of 2˚C from 1990 till 2050, and an increased occurrence of mild wet winters and warm dry summers for the W[+] scenario (see http://www.knmi.nl/research/climate_services/). Climate change is likely to be manifested by fewer cold and frost days (IPCC 2001; IPCC 2007), and hence by more frequent occurrence of mild winters (Fig. 3.4a), as well as warm springs (Fig. 3.4c). Based on our results, we can hypothesize that in general more frequent occurrence of mild winters and warm springs is expected to be detrimental to insectivorous long-distance migrants (marshland and forest species) in the Netherlands. Waterfowl species in the Netherlands are expected to profit from the more frequent occurrence of mild winters. It is unclear how the precipitation sum over the non-breeding season and over the breeding season will alter in the future climate (Fig. 3.4b and d). For the non-breeding season, the precipitation sum might increase, but this increase is only significant in 2100 under the W[+] scenario. Under the W[+] scenario the precipitation sum in the breeding season will decrease from present to 2100, while under the W scenario the precipitation sum in 2100 will remain similar to the present sum (no significant difference). Subsequently, it is unclear if species will be harmed by future precipitation.

Based on species specific regression coefficients $b_k$ resulting from the LTE analyses (Appendix 3.6) we can point out the species that are expected to respond positively or negatively to a more frequent occurrence of mild winters. Most of the species that are expected to respond positively to climate change or a more frequent occurrence of mild winters based on their $b_k$'s (listed in Table 3.4a) can indeed be characterized as waterfowl (Fig. 3.3a; a.o. Teal *Anas crecca* and Mute swan *Cygnus olor*). Most of the species that are expected to respond negatively to climate change (listed in Table 3.4b) can be characterized as insectivorous long-distance migrants (Fig. 3.3b; a.o. Icterine warbler *Hippolais icterina* and Golden oriole *Oriolus oriolus*).



(a)



(b)



(c)



(d)
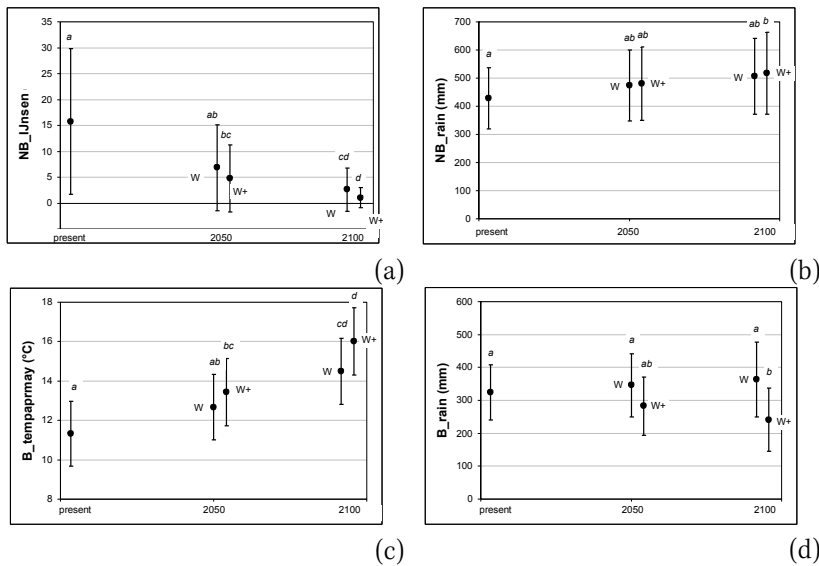
**Figure 3.4**

Weather variable values and SDs for present (1984-2004), 2050 (range 2037-2065), and 2100 (range 2087-2115) for IJnsen (a), total precipitation sum over non-breeding season (b), mean temperature from 16 April to 15 May (c), and total precipitation sum over breeding season (d); expectation based on data KNMI scenarios W and W$^+$ (http://climexp.knmi.nl/Scenarios_monthly/; for explanation on scenarios, see http://www.knmi.nl/research/climate_services/). Within each weather variable, bars sharing the same letter are not significantly different (P > 0.05). For abbreviations of weather variables, see Table 3.2.

Our results show that impacts of climate change on species dynamics may interfere with aims set in nature conservation programmes, which often concern the presence and abundance of specific target species in protected areas. In recent literature on ecosystem resilience it is argued that future nature conservation programmes should focus on the functioning of ecosystems and the distribution of functional groups of species over ecosystems, rather than setting conservation

Table 3.4

Species expected to respond most positively (a) and negatively (b) to the expected increased occurrence of mild winters, which can be expected from their species specific regression coefficient ($b_k$) values. For abbreviations of traits, see Table 3.1.

a: species expected to respond most positively

| abbreviation | scientific name | English name | lownest | fdpl | altr | resid | habitat (marshland species (M); forest species (F); both (M&F)) |
|---|---|---|---|---|---|---|---|
| ACAU | *Aegithalos caudatus* | Long-tailed tit | 0 | 0 | 1 | 1 | M&F |
| ACRE | *Anas crecca* | Teal | 1 | 1 | 0 | 0 | M |
| ASTR | *Anas strepera* | Gadwall | 1 | 1 | 0 | 0 | M |
| BSTE | *Botaurus stellaris* | Bittern | 1 | 0 | 1 | 1 | M |
| COLO | *Cygnus olor* | Mute swan | 1 | 1 | 0 | 1 | M |
| GCHL | *Gallinula chloropus* | Moorhen | 1 | 0 | 0 | 1 | M |
| LMEG | *Luscinia megarhynchos* | Nightingale | 0 | 0 | 1 | 0 | M&F |
| RAQU | *Rallus aquaticus* | Water rail | 1 | 0 | 0 | 0 | M |
| SATR | *Sylvia atricapilla* | Blackcap | 0 | 0 | 1 | 0 | M&F |
| TRUF | *Tachybaptus ruficollis* | Little grebe | 1 | 0 | 0 | 0 | M |

b: species expected to respond most negatively

| abbreviation | scientific name | English name | fdinvert | migr | habitat (marshland species (M); forest species (F); both (M&F)) |
|---|---|---|---|---|---|
| ECIT | *Emberiza citrinella* | Yellowhammer | 1 | 0 | F |
| FSUB | *Falco subbuteo* | Hobby | 1 | 1 | F |
| HICT | *Hippolais icterina* | Icterine warbler | 1 | 1 | F |
| OORI | *Oriolus oriolus* | Golden oriole | 1 | 1 | F |
| PCOLL | *Phylloscopus collybita* | Chiffchaff | 1 | 1 | M&F |
| PSIB | *Phylloscopus sibilatrix* | Wood warbler | 1 | 1 | F |
| RIGN | *Regulus ignicapillus* | Firecrest | 1 | 0 | F |
| SATR | *Sylvia atricapilla* | Blackcap | 1 | 1 | M&F |
| SBOR | *Sylvia borin* | Garden warbler | 1 | 1 | M&F |
| SCOM | *Sylvia communis* | Whitethroat | 1 | 1 | M&F |
| STUR | *Streptopelia turtur* | Turtle dove | 0 | 1 | M&F |
| TTRO | *Troglodytes troglodytes* | Winter wren | 1 | 0 | M&F |
| TVIS | *Turdus viscivorus* | Mistle thrush | 1 | 0 | F |

targets on specific rare or declining species (Turner et al. 2007). Species traits play an important role in constructing functional groups that help to understand the relationship between biodiversity and ecosystem functioning. In addition, our study shows that trait analysis also helps to gain insight into the responses to climate change which could be linked to these functional groups. In this way, our approach presents a generalized view on the responses of species to weather variability.

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## ACKNOWLEDGMENTS

## APPENDIX

### Appendix 3.1

Species, used for analysis in **Y** and **Z** matrix, and their traits (1: species holds trait; 0: species does not hold trait). For abbreviations of traits, see Table 3.1

| abbreviation | scientific name | English name | lownest | fdpl | fdinvert | fdpisci | fdmeat | altr | resid | pmigr | migr | habitat (marshland species (M); forest species (F); both (M&F)) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AARU | *Acrocephalus arundinaceus* | Great reed warbler | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | M |
| ACAU | *Aegithalos caudatus* | Long-tailed tit | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | M&F |
| ACLY | *Anas clypeata* | Northern shoveler | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | M |
| ACRE | *Anas crecca* | Teal | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | M |
| AFUL | *Aythya fuligula* | Tufted duck | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | M |
| AGEN | *Accipiter gentilis* | Goshawk | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | F |
| ANIS | *Accipiter nisus* | Sparrowhawk | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | F |
| AOTU | *Asio otus* | Long-eared owl | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | F |
| APAL | *Acrocephalus palustris* | Marsh warbler | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | M |
| APUR | *Ardea purpurea* | Purple heron | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | M |
| ASCH | *Acrocephalus schoenobaenus* | Sedge warbler | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | M |
| ASCI | *Acrocephalus scirpaceus* | Reed warbler | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | M |
| ASTR | *Anas strepera* | Gadwall | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | M |
| BBUT | *Buteo buteo* | Buzzard | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | F |
| BSTE | *Botaurus stellaris* | Bittern | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | M |
| CAER | *Circus aeruginosus* | Western marsh harrier | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | M |
| CBRA | *Certhia brachydactyla* | Short-toed treecreeper | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | F |
| CCANN | *Carduelis cannabina* | Linnet | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | F |
| CCANO | *Cuculus canorus* | Cuckoo | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | M&F |

| abbreviation | scientific name | English name | lownest | fdpl | fdinvert | fdpisci | fdmeat | altr | resid | pmigr | migr | habitat (marshland species (M); forest species (F); both (M&F)) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CCHL | *Chloris chloris* | Greenfinch | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | F |
| CCOR | *Corvus corone* | Carrion crow | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | F |
| CMON | *Corvus monedula* | Jackdaw | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | F |
| COEN | *Columba oenas* | Stock pigeon | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | F |
| COLO | *Cygnus olor* | Mute swan | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | M |
| CPAL | *Columba palumbus* | Wood pigeon | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | M&F |
| DMAJ | *Dendrocopos major* | Great spotted woodpecker | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | M&F |
| DMIN | *Dendrocopos minor* | Lesser spotted woodpecker | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | F |
| ECIT | *Emberiza citrinella* | Yellowhammer | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | F |
| ERUB | *Erithacus rubecula* | Robin | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | M&F |
| ESCH | *Emberiza schoeniclus* | Reed bunting | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | M |
| FATR | *Fulica atra* | Coot | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | M |
| FCOE | *Fringilla coelebs* | Chaffinch | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | F |
| FHYP | *Ficedula hypoleuca* | Pied flycatcher | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | F |
| FSUB | *Falco subbuteo* | Hobby | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | F |
| FTIN | *Falco tinnunculus* | Kestrel | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | F |
| GCHL | *Gallinula chloropus* | Moorhen | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | M |
| GGLA | *Garrulus glandarius* | Jay | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | M&F |
| HICT | *Hippolais icterina* | Icterine warbler | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | F |
| LLUS | *Locustella luscinioides* | Savi's warbler | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | M |
| LMEG | *Luscinia megarhynchos* | Nightingale | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | M&F |
| LNAE | *Locustella naevia* | Grasshopper warbler | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | M |
| LSVE | *Luscinia svecica* | Bluethroat | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | M |
| MSTRI | *Muscicapa striata* | Spotted flycatcher | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | F |

**Appendix 3.1 (continued)**

| abbreviation | scientific name | English name | lownest | fdpl | fdinvert | fdpisci | fdmeat | altr | resid | pmigr | migr | habitat (marshland species (M); forest species (F); both (M&F)) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| OORI | *Oriolus oriolus* | Golden oriole | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | F |
| PACRI | *Parus cristatus* | Crested tit | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | F |
| PATE | *Parus ater* | Coal tit | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | F |
| PCAE | *Parus caeruleus* | Blue tit | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | M&F |
| PCAR | *Phalacrocorax carbo* | Cormorant | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | M |
| PCOLC | *Phasianus colchicus* | Pheasant | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | F |
| PCOLL | *Phylloscopus collybita* | Chiffchaff | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | M&F |
| PLEU | *Platalea leucorodia* | Spoonbill | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | M |
| PMAJ | *Parus major* | Great tit | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | M&F |
| PMOD | *Prunella modularis* | Dunnock | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | M&F |
| PMON | *Parus montanus* | Willow tit | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | M&F |
| POCRI | *Podiceps cristatus* | Great crested grebe | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | M |
| PPAL | *Parus palustris* | Marsh tit | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | F |
| PPHO | *Phoenicurus phoenicurus* | Redstart | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | F |
| PPIC | *Pica pica* | Magpie | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | F |
| PPYR | *Pyrrhula pyrrhula* | Bullfinch | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | F |
| PSIB | *Phylloscopus sibilatrix* | Wood warbler | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | F |
| PTRO | *Phylloscopus trochilus* | Willow warbler | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | M&F |
| PVIR | *Picus viridis* | Green woodpecker | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | F |
| RAQU | *Rallus aquaticus* | Water rail | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | M |
| RIGN | *Regulus ignicapillus* | Firecrest | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | F |
| RPEN | *Remiz pendulinus* | Penduline tit | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | M |
| RREG | *Regulus regulus* | Goldcrest | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | F |

| abbreviation | scientific name | English name | lownest | fdpl | fdinvert | fdpisci | fdmeat | altr | resid | pmigr | migr | habitat (marshland species (M); forest species (F); both (M&F)) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SATR | *Sylvia atricapilla* | Blackcap | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | M&F |
| SBOR | *Sylvia borin* | Garden warbler | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | M&F |
| SCOM | *Sylvia communis* | Whitethroat | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | M&F |
| SEUR | *Sitta europaea* | Nuthatch | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | F |
| STUR | *Streptopelia turtur* | Turtle dove | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | M&F |
| SVUL | *Sturnus vulgaris* | Starling | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | F |
| TMER | *Turdus merula* | Blackbird | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | M&F |
| TPHI | *Turdus philomelos* | Song thrush | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | F |
| TRUF | *Tachybaptus ruficollis* | Little grebe | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | M |
| TTRO | *Troglodytes troglodytes* | Winter wren | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | M&F |
| TVIS | *Turdus viscivorus* | Mistle thrush | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | F |

**Appendix 3.2**

Occurrence of weather variables in 1984-2005. For abbreviations of weather variables, see Table 3.2
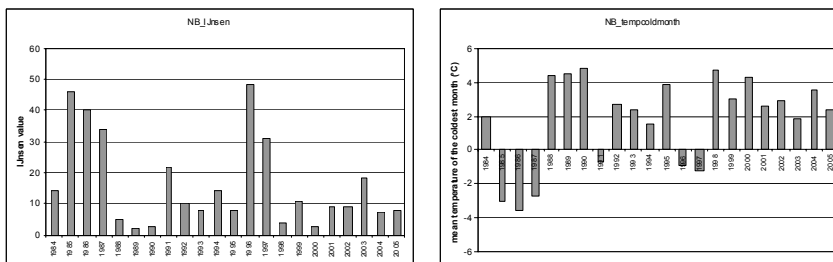
## Appendix 3.2 (continued)
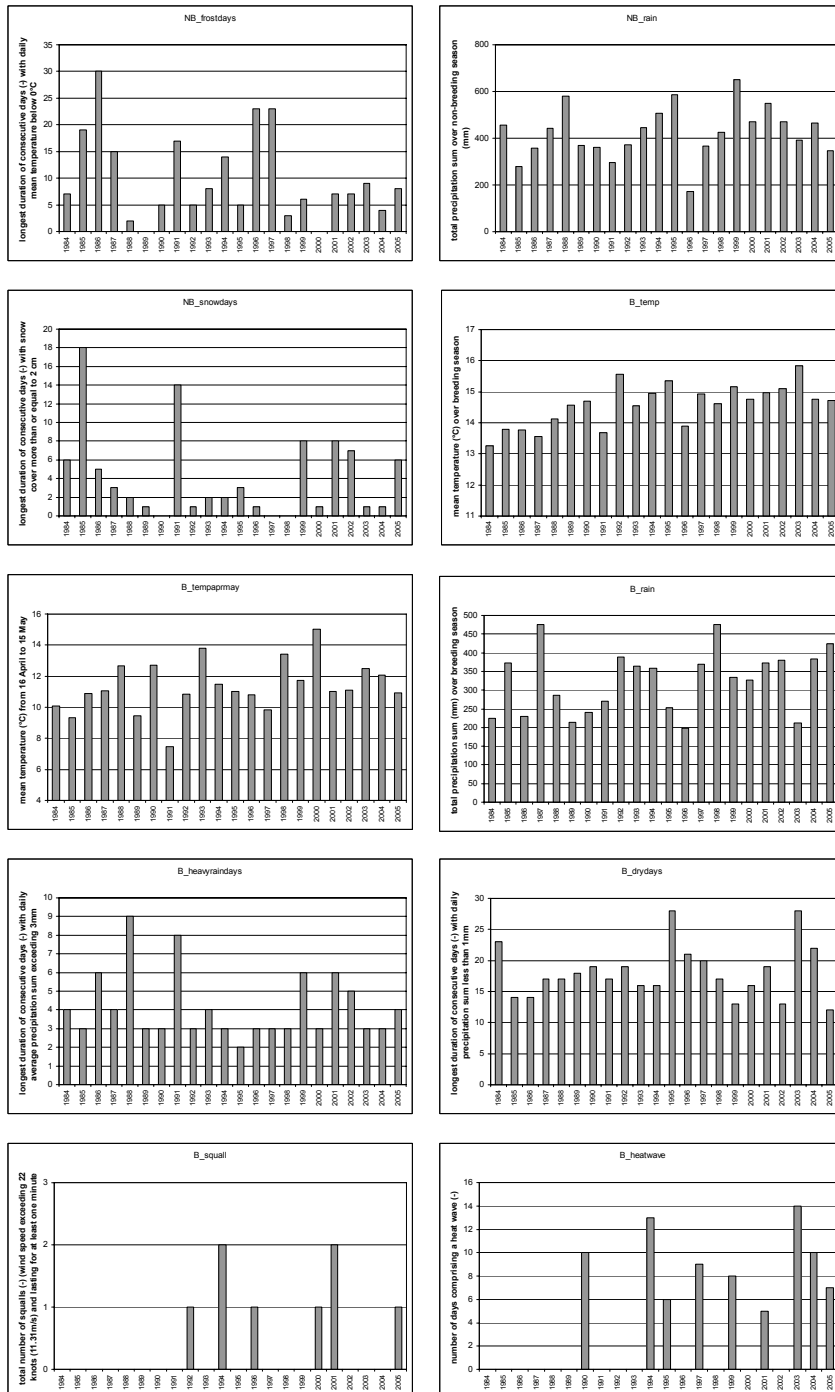
## Appendix 3.3

Correlations between weather variables; grey shading: relatively high Pearson score. For abbreviations of weather variables, see Table 3.2

| | NB_IJnsen | NB_IJnsen t-1 | NB_tempcoldmonth | NB_tempcoldmonth t-1 | NB_frostdays | NB_frostdays t-1 | NB_rain | NB_rain t-1 | NB_snowdays | NB_snowdays t-1 | B_temp | B_temp t-1 | B_tempaprmay | B_tempaprmay t-1 | B_rain | B_rain t-1 | B_heavyraindays | B_heavyraindays t-1 | B_drydays | B_drydays t-1 | B_squall | B_squall t-1 | B_heatwave | B_heatwave t-1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| NB_IJnsen | - | 0.31 | -0.87 | -0.29 | 0.90 | 0.37 | -0.49 | -0.35 | 0.38 | 0.27 | -0.41 | -0.29 | -0.50 | -0.13 | -0.04 | -0.30 | -0.25 | 0.04 | -0.02 | 0.17 | -0.02 | -0.04 | -0.07 | -0.17 |
| NB_IJnsen t-1 | 0.31 | - | -0.41 | -0.86 | 0.18 | 0.90 | 0.05 | -0.50 | -0.27 | 0.40 | -0.19 | -0.39 | 0.12 | -0.51 | 0.31 | -0.03 | 0.19 | -0.28 | 0.04 | -0.04 | -0.26 | 0.00 | -0.28 | -0.06 |
| NB_tempcoldmonth | -0.87 | -0.41 | - | 0.48 | -0.74 | -0.37 | 0.46 | 0.39 | -0.39 | -0.39 | 0.64 | 0.50 | 0.47 | 0.25 | 0.03 | 0.34 | 0.34 | 0.12 | 0.22 | 0.00 | 0.15 | 0.16 | 0.28 | 0.26 |
| NB_tempcoldmonth t-1 | -0.29 | -0.86 | 0.48 | - | -0.20 | -0.75 | -0.13 | 0.48 | 0.14 | -0.40 | 0.38 | 0.55 | -0.07 | 0.46 | -0.25 | -0.01 | -0.18 | 0.38 | 0.06 | 0.28 | 0.27 | 0.13 | 0.35 | 0.26 |
| NB_frostdays | 0.90 | 0.18 | -0.74 | -0.20 | - | 0.22 | -0.42 | -0.49 | 0.33 | 0.07 | -0.32 | -0.19 | -0.46 | -0.13 | 0.02 | -0.25 | -0.21 | -0.05 | -0.07 | 0.23 | -0.01 | 0.08 | 0.12 | -0.17 |
| NB_frostdays t-1 | 0.37 | 0.90 | -0.37 | -0.75 | 0.22 | - | 0.03 | -0.42 | -0.16 | 0.33 | -0.14 | -0.29 | 0.00 | -0.46 | 0.29 | 0.02 | 0.25 | -0.20 | 0.06 | -0.06 | -0.29 | -0.02 | -0.29 | 0.11 |
| NB_rain | -0.49 | 0.05 | 0.46 | -0.13 | -0.42 | 0.03 | - | 0.04 | 0.04 | -0.15 | 0.45 | 0.05 | 0.41 | 0.36 | 0.34 | 0.55 | 0.23 | 0.05 | -0.03 | -0.49 | -0.05 | 0.32 | 0.31 | -0.12 |
| NB_rain t-1 | -0.35 | -0.50 | 0.39 | 0.48 | -0.49 | -0.42 | 0.04 | - | 0.22 | 0.08 | 0.06 | 0.38 | 0.22 | 0.39 | -0.26 | 0.35 | -0.05 | 0.22 | -0.02 | -0.06 | 0.27 | -0.03 | -0.13 | 0.33 |
| NB_snowdays | 0.38 | -0.27 | -0.39 | 0.14 | 0.33 | -0.16 | 0.04 | 0.22 | - | 0.04 | -0.30 | -0.20 | -0.50 | 0.34 | 0.12 | 0.19 | -0.33 | 0.22 | -0.49 | -0.01 | 0.03 | 0.12 | -0.17 | 0.02 |
| NB_snowdays t-1 | 0.27 | 0.40 | -0.39 | -0.40 | 0.07 | 0.33 | -0.15 | 0.08 | 0.04 | - | 0.00 | -0.36 | 0.07 | -0.51 | -0.17 | 0.02 | -0.20 | -0.26 | -0.01 | -0.38 | 0.09 | -0.04 | -0.35 | -0.25 |
| B_temp | -0.41 | -0.19 | 0.64 | 0.38 | -0.32 | -0.14 | 0.45 | 0.06 | -0.30 | 0.00 | - | 0.31 | 0.31 | 0.07 | 0.03 | 0.30 | 0.26 | 0.10 | 0.37 | -0.22 | 0.19 | 0.34 | 0.58 | -0.01 |
| B_temp t-1 | -0.29 | -0.39 | 0.50 | 0.55 | -0.19 | -0.29 | 0.05 | 0.38 | -0.20 | -0.36 | 0.31 | - | 0.42 | 0.35 | -0.08 | 0.14 | 0.05 | 0.19 | 0.27 | 0.25 | 0.12 | 0.22 | 0.27 | 0.59 |
| B_tempaprmay | -0.50 | 0.12 | 0.47 | -0.07 | -0.46 | 0.00 | 0.41 | 0.22 | -0.50 | 0.07 | 0.31 | 0.42 | - | -0.12 | 0.15 | 0.43 | 0.19 | 0.05 | 0.05 | -0.26 | 0.09 | -0.03 | 0.08 | 0.04 |
| B_tempaprmay t-1 | -0.13 | -0.51 | 0.25 | 0.46 | -0.13 | -0.46 | 0.36 | 0.39 | 0.34 | -0.51 | 0.07 | 0.35 | -0.12 | - | 0.02 | 0.21 | -0.12 | 0.15 | -0.04 | -0.02 | 0.34 | 0.12 | 0.40 | 0.12 |
| B_rain | -0.04 | 0.31 | 0.03 | -0.25 | 0.02 | 0.29 | 0.34 | -0.26 | 0.12 | -0.17 | 0.03 | -0.08 | 0.15 | 0.02 | - | -0.02 | 0.17 | -0.03 | -0.42 | 0.13 | 0.15 | 0.11 | -0.03 | 0.08 |
| B_rain t-1 | -0.30 | -0.03 | 0.34 | -0.01 | -0.25 | 0.02 | 0.55 | 0.35 | 0.19 | 0.02 | 0.30 | 0.14 | 0.43 | 0.21 | -0.02 | - | 0.21 | 0.19 | -0.27 | -0.41 | 0.09 | 0.12 | -0.01 | -0.04 |
| B_heavyraindays | -0.25 | 0.19 | 0.34 | -0.18 | -0.21 | 0.25 | 0.23 | -0.05 | -0.33 | -0.20 | 0.26 | 0.05 | 0.19 | -0.12 | 0.17 | 0.21 | - | -0.12 | 0.28 | -0.07 | 0.13 | 0.05 | -0.06 | 0.21 |

**Appendix 3.3 (continued)**

| | NB_ljnsen | NB_ljnsen t-1 | NB_tempcoldmonth | NB_tempcoldmonth t-1 | NB_frostdays | NB_frostdays t-1 | NB_rain | NB_rain t-1 | NB_snowdays | NB_snowdays t-1 | B_temp | B_temp t-1 | B_tempaprmay | B_tempaprmay t-1 | B_rain | B_rain t-1 | B_heavyraindays | B_heavyraindays t-1 | B_drydays | B_drydays t-1 | B_squall | B_squall t-1 | B_heatwave | B_heatwave t-1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| B_heavyraindays t-1 | 0.04 | -0.28 | 0.12 | 0.38 | -0.05 | -0.20 | 0.05 | 0.22 | 0.22 | -0.26 | 0.10 | 0.19 | 0.05 | 0.15 | -0.03 | 0.19 | -0.12 | - | -0.22 | 0.23 | -0.22 | 0.19 | -0.05 | -0.03 |
| B_drydays | -0.02 | 0.04 | 0.22 | 0.06 | -0.07 | 0.06 | -0.03 | -0.02 | -0.49 | -0.01 | 0.37 | 0.27 | 0.05 | -0.04 | -0.42 | -0.27 | 0.28 | -0.22 | - | -0.06 | -0.08 | 0.17 | 0.34 | 0.09 |
| B_drydays t-1 | 0.17 | -0.04 | 0.00 | 0.28 | 0.23 | -0.06 | -0.49 | -0.06 | -0.01 | -0.38 | -0.22 | 0.25 | -0.26 | -0.02 | 0.13 | -0.41 | -0.07 | 0.23 | -0.06 | - | -0.05 | -0.01 | 0.01 | 0.40 |
| B_squall | -0.02 | -0.26 | 0.15 | 0.27 | -0.01 | -0.29 | -0.05 | 0.27 | 0.03 | 0.09 | 0.19 | 0.12 | 0.09 | 0.34 | 0.15 | 0.09 | 0.13 | -0.22 | -0.08 | -0.05 | - | -0.08 | 0.16 | 0.02 |
| B_squall t-1 | -0.04 | 0.00 | 0.16 | 0.13 | 0.08 | -0.02 | 0.32 | -0.03 | 0.12 | -0.04 | 0.34 | 0.22 | -0.03 | 0.12 | 0.11 | 0.12 | 0.05 | 0.19 | 0.17 | -0.01 | -0.08 | - | 0.09 | 0.13 |
| B_heatwave | -0.07 | -0.28 | 0.28 | 0.35 | 0.12 | -0.29 | 0.31 | -0.13 | -0.17 | -0.35 | 0.58 | 0.27 | 0.08 | 0.40 | -0.03 | -0.01 | -0.06 | -0.05 | 0.34 | 0.01 | 0.16 | 0.09 | - | -0.05 |
| B_heatwave t-1 | -0.17 | -0.06 | 0.26 | 0.26 | -0.17 | 0.11 | -0.12 | 0.33 | 0.02 | -0.25 | -0.01 | 0.59 | 0.04 | 0.12 | 0.08 | -0.04 | 0.21 | -0.03 | 0.09 | 0.40 | 0.02 | 0.13 | -0.05 | - |

## Appendix 3.4

In this appendix we describe the linear trait-environment (LTE) method, which is the linear counter part of the fourth-corner method of Dray and Legendre (2008). See below for a detailed comparison. The LTE method relates the quantitative environmental variable x to the quantitative species trait $z$ via the species-site data $y$. It differs from the fourth-corner method by using multivariate linear regression model for the species-site data, thus allowing negative values $y$. In our application, sites are years and $y_{ik} = \ln[\text{index }_{\text{year\_i,species\_k}} / \text{index }_{\text{year\_i-1,species\_k}}]$.

*Notation*: Denote the value of environmental variable $x$ at site $i$ by $x_i$, the value of the trait $z$ of species k by $z_k$, and the population growth rate $y$ of species $k$ in site $i$ by $y_{ik}$ ($i = 1,..., n, k = 1, ..., m$). All these values are interval scaled taking values on the real line.

*Model*: The LTE method starts from a multivariate linear regression of the species-site data using a single predictor variable $x$. This regression can be expressed as m separate simple linear regressions, one for each species,

$$y_{ik} = a_k + b_k x_i + \varepsilon_{ik}, \tag{1}$$

where $a_k$ and $b_k$ are the intercept and slope for species k with respect to environmental variable $x$ and $\varepsilon_{ik}$ is a noise variable with mean 0 and a species-specific variance. This models the environmentally structured variation in the species-site data. We define the amount of environmentally structured variation by the sum across species of the regression sum of squares, say $SS$x. We now relate this variation to the species trait z by a simple regression of the species-specific slopes ($b_k$) on to the trait $z$, that is

$$b_k = c + dz_k + \delta_k,$$

where $c$ and $d$ are the intercept and slope for trait $z$ and $\delta_k$ is species specific noise variable with mean 0. By inserting this equation in the previous we obtain one regression model for all $n \times m$ data points

$$y_{ik} = a_k + cx_i + dz_k x_i + \varepsilon_{ik}^* \tag{2}$$

with $\varepsilon_{ik}^* = \varepsilon_{ik} + \delta_k x_i$, an error term with mean zero. Note that the errors are no longer independent. The trait-environment relation is represented by the coefficient d and the amount of trait-environment variation is expressed as the sum of squares, say $SS$xz, associated with the term $z_k x_i$. Equation (2) could also be ex-

pressed as a linear mixed model, but we do not do so because we estimate parameters by least-squares and perform statistical tests by Monte Carlo permutation.

*Fitting the model:* The least-squares estimate, $\hat{d}$, of the coefficient $d$ can be calculated most easily by subtracting the mean of $x$ and of $z$ from $x_i$ and $z_k$ and by continuing with the centered versions, denoted by the vectors $\mathbf{x}$ and $\mathbf{z}$. With $\mathbf{Y} = [y_{ik}]$, the matrix with species-site data, we then have (see also Takane et al. 1991; Takane & Hunter 2001)

$$\hat{d} = (\mathbf{x}^T\mathbf{x})^{-1}\mathbf{x}^T\mathbf{Y}\mathbf{z}(\mathbf{z}^T\mathbf{z})^{-1} \text{ and } \mathrm{SS}_{xz} = \hat{d}^2\sum_{i,k}(x_iz_k)^2 \tag{3}$$

These results can be derived by noting that the term $z_k x_i$ is orthogonal to all terms $a_k$ and $x_i$, e.g. for the latter

$$\sum_{i,k} z_k x_i^2 = 0,$$

so that $\hat{d}$ can be obtained by regressing a response with elements $y_{ik}$ on the single predictor with elements $x_iz_k$ using all $n \times m$ data points and by re-expressing the least-squares estimate in terms of the vectors $\mathbf{x}$ and $\mathbf{z}$ and matrix $\mathbf{Y}$.

*Testing statistical significance:* Dray and Legendre (2008) evaluated six permutation-based significance tests for testing the trait-environment relationship, but none faithfully controlled the type I error. This means that these tests may more frequently indicate a trait-environment relationship than the nominal significance level (e.g. 0.05) in the case no such relationship exists. Ter Braak et al. (in prep.) showed that their sixth method (the combined method) can be transformed into a sequential test that does control the type I error. The new test is carried out as follows.

(1) Select a test statistic that is sensitive to the strength of the trait-environment relationship, for which we use *SS*xz, and compute its value for the data, yielding $F_0$.

(2) Randomly permute the values in $x$ and compute the statistic using the permuted $x$, yielding $F_1$. Repeat this operation so as to yield the additional values $F_2, \dots F_K$, with $K$ the number of permutations. We used $K = 999$.

(3) Compute the Monte Carlo significance level, i.e. compute the number of values $F_0, F_1, \dots F_K$ that is greater than or equal to $F_0$ (this number is thus at least 1), and divide by $K+1$. Denote the result by $\alpha_1$.

(4) Randomly permute the values in $z$ and compute the statistic using the permuted $z$, yielding $G_1$. Repeat this operation so as to yield the additional values $G_2, \ldots G_K$, with $K$ the number of permutations.

(5) Compute the Monte Carlo significance level, i.e. compute the number of values $F_0, G_1, \ldots G_K$ that is greater than or equal to $F_0$ (this number is thus at least 1), and divide by $K+1$. Denote the result by $\alpha_2$.

(6) The final Monte Carlo significance level, $\alpha$, is the maximum of the two significance levels, i.e. $\alpha = \max(\alpha_1, \alpha_2)$.

*Trait-environment correlation*: The fourth-corner problem linking two quantitative variables yields an easy to interpret correlation (Dray & Legendre 2008). For the LTE method we define the trait-environment correlation ($R$) as the Pearson correlation between the species-specific slopes ($b_k$) and the trait $z$. It can be shown that $R^2$ is the fraction of the environmentally structured variation that can be explained by the trait, i.e. $R^2 = SSxz/SSx$. Note the caveat in the interpretation of $R$ that $R$ can be high even when the environmentally structured variation is small. For this reason, the squared correlation is less suited for testing.

*Discussion*: One may wonder why we use the simple test statistic $SSxz$ instead of an $F$-type statistic which compares the regression mean square to the error mean square as is optimal in permutation tests for testing the significance of one or more regression terms in the presence of other (so called nuisance) terms (Anderson & Legendre 1999; Anderson & Robinson 2001; Ter Braak & Šmilauer 2002). The reason is that the other models than model (2) can be formulated that are equally appealing but that yield another error mean square. For example, by also expressing $a_k$ as a linear function of $z$ we obtain a standard model with main effects for $x$ and $z$ and the interaction between $x$ and $z$, that is

$$y_{ik} = c_0 + c_1 x_i + c_2 z_k + c_3 x_i z_k + \varepsilon_{ik}^{**} . \tag{4}$$

One can verify that the least-squares estimates of $d$ in model (2) and of $c_3$ in model (4) are equal. The amounts of trait-environment variation are equal as well. A third model with the same interaction parameter and the same amount of trait-environment variation is a model with free parameters for sites (rows) and species (species) and an interaction term between $x$ and $z$, that is

$$y_{ik} = r_i + c_k + dx_i z_k + \varepsilon_{ik}^{***} . \tag{5}$$

This model can simply be expressed as

$$\widetilde{y}_{ik} = dx_i z_k + \varepsilon_{ik}^{***}. \tag{6}$$

with $\widetilde{y}_{ik}$ the double centered version of $y_{ik}$, i.e.

$\widetilde{y}_{ik} = y_{ik} - y_{i+}/m - y_{+k}/n + y_{++}/nm$, where we use the notation that a '+' replacing an index means the sum over the index. So, only one term remains, making it unnecessary to use an $F$–type statistic. The proposed permutation test is thus based on a model with all variation that is either environmentally structured or trait-structured but not both removed. Here 'all' means not only variation related to our specific $x$ or to $z$, but to any environmental variable or trait.

*Comparison of LTE with the fourth-corner method*: The fourth-corner method (Dray & Legendre 2008) calculates a weighted Pearson correlation between the trait and the environmental variable by using all species-site combinations as cases, the measure of abundance as a weight and by assigning to each case the trait and the environmental value of the combination. This generates a weighted data set of $n \times m$ cases with two variables. As zero abundance implies zero weight, the standard fourth-corner method calculates the correlation between trait and environmental variable for the species-site combinations with positive abundance. The method thus has particular appeal for presence/absence data for which it was originally developed (Legendre et al. 1997) and for abundance data with many zeroes. As weights must be non-negative, the method cannot be used with a measure of (change in) abundance that can be negative, for example, when an index value decreases from one year to the next.

Whereas the standard fourth-corner method relates to doubly constrained correspondence analysis and the method of weighted averaging (that is, methods that have appeal for unimodal relationships in niche studies, Ter Braak & Prentice 1988), the LTE method relates similarly to doubly constrained principal component analysis and linear regression. This relationship to linear methods may appear a step in the wrong direction in terms of model complexity. However, because we apply the method to log-ratios or population growth rates, the method is well suited to analyze unimodal data, as shown in section 3.9 of Ter Braak and Šmilauer (2002).

## Appendix 3.5

Correlations between traits; grey shading: relatively high Pearson score. For abbreviations of traits, see Table 3.1

a: marshland species

|          | lownest | fdpl  | fdinvert | fdpisci | fdmeat | altr  | resid | pmigr | migr  |
|----------|---------|-------|----------|---------|--------|-------|-------|-------|-------|
| lownest  | -       | 0.28  | -0.32    | 0.04    | 0.21   | -0.75 | -0.13 | 0.37  | -0.23 |
| fdpl     | 0.28    | -     | -0.69    | -0.17   | -0.07  | -0.44 | -0.03 | 0.34  | -0.28 |
| fdinvert | -0.32   | -0.69 | -        | -0.52   | -0.22  | 0.32  | 0.10  | -0.30 | 0.19  |
| fdpisci  | 0.04    | -0.17 | -0.52    | -       | -0.06  | 0.03  | -0.06 | 0.08  | -0.01 |
| fdmeat   | 0.21    | -0.07 | -0.22    | -0.06   | -      | 0.08  | -0.10 | -0.10 | 0.18  |
| altr     | -0.75   | -0.44 | 0.32     | 0.03    | 0.08   | -     | 0.10  | -0.60 | 0.47  |
| resid    | -0.13   | -0.03 | 0.10     | -0.06   | -0.10  | 0.10  | -     | -0.41 | -0.53 |
| pmigr    | 0.37    | 0.34  | -0.30    | 0.08    | -0.10  | -0.60 | -0.41 | -     | -0.56 |
| migr     | -0.23   | -0.28 | 0.19     | -0.01   | 0.18   | 0.47  | -0.53 | -0.56 | -     |

b: forest species

|          | lownest | fdpl  | fdinvert | fdmeat | altr  | resid | pmigr | migr  |
|----------|---------|-------|----------|--------|-------|-------|-------|-------|
| lownest  | -       | 0.12  | -0.03    | -0.08  | -0.57 | -0.06 | -0.15 | 0.21  |
| fdpl     | 0.12    | -     | -0.67    | -0.14  | -0.33 | -0.07 | 0.23  | -0.15 |
| fdinvert | -0.03   | -0.67 | -        | -0.51  | 0.22  | 0.07  | -0.38 | 0.30  |
| fdmeat   | -0.08   | -0.14 | -0.51    | -      | 0.04  | -0.16 | 0.39  | -0.20 |
| altr     | -0.57   | -0.33 | 0.22     | 0.04   | -     | -0.15 | 0.08  | 0.09  |
| resid    | -0.06   | -0.07 | 0.07     | -0.16  | -0.15 | -     | -0.55 | -0.57 |
| pmigr    | -0.15   | 0.23  | -0.38    | 0.39   | 0.08  | -0.55 | -     | -0.38 |
| migr     | 0.21    | -0.15 | 0.30     | -0.20  | 0.09  | -0.57 | -0.38 | -     |

# Appendix 3.6

Species specific regression coefficients $b_k$ resulting from the LTE analyses. For abbreviations of species names, see Appendix 3.1; for abbreviations of weather variables, see Table 3.2

a: marshland species

| abbreviation | NB_Jnsen | NB_Jnsen t-1 | NB_tempcoldmonth | NB_tempcoldmonth t-1 | NB_frostdays | NB_frostdays t-1 | NB_rain | NB_rain t-1 | NB_snowdays | NB_snowdays t-1 | B_temp | B_temp t-1 | B_tempmay | B_tempmay t-1 | B_rain | B_rain t-1 | B_heavyraindays | B_heavyraindays t-1 | B_drydays | B_drydays t-1 | B_squall | B_squall t-1 | B_heatwave | B_heatwave t-1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AARU | 0.08 | 0.06 | -0.13 | -0.13 | 0.07 | 0.05 | 0.02 | -0.08 | 0.05 | 0.02 | -0.09 | 0.00 | 0.00 | 0.01 | 0.11 | 0.10 | 0.04 | -0.08 | -0.12 | -0.14 | 0.08 | -0.01 | -0.03 | 0.00 |
| ACAU | -0.05 | -0.09 | 0.14 | 0.08 | -0.04 | -0.05 | -0.10 | 0.21 | -0.06 | -0.06 | 0.00 | 0.14 | 0.01 | 0.03 | -0.02 | -0.17 | 0.21 | -0.02 | 0.26 | 0.08 | 0.17 | 0.07 | -0.02 | 0.07 |
| ACLY | 0.00 | -0.01 | -0.01 | 0.01 | 0.00 | -0.02 | -0.10 | 0.04 | 0.05 | -0.08 | -0.09 | -0.06 | -0.04 | 0.02 | 0.17 | 0.02 | -0.06 | 0.12 | -0.37 | 0.42 | -0.03 | -0.04 | -0.02 | 0.00 |
| ACRE | -0.01 | -0.08 | 0.05 | 0.16 | -0.05 | -0.06 | -0.09 | 0.29 | 0.11 | -0.09 | -0.08 | 0.00 | -0.02 | 0.05 | -0.12 | 0.39 | -0.26 | 0.71 | -0.39 | 0.25 | -0.12 | 0.07 | -0.09 | -0.04 |
| AFUL | 0.01 | 0.00 | -0.03 | 0.01 | 0.00 | 0.01 | -0.01 | -0.01 | 0.03 | 0.01 | 0.00 | -0.05 | -0.02 | 0.01 | 0.13 | -0.03 | -0.10 | -0.03 | -0.18 | 0.01 | 0.05 | -0.07 | 0.00 | -0.01 |
| APAL | 0.07 | 0.01 | -0.09 | -0.01 | 0.06 | -0.01 | -0.11 | 0.06 | 0.05 | 0.05 | -0.06 | -0.01 | 0.00 | -0.01 | -0.06 | -0.02 | -0.11 | 0.07 | -0.09 | 0.17 | 0.07 | 0.06 | -0.01 | 0.00 |
| APUR | 0.02 | 0.03 | -0.01 | -0.01 | 0.02 | 0.04 | 0.00 | -0.01 | 0.01 | 0.04 | 0.05 | 0.02 | 0.01 | -0.02 | 0.12 | 0.05 | 0.22 | -0.03 | -0.03 | 0.06 | 0.09 | -0.02 | 0.00 | 0.04 |
| ASCH | 0.02 | 0.06 | -0.04 | -0.09 | 0.00 | 0.07 | 0.07 | 0.06 | 0.00 | 0.06 | -0.03 | 0.03 | 0.01 | -0.01 | -0.02 | 0.04 | 0.19 | -0.08 | 0.15 | -0.06 | 0.03 | 0.06 | -0.03 | 0.04 |
| ASCI | 0.05 | 0.01 | -0.08 | -0.01 | 0.04 | 0.01 | -0.05 | -0.05 | 0.04 | 0.06 | 0.03 | -0.03 | -0.02 | -0.02 | -0.03 | 0.00 | -0.01 | 0.00 | -0.04 | -0.06 | 0.05 | 0.03 | 0.01 | 0.00 |
| ASTR | -0.09 | -0.12 | 0.16 | 0.19 | -0.09 | -0.07 | 0.03 | 0.24 | -0.02 | -0.10 | 0.06 | 0.09 | -0.02 | 0.06 | -0.06 | -0.11 | -0.02 | 0.15 | 0.13 | 0.08 | 0.07 | -0.06 | 0.04 | 0.04 |
| BSTE | -0.09 | 0.04 | 0.11 | -0.06 | -0.09 | 0.04 | 0.35 | -0.02 | -0.01 | -0.01 | 0.10 | -0.05 | 0.02 | 0.01 | 0.21 | 0.32 | 0.23 | 0.06 | -0.12 | -0.33 | -0.06 | 0.08 | -0.02 | -0.02 |
| CAER | 0.02 | 0.01 | -0.03 | -0.03 | 0.02 | 0.00 | 0.05 | -0.05 | 0.01 | 0.01 | -0.03 | -0.02 | 0.00 | 0.01 | -0.09 | 0.09 | -0.01 | -0.11 | -0.06 | -0.10 | 0.06 | -0.01 | 0.01 | 0.00 |
| CCANO | 0.05 | 0.00 | -0.06 | 0.04 | 0.03 | 0.01 | -0.15 | 0.04 | 0.04 | 0.02 | -0.02 | 0.01 | -0.01 | -0.01 | -0.03 | -0.07 | -0.08 | 0.13 | 0.00 | 0.16 | 0.02 | 0.01 | -0.01 | 0.02 |
| COLO | -0.08 | -0.09 | 0.17 | 0.09 | -0.08 | -0.03 | 0.18 | 0.14 | -0.03 | -0.14 | 0.04 | 0.10 | -0.02 | 0.07 | 0.08 | -0.16 | -0.05 | 0.10 | 0.32 | -0.08 | -0.06 | 0.09 | 0.04 | 0.04 |

| abbreviation | NB_lJnsen | NB_lJnsen t-1 | NB_tempcoldmonth | NB_tempcoldmonth t-1 | NB_frostdays | NB_frostdays t-1 | NB_rain | NB_rain t-1 | NB_snowdays | NB_snowdays t-1 | B_temp | B_temp t-1 | B_tempazrmay | B_tempazrmayy t-1 | B_rain | B_rain t-1 | B_heavyraindays | B_heavyraindays t-1 | B_drydays | B_drydays t-1 | B_squall | B_squall t-1 | B_heatwave | B_heatwave t-1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CPAL | 0.03 | -0.01 | -0.02 | 0.03 | 0.02 | -0.01 | -0.06 | 0.06 | 0.01 | 0.03 | 0.02 | 0.01 | 0.00 | 0.00 | -0.19 | 0.03 | 0.02 | -0.05 | 0.12 | -0.01 | 0.02 | -0.06 | 0.02 | 0.00 |
| DMAJ | 0.04 | -0.04 | -0.06 | 0.08 | 0.06 | -0.05 | -0.17 | 0.03 | 0.06 | 0.01 | -0.07 | 0.03 | 0.01 | -0.01 | -0.07 | 0.06 | -0.08 | -0.02 | -0.27 | 0.24 | 0.06 | 0.00 | -0.02 | 0.01 |
| ERUB | -0.09 | -0.02 | 0.07 | 0.04 | -0.07 | -0.03 | -0.04 | -0.08 | -0.09 | 0.03 | 0.10 | 0.05 | 0.00 | -0.02 | -0.35 | 0.15 | 0.10 | -0.08 | 0.08 | -0.24 | -0.04 | -0.01 | -0.01 | 0.00 |
| ESCH | 0.03 | -0.01 | -0.01 | 0.02 | 0.03 | 0.00 | -0.01 | -0.01 | 0.04 | -0.01 | 0.00 | 0.02 | -0.01 | 0.01 | 0.02 | 0.10 | -0.05 | 0.05 | -0.10 | 0.07 | 0.03 | 0.02 | 0.01 | 0.01 |
| FATR | 0.04 | -0.02 | -0.04 | 0.03 | 0.05 | -0.01 | -0.01 | -0.07 | 0.05 | 0.00 | 0.03 | -0.03 | -0.02 | 0.00 | 0.01 | -0.04 | 0.01 | 0.01 | -0.02 | -0.02 | -0.01 | -0.02 | 0.02 | -0.01 |
| GCHL | -0.13 | -0.04 | 0.18 | 0.05 | -0.10 | -0.04 | 0.22 | 0.16 | -0.06 | -0.05 | 0.07 | 0.09 | 0.04 | 0.02 | 0.13 | 0.11 | 0.22 | 0.04 | -0.03 | -0.01 | 0.08 | -0.01 | 0.01 | 0.03 |
| GGLA | 0.08 | 0.00 | -0.07 | -0.05 | 0.03 | 0.05 | -0.17 | 0.13 | 0.03 | -0.03 | -0.14 | 0.03 | -0.02 | 0.02 | 0.21 | -0.33 | -0.03 | 0.00 | 0.19 | 0.03 | -0.01 | -0.12 | -0.06 | 0.03 |
| LLUS | -0.03 | 0.03 | 0.03 | -0.05 | -0.02 | 0.01 | 0.20 | 0.01 | -0.02 | 0.00 | 0.03 | 0.01 | 0.03 | 0.00 | 0.05 | 0.16 | 0.10 | 0.02 | -0.05 | -0.10 | 0.00 | 0.03 | 0.02 | -0.01 |
| LMEG | -0.07 | -0.07 | 0.02 | 0.18 | -0.06 | -0.08 | -0.34 | 0.06 | -0.01 | 0.00 | -0.03 | 0.04 | -0.06 | 0.02 | -0.76 | 0.21 | -0.24 | -0.05 | -0.15 | 0.25 | 0.01 | -0.03 | -0.04 | 0.02 |
| LNAE | 0.03 | 0.01 | -0.01 | -0.01 | 0.02 | 0.01 | -0.16 | 0.08 | -0.04 | -0.01 | -0.07 | 0.07 | -0.01 | -0.01 | -0.11 | -0.14 | -0.09 | -0.10 | 0.23 | 0.31 | -0.01 | -0.13 | 0.02 | 0.05 |
| LSVE | 0.09 | 0.02 | -0.13 | -0.04 | 0.08 | 0.03 | -0.07 | -0.09 | 0.05 | 0.05 | -0.05 | -0.03 | -0.01 | -0.01 | -0.10 | -0.05 | -0.08 | -0.11 | 0.07 | -0.08 | -0.07 | -0.01 | 0.00 | -0.01 |
| PCAE | 0.03 | 0.00 | -0.01 | -0.02 | 0.01 | -0.01 | -0.15 | 0.18 | -0.02 | 0.07 | -0.01 | 0.01 | 0.03 | -0.02 | -0.05 | 0.02 | 0.08 | 0.03 | -0.01 | 0.07 | 0.17 | -0.12 | -0.02 | 0.00 |
| PCAR | 0.02 | 0.01 | -0.06 | -0.02 | 0.02 | 0.00 | -0.16 | 0.01 | 0.01 | 0.05 | -0.05 | 0.00 | 0.00 | -0.04 | -0.28 | -0.05 | 0.05 | 0.00 | 0.14 | 0.01 | -0.16 | 0.02 | -0.04 | 0.02 |
| PCOLL | 0.05 | 0.07 | -0.06 | -0.06 | 0.05 | 0.04 | -0.13 | -0.21 | -0.07 | 0.07 | 0.05 | -0.01 | 0.00 | -0.05 | -0.06 | -0.32 | 0.06 | -0.19 | 0.51 | 0.00 | -0.10 | 0.14 | 0.01 | -0.02 |
| PLEU | -0.07 | 0.13 | 0.00 | -0.12 | -0.02 | 0.07 | 0.76 | -0.63 | 0.01 | 0.00 | 0.17 | -0.16 | 0.00 | 0.01 | 0.45 | -0.11 | -0.13 | -0.35 | -0.10 | -0.48 | -0.30 | 0.51 | 0.10 | -0.06 |
| PMAJ | 0.08 | 0.01 | -0.09 | -0.02 | 0.07 | 0.00 | -0.27 | 0.03 | 0.01 | 0.04 | -0.05 | 0.03 | -0.01 | -0.03 | -0.06 | -0.10 | -0.05 | 0.04 | 0.05 | 0.12 | 0.03 | -0.05 | -0.01 | 0.02 |
| PMOD | -0.04 | 0.01 | 0.05 | -0.01 | -0.02 | -0.01 | -0.05 | 0.01 | -0.09 | 0.03 | 0.05 | 0.08 | 0.05 | -0.03 | -0.10 | 0.04 | 0.02 | -0.04 | 0.16 | -0.04 | 0.04 | -0.04 | 0.01 | 0.01 |
| PMON | 0.00 | 0.00 | -0.06 | -0.01 | -0.01 | 0.01 | -0.17 | 0.05 | 0.00 | 0.01 | -0.07 | 0.03 | -0.01 | -0.01 | -0.15 | 0.01 | 0.17 | -0.08 | -0.07 | -0.11 | 0.00 | -0.01 | -0.05 | 0.05 |
| POCRI | 0.01 | -0.04 | -0.01 | 0.03 | 0.00 | -0.03 | 0.02 | 0.15 | 0.06 | -0.02 | -0.07 | -0.05 | -0.01 | 0.03 | 0.09 | -0.01 | -0.10 | -0.08 | -0.26 | -0.02 | 0.11 | -0.13 | 0.01 | 0.01 |

**Appendix 3.6 (continued)**

| abbreviation | NB_lJnsen | NB_lJnsen t-1 | NB_tempcoldmonth | NB_tempcoldmonth t-1 | NB_frostdays | NB_frostdays t-1 | NB_rain | NB_rain t-1 | NB_snowdays | NB_snowdays t-1 | B_temp | B_temp t-1 | B_tempaprmay | B_tempaprmay t-1 | B_rain | B_rain t-1 | B_heavyraindays | B_heavyraindays t-1 | B_drydays | B_drydays t-1 | B_squall | B_squall t-1 | B_heatwave | B_heatwave t-1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PTRO | 0.06 | 0.01 | -0.08 | 0.00 | 0.05 | 0.01 | -0.07 | -0.05 | 0.03 | -0.01 | -0.04 | -0.01 | -0.01 | 0.00 | -0.03 | -0.03 | -0.15 | 0.00 | -0.01 | 0.10 | -0.05 | -0.04 | 0.02 | -0.01 |
| RAQU | -0.05 | 0.03 | 0.05 | -0.05 | -0.03 | 0.04 | 0.32 | -0.12 | -0.01 | -0.05 | 0.06 | -0.05 | 0.02 | 0.02 | 0.22 | 0.35 | 0.12 | -0.01 | -0.20 | -0.34 | -0.06 | -0.06 | 0.02 | -0.06 |
| RPEN | 0.17 | -0.05 | -0.30 | -0.08 | 0.12 | -0.05 | -0.56 | -0.26 | 0.09 | -0.05 | -0.31 | -0.32 | -0.14 | -0.03 | 0.10 | -1.00 | -0.48 | 0.06 | -0.07 | 0.29 | -0.26 | -0.26 | -0.06 | -0.13 |
| SATR | -0.01 | 0.02 | 0.04 | -0.02 | 0.00 | 0.00 | 0.03 | -0.04 | -0.01 | -0.02 | -0.01 | 0.01 | 0.03 | -0.02 | 0.12 | -0.05 | -0.06 | 0.03 | 0.06 | 0.11 | -0.07 | 0.03 | 0.00 | 0.01 |
| SBOR | 0.10 | 0.01 | -0.11 | 0.00 | 0.09 | 0.01 | -0.15 | -0.04 | 0.07 | 0.01 | -0.06 | -0.01 | -0.03 | 0.00 | 0.09 | -0.18 | -0.12 | -0.02 | -0.04 | 0.23 | 0.04 | 0.01 | 0.01 | 0.02 |
| SCOM | 0.08 | 0.04 | -0.16 | -0.03 | 0.06 | 0.03 | -0.27 | -0.06 | 0.01 | 0.09 | -0.06 | -0.04 | -0.01 | -0.03 | -0.03 | -0.21 | -0.23 | -0.08 | -0.06 | 0.08 | 0.05 | -0.10 | -0.02 | -0.02 |
| STUR | -0.03 | 0.02 | 0.03 | 0.05 | -0.01 | -0.01 | -0.23 | -0.11 | -0.09 | 0.05 | 0.07 | -0.05 | 0.00 | -0.04 | -0.03 | -0.24 | -0.01 | -0.37 | 0.06 | 0.20 | 0.15 | -0.14 | 0.03 | 0.00 |
| TMER | -0.01 | 0.03 | 0.03 | -0.06 | 0.01 | 0.01 | 0.07 | -0.02 | -0.06 | 0.02 | 0.03 | 0.03 | 0.04 | -0.01 | -0.13 | 0.26 | 0.10 | -0.03 | 0.06 | -0.13 | 0.04 | 0.00 | 0.02 | -0.02 |
| TRUF | -0.23 | -0.04 | 0.43 | 0.08 | -0.19 | -0.03 | 0.93 | 0.20 | -0.09 | -0.10 | 0.34 | 0.05 | 0.11 | 0.05 | 0.29 | 0.59 | 0.35 | 0.49 | 0.20 | -0.38 | 0.04 | 0.24 | 0.12 | -0.06 |
| TTRO | -0.18 | 0.08 | 0.21 | -0.16 | -0.14 | 0.04 | 0.62 | -0.21 | -0.13 | 0.00 | 0.20 | -0.01 | 0.09 | -0.03 | 0.29 | 0.34 | 0.30 | -0.09 | 0.07 | -0.64 | -0.14 | 0.10 | 0.03 | -0.05 |

b: forest species

| abbreviation | NB_lJnsen | NB_lJnsen t-1 | NB_tempcoldmonth | NB_tempcoldmonth t-1 | NB_frostdays | NB_frostdays t-1 | NB_rain | NB_rain t-1 | NB_snowdays | NB_snowdays t-1 | B_temp | B_temp t-1 | B_tempaprmay | B_tempaprmay t-1 | B_rain | B_rain t-1 | B_heavyraindays | B_heavyraindays t-1 | B_drydays | B_drydays t-1 | B_squall | B_squall t-1 | B_heatwave | B_heatwave t-1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ACAU | 0.01 | 0.00 | -0.01 | 0.03 | -0.01 | 0.00 | -0.05 | 0.07 | 0.00 | 0.05 | 0.03 | -0.03 | 0.00 | 0.00 | -0.04 | -0.05 | 0.01 | -0.10 | 0.07 | -0.11 | 0.10 | -0.04 | 0.01 | -0.02 |
| AGEN | 0.04 | -0.06 | -0.13 | 0.07 | 0.04 | -0.06 | -0.19 | 0.06 | 0.09 | 0.01 | -0.11 | -0.06 | -0.04 | -0.01 | -0.16 | -0.12 | -0.16 | 0.05 | -0.26 | 0.12 | -0.10 | -0.10 | 0.04 | -0.01 |

**Appendix 3.6 (continued)**

| abbreviation | NB_llnsen | NB_llnsen t-1 | NB_tempcoldmonth | NB_tempcoldmonth t-1 | NB_frostdays | NB_frostdays t-1 | NB_rain | NB_rain t-1 | NB_snowdays | NB_snowdays t-1 | B_temp | B_temp t-1 | B_tempaprmay | B_tempaprmay t-1 | B_rain | B_rain t-1 | B_heavyraindays | B_heavyraindays t-1 | B_drydays | B_drydays t-1 | B_squall | B_squall t-1 | B_heatwave | B_heatwave t-1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ANIS | -0.07 | -0.07 | 0.10 | 0.02 | -0.06 | -0.06 | -0.02 | 0.09 | -0.06 | -0.04 | 0.01 | -0.04 | 0.00 | -0.01 | -0.17 | -0.17 | -0.07 | -0.04 | 0.28 | -0.14 | -0.10 | -0.08 | -0.07 | -0.03 |
| AOTU | -0.10 | -0.08 | 0.15 | 0.09 | -0.09 | -0.07 | -0.09 | 0.37 | -0.01 | -0.01 | 0.02 | 0.10 | 0.02 | 0.01 | -0.58 | 0.58 | -0.02 | 0.29 | -0.06 | -0.02 | 0.02 | -0.07 | -0.10 | 0.03 |
| BBUT | 0.02 | -0.04 | -0.05 | 0.03 | 0.02 | -0.02 | -0.05 | 0.09 | 0.07 | 0.01 | -0.04 | -0.06 | -0.02 | -0.01 | -0.02 | -0.02 | -0.07 | 0.05 | -0.13 | -0.03 | -0.01 | -0.04 | 0.02 | -0.01 |
| CBRA | 0.01 | -0.03 | 0.01 | 0.04 | 0.01 | -0.02 | 0.00 | 0.00 | 0.00 | 0.01 | 0.04 | -0.01 | -0.01 | 0.01 | 0.00 | -0.05 | -0.11 | 0.00 | -0.01 | -0.05 | 0.07 | -0.01 | 0.01 | -0.02 |
| CCANN | -0.01 | 0.01 | 0.01 | 0.02 | 0.01 | 0.00 | 0.08 | -0.08 | -0.04 | -0.02 | 0.04 | 0.09 | 0.02 | 0.02 | 0.00 | -0.04 | -0.02 | -0.11 | 0.09 | 0.11 | 0.00 | 0.03 | -0.01 | 0.01 |
| CCANO | 0.02 | 0.01 | -0.02 | 0.00 | 0.04 | 0.00 | 0.07 | -0.11 | 0.03 | 0.02 | 0.05 | -0.02 | 0.00 | -0.01 | 0.21 | -0.02 | -0.07 | 0.06 | -0.10 | 0.07 | 0.04 | 0.14 | 0.02 | -0.02 |
| CCHL | -0.04 | 0.01 | 0.07 | -0.01 | -0.02 | 0.01 | 0.18 | 0.00 | -0.02 | -0.02 | 0.05 | 0.05 | 0.03 | 0.01 | 0.02 | 0.12 | 0.12 | -0.14 | 0.18 | -0.07 | -0.07 | 0.03 | -0.04 | 0.01 |
| CCOR | 0.04 | -0.02 | -0.07 | 0.05 | 0.01 | -0.02 | -0.04 | -0.02 | 0.05 | 0.00 | -0.03 | -0.05 | -0.04 | 0.01 | 0.06 | -0.26 | -0.14 | 0.11 | -0.09 | 0.13 | -0.01 | 0.00 | 0.04 | -0.01 |
| CMON | 0.00 | 0.01 | -0.02 | -0.03 | 0.02 | 0.01 | 0.13 | -0.10 | 0.04 | -0.05 | -0.02 | -0.02 | -0.02 | 0.01 | 0.19 | -0.01 | 0.06 | 0.03 | -0.10 | 0.04 | -0.10 | 0.07 | 0.00 | 0.00 |
| COEN | 0.02 | 0.02 | -0.02 | 0.00 | 0.01 | 0.03 | -0.10 | -0.03 | -0.03 | -0.01 | -0.01 | 0.01 | -0.01 | -0.01 | -0.06 | -0.12 | 0.10 | -0.08 | 0.22 | 0.07 | -0.05 | -0.03 | 0.02 | 0.02 |
| CPAL | 0.01 | 0.01 | 0.00 | 0.04 | 0.00 | -0.01 | -0.04 | 0.05 | 0.03 | -0.01 | -0.01 | 0.01 | -0.02 | 0.01 | -0.03 | 0.00 | 0.00 | 0.04 | -0.02 | 0.09 | 0.02 | -0.01 | 0.01 | 0.02 |
| DMAJ | 0.02 | 0.02 | -0.02 | -0.02 | 0.02 | 0.01 | 0.06 | -0.04 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.04 | 0.02 | -0.03 | 0.04 | -0.01 | -0.04 | 0.00 | 0.06 | 0.02 | 0.00 |
| DMIN | 0.00 | -0.03 | 0.03 | 0.04 | 0.03 | -0.04 | -0.08 | 0.02 | -0.01 | -0.05 | -0.02 | 0.06 | 0.01 | 0.00 | 0.08 | -0.07 | -0.01 | 0.05 | 0.04 | 0.28 | 0.02 | 0.14 | 0.00 | 0.02 |
| ECIT | 0.03 | 0.05 | -0.07 | -0.10 | 0.05 | 0.02 | -0.08 | -0.22 | -0.06 | 0.08 | 0.01 | -0.06 | 0.02 | -0.06 | 0.09 | -0.10 | -0.03 | -0.15 | -0.08 | -0.08 | 0.05 | -0.08 | 0.03 | -0.07 |
| ERUB | -0.09 | 0.00 | 0.10 | -0.02 | -0.07 | -0.01 | 0.23 | 0.02 | -0.01 | -0.01 | 0.05 | 0.02 | 0.03 | 0.00 | -0.03 | 0.30 | 0.14 | 0.06 | -0.13 | -0.18 | -0.01 | 0.05 | -0.09 | 0.00 |
| FCOE | 0.01 | -0.03 | -0.01 | 0.03 | 0.01 | -0.02 | -0.05 | 0.06 | 0.02 | 0.00 | 0.00 | 0.02 | -0.02 | 0.01 | -0.07 | -0.03 | 0.03 | 0.01 | 0.00 | -0.02 | 0.05 | -0.01 | 0.01 | 0.02 |
| FHYP | 0.03 | 0.01 | 0.02 | 0.05 | 0.01 | 0.03 | -0.02 | -0.07 | -0.03 | -0.02 | 0.11 | 0.01 | -0.03 | 0.01 | 0.12 | -0.26 | 0.12 | 0.07 | 0.35 | 0.12 | 0.02 | 0.14 | 0.03 | 0.02 |
| FSUB | 0.14 | 0.04 | -0.18 | -0.20 | 0.15 | 0.06 | -0.20 | -0.31 | 0.06 | 0.03 | -0.18 | -0.23 | -0.04 | -0.06 | 0.25 | -0.23 | 0.26 | -0.41 | -0.24 | -0.17 | 0.07 | -0.17 | 0.14 | -0.04 |
| FTIN | -0.09 | -0.17 | 0.12 | 0.17 | -0.06 | -0.14 | -0.25 | 0.45 | -0.02 | -0.08 | -0.09 | 0.08 | -0.01 | 0.06 | -0.37 | 0.13 | -0.25 | -0.17 | -0.19 | 0.03 | 0.20 | -0.21 | -0.09 | 0.03 |

| abbreviation | NB_lJnsen | NB_lJnsen t-1 | NB_tempcoldmonth | NB_tempcoldmonth t-1 | NB_frostdays | NB_frostdays t-1 | NB_rain | NB_rain t-1 | NB_snowdays | NB_snowdays t-1 | B_temp | B_temp t-1 | B_tempprmay | B_tempprmay t-1 | B_rain | B_rain t-1 | B_heavyraindays | B_heavyraindays t-1 | B_drydays | B_drydays t-1 | B_squall | B_squall t-1 | B_heatwave | B_heatwave t-1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| GGLA | 0.06 | -0.03 | -0.06 | 0.05 | 0.04 | -0.01 | -0.13 | 0.00 | 0.04 | -0.01 | -0.02 | 0.01 | -0.04 | 0.02 | -0.12 | -0.08 | -0.17 | 0.10 | 0.02 | 0.02 | 0.00 | 0.00 | 0.06 | 0.00 |
| HICT | -0.07 | 0.04 | 0.10 | -0.01 | -0.07 | 0.04 | 0.06 | 0.08 | -0.04 | -0.03 | 0.02 | 0.15 | 0.04 | 0.00 | 0.31 | -0.08 | 0.26 | -0.27 | 0.14 | 0.22 | 0.01 | -0.08 | -0.07 | 0.11 |
| LMEG | -0.01 | 0.07 | -0.05 | -0.09 | 0.00 | 0.06 | 0.16 | -0.10 | 0.02 | -0.03 | -0.05 | 0.00 | 0.00 | 0.03 | 0.12 | 0.18 | -0.09 | -0.16 | -0.20 | -0.15 | -0.06 | 0.04 | -0.01 | 0.01 |
| MSTR | -0.02 | 0.05 | 0.04 | -0.01 | -0.03 | 0.05 | 0.14 | -0.13 | -0.02 | -0.01 | 0.08 | -0.02 | 0.00 | 0.01 | 0.14 | 0.00 | 0.08 | -0.06 | 0.10 | -0.04 | 0.00 | 0.08 | -0.02 | 0.00 |
| OORI | 0.05 | 0.05 | -0.08 | -0.09 | 0.05 | 0.05 | 0.01 | -0.17 | -0.01 | 0.02 | -0.04 | 0.06 | 0.01 | -0.01 | 0.35 | -0.18 | -0.10 | 0.02 | -0.04 | -0.05 | 0.03 | 0.10 | 0.05 | 0.00 |
| PACRI | 0.09 | -0.02 | -0.11 | 0.04 | 0.06 | -0.02 | -0.23 | 0.02 | 0.07 | 0.02 | -0.08 | -0.06 | -0.03 | -0.01 | -0.06 | -0.13 | -0.10 | 0.17 | -0.15 | 0.25 | 0.01 | -0.08 | 0.09 | -0.02 |
| PATE | 0.01 | -0.05 | 0.00 | 0.11 | 0.00 | -0.06 | -0.14 | 0.04 | 0.00 | 0.00 | 0.00 | 0.05 | 0.00 | 0.00 | -0.14 | -0.16 | -0.15 | 0.24 | 0.02 | 0.21 | 0.01 | 0.03 | 0.01 | 0.00 |
| PCAE | 0.05 | -0.03 | -0.03 | 0.03 | 0.04 | -0.01 | -0.15 | 0.08 | 0.04 | -0.02 | -0.07 | 0.04 | -0.02 | 0.02 | -0.09 | 0.02 | -0.03 | 0.01 | -0.02 | 0.11 | 0.04 | -0.06 | 0.05 | 0.03 |
| PCOLC | 0.05 | -0.01 | -0.08 | 0.02 | 0.05 | -0.01 | -0.14 | -0.03 | 0.05 | 0.00 | -0.06 | 0.01 | -0.03 | 0.01 | -0.04 | -0.01 | -0.13 | -0.05 | -0.19 | 0.13 | 0.04 | -0.08 | 0.05 | 0.01 |
| PCOLL | 0.00 | 0.09 | 0.00 | -0.10 | 0.00 | 0.05 | 0.03 | -0.21 | -0.09 | 0.07 | 0.07 | -0.07 | 0.00 | -0.05 | 0.06 | -0.23 | 0.17 | -0.23 | 0.40 | -0.05 | -0.08 | 0.12 | 0.00 | -0.05 |
| PMAJ | 0.05 | -0.03 | -0.04 | 0.02 | 0.06 | -0.01 | -0.17 | 0.03 | 0.02 | 0.00 | -0.04 | 0.06 | -0.01 | 0.01 | -0.15 | 0.03 | -0.01 | -0.02 | 0.02 | 0.08 | 0.06 | -0.01 | 0.05 | 0.03 |
| PMOD | -0.02 | 0.00 | 0.03 | 0.01 | -0.02 | 0.01 | 0.06 | 0.01 | 0.00 | 0.00 | 0.05 | 0.01 | -0.01 | 0.01 | -0.03 | 0.09 | 0.07 | -0.07 | 0.04 | -0.17 | 0.02 | 0.05 | -0.02 | 0.01 |
| PMON | 0.06 | -0.02 | -0.08 | 0.04 | 0.06 | -0.01 | -0.19 | -0.05 | 0.04 | -0.01 | -0.06 | -0.03 | -0.01 | 0.01 | -0.11 | -0.07 | -0.22 | -0.02 | -0.10 | 0.13 | 0.02 | -0.08 | 0.06 | -0.01 |
| PPAL | 0.04 | -0.06 | -0.02 | 0.08 | 0.04 | -0.04 | -0.16 | 0.05 | 0.03 | -0.03 | -0.04 | 0.06 | -0.01 | 0.00 | -0.12 | -0.11 | -0.08 | 0.00 | 0.08 | 0.13 | -0.01 | 0.00 | 0.04 | 0.03 |
| PHO | 0.03 | 0.01 | -0.06 | -0.02 | 0.03 | 0.02 | -0.10 | -0.06 | -0.02 | -0.01 | -0.05 | 0.03 | 0.00 | 0.01 | 0.00 | -0.04 | -0.10 | -0.04 | -0.07 | -0.01 | 0.03 | -0.02 | 0.03 | 0.00 |
| PPIC | 0.01 | 0.01 | -0.03 | -0.01 | -0.02 | 0.01 | -0.06 | 0.02 | 0.01 | -0.01 | -0.07 | -0.02 | -0.01 | 0.00 | -0.07 | -0.09 | -0.10 | 0.07 | -0.07 | 0.12 | -0.09 | -0.18 | 0.01 | 0.03 |
| PPYR | 0.03 | -0.05 | -0.03 | 0.10 | 0.02 | -0.05 | -0.17 | 0.13 | 0.04 | -0.03 | -0.05 | -0.02 | -0.02 | 0.02 | 0.00 | -0.13 | -0.23 | 0.08 | -0.09 | 0.31 | 0.01 | -0.05 | 0.03 | -0.01 |
| PSIB | 0.00 | 0.08 | -0.09 | -0.14 | -0.01 | 0.00 | 0.11 | 0.06 | 0.06 | 0.12 | -0.10 | -0.08 | 0.07 | -0.07 | -0.02 | 0.30 | -0.21 | 0.28 | -0.26 | -0.09 | -0.26 | 0.08 | 0.00 | -0.08 |
| PTRO | 0.04 | 0.03 | -0.05 | -0.01 | 0.02 | 0.03 | -0.02 | -0.03 | 0.01 | 0.00 | -0.01 | -0.02 | -0.02 | 0.01 | -0.02 | -0.02 | -0.04 | 0.06 | 0.04 | 0.11 | -0.03 | -0.05 | 0.04 | 0.00 |

**Appendix 3.6 (continued)**

| abbreviation | NB_ljnsen | NB_ljnsen t-1 | NB_tempcoldmonth | NB_tempcoldmonth t-1 | NB_frostdays | NB_frostdays t-1 | NB_rain | NB_rain t-1 | NB_snowdays | NB_snowdays t-1 | B_temp | B_temp t-1 | B_tempaprmay | B_tempaprmay t-1 | B_rain | B_rain t-1 | B_heavyraindays | B_heavyraindays t-1 | B_drydays | B_drydays t-1 | B_squall | B_squall t-1 | B_heatwave | B_heatwave t-1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PVIR | -0.04 | -0.03 | 0.02 | 0.04 | -0.03 | -0.03 | 0.09 | 0.01 | 0.02 | 0.00 | 0.03 | 0.00 | -0.01 | 0.02 | 0.03 | -0.04 | -0.11 | -0.04 | -0.13 | -0.11 | 0.04 | -0.02 | -0.04 | 0.01 |
| RIGN | -0.18 | 0.10 | 0.28 | -0.10 | -0.15 | 0.05 | 0.49 | 0.04 | -0.23 | 0.04 | 0.23 | 0.07 | 0.12 | -0.05 | -0.06 | 0.27 | 0.52 | 0.02 | 0.59 | -0.19 | 0.02 | 0.15 | -0.18 | -0.01 |
| RREG | -0.13 | 0.01 | 0.23 | 0.03 | -0.16 | -0.01 | 0.30 | 0.37 | -0.12 | -0.01 | 0.15 | 0.04 | 0.09 | -0.01 | -0.02 | 0.26 | 0.31 | 0.52 | 0.36 | -0.13 | -0.06 | 0.04 | -0.13 | -0.03 |
| SATR | -0.02 | 0.05 | 0.02 | -0.05 | -0.02 | 0.03 | 0.12 | -0.11 | -0.02 | 0.03 | 0.06 | -0.06 | 0.00 | -0.01 | 0.15 | -0.01 | 0.08 | -0.10 | 0.00 | -0.06 | 0.04 | 0.00 | -0.02 | -0.02 |
| SBOR | 0.06 | 0.02 | -0.05 | -0.03 | 0.05 | 0.03 | -0.08 | -0.05 | 0.03 | 0.01 | -0.01 | -0.01 | -0.03 | 0.00 | 0.03 | -0.06 | 0.01 | -0.08 | 0.07 | 0.13 | 0.03 | -0.01 | 0.06 | 0.01 |
| SCOM | 0.07 | 0.06 | -0.13 | -0.04 | 0.03 | 0.05 | -0.22 | -0.01 | 0.01 | 0.08 | -0.09 | 0.02 | 0.00 | -0.01 | -0.20 | 0.02 | -0.06 | 0.03 | -0.02 | 0.06 | 0.04 | -0.12 | 0.07 | 0.02 |
| SEUR | 0.06 | -0.07 | -0.06 | 0.05 | 0.07 | -0.04 | -0.05 | -0.01 | 0.06 | -0.02 | -0.04 | 0.05 | -0.02 | 0.03 | -0.13 | 0.05 | -0.19 | 0.01 | -0.12 | -0.15 | 0.04 | 0.04 | 0.06 | 0.01 |
| STUR | 0.00 | 0.06 | -0.02 | -0.07 | 0.00 | 0.05 | 0.03 | -0.19 | 0.02 | 0.01 | 0.05 | -0.08 | -0.02 | -0.03 | 0.20 | 0.00 | 0.03 | 0.04 | -0.04 | -0.06 | -0.10 | 0.14 | 0.00 | 0.00 |
| SVUL | 0.03 | 0.03 | -0.06 | -0.01 | 0.03 | 0.03 | -0.03 | -0.06 | 0.05 | 0.00 | -0.02 | -0.01 | -0.02 | 0.00 | 0.04 | 0.10 | -0.05 | 0.02 | -0.17 | 0.08 | 0.01 | 0.01 | 0.03 | 0.03 |
| TMER | -0.03 | 0.00 | 0.03 | -0.01 | -0.02 | 0.00 | 0.07 | 0.03 | 0.00 | -0.01 | 0.01 | -0.01 | 0.00 | 0.01 | 0.00 | 0.10 | 0.09 | -0.02 | -0.06 | -0.10 | 0.01 | 0.02 | -0.03 | 0.00 |
| TPHI | -0.09 | -0.02 | 0.15 | 0.02 | -0.07 | -0.01 | 0.20 | 0.11 | -0.05 | -0.05 | 0.06 | 0.05 | 0.03 | 0.02 | 0.09 | 0.21 | 0.20 | 0.02 | -0.03 | -0.11 | 0.08 | 0.03 | -0.09 | 0.01 |
| TTRO | -0.18 | 0.05 | 0.20 | -0.10 | -0.14 | 0.03 | 0.55 | -0.11 | -0.09 | -0.03 | 0.15 | -0.02 | 0.06 | 0.00 | 0.23 | 0.32 | 0.40 | -0.13 | -0.05 | -0.51 | -0.07 | 0.05 | -0.18 | -0.03 |
| TVIS | -0.02 | 0.01 | 0.03 | -0.04 | -0.01 | 0.01 | 0.14 | -0.14 | -0.02 | 0.01 | 0.06 | -0.03 | 0.00 | -0.01 | 0.07 | -0.09 | 0.08 | -0.09 | 0.15 | -0.20 | -0.03 | 0.04 | -0.02 | -0.02 |

# 4

# Population dynamics of Great bittern (*Botaurus stellaris*) in the Netherlands: interaction effects of weather variability and habitat fragmentation

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## ABSTRACT

In Western Europe, Great bitterns *Botaurus stellaris* are found to be susceptible to continuous loss of suitable habitat due to succession and fragmentation. Moreover, year-to-year fluctuations in local bittern populations can be caused by severe winter weather. The enlarged variability in weather as a result of climate change is expected to have population dynamical consequences, because it will likely lead to increased variation in vital demographic rates (survival, reproduction) in these populations. With regard to habitat loss and the expected increase in weather variability, it is relevant to understand the relation between the effect of weather variability on bittern population dynamics and possible remediating effects of the landscape structure. We obtained bittern population numbers from 28 sites scattered over the Netherlands. Bittern habitat surrounding these sites differ in area, quality, and spatial cohesion. Our results show that severe winter weather has a significant negative impact on bittern population growth rates. Furthermore, we found that an increased carrying capacity and spatial cohesion contributes to an increase in mean growth rates over the years. Thus, recovery from negative effects of severe winters on bittern population numbers is faster in large, well-connected habitats. Although the frequency of severe winters is predicted to diminish under climate change, it is expected that weather variability especially during the breeding season will increase (more droughts and floodings), which might result in increased population fluctuations. To compensate for the effects of increased weather variability, growth and recovery rates of populations need to be enhanced. Therefore, from a conservational point of view one should invest in more large, well-connected patches, in order to support larger populations.

## 4.1 INTRODUCTION

In Western Europe, Great bitterns *Botaurus stellaris* show a scattered distribution reflecting the presence of its habitat, lowland marshlands. It has long been known that large year-to-year fluctuations in local populations occur, caused by severe winters (Rivière 1930). An increase in weather variability as a result of climate change (IPCC 2001; IPCC 2007) – e.g. flooding and extreme drought during the breeding season - might cause additional population fluctuations, thus increasing extinction probabilities (Akçakaya & Baur 1996; Easterling et al. 2000; Easterling et al. 2000). In this respect, we investigated the potential remediating effect of landscape structure on population recovery.

Bitterns mainly breed in wetlands with reedbeds that are permanently or periodically inundated (Gilbert et al. 2005). Nests are usually built in reed (*Phragmites australis)* or bulrush (*Typha* sp.) vegetation that has not been mown for several years (Cramp & Simmons 1977-1994). Bitterns are found to be susceptible to vegetation succession of their habitat. Tyler et al. (1998) showed for the UK that bittern numbers declined in sites with increased shrub encroachment and presence of wetland herb species. Loss of early hydroseral succession stages consisting of reed vegetations lead to a decrease in area of suitable breeding and foraging habitat. Loss of suitable habitat leads to an increase of the degree of fragmentation, which makes habitat fragmentation a significant factor in the decline in bittern numbers and distribution (Foppen 2001).

The study of Tyler et al. (1998) solely considered whether trends decreased or increased over a 16-year period. However, population numbers also fluctuate between years. These year-to-year fluctuations in local bittern populations can be caused by severe winter weather that temporarily affects population levels or even distributions (Cramp & Simmons 1977-1994; Bibby 1981; Van Turnhout et al. 2010). Year-to-year fluctuations in local bittern populations reflect reproduction and survival rates. Adult survival is mostly correlated to extreme weather during the non-breeding season (e.g. Sæther et al. 2000). In combination with density dependence, these weather conditions determine the number of individuals surviving during the non-breeding season (tub-hypothesis, Lack 1954; Sæther et al. 2004).

In order to survive severe winters, part of the bittern populations may migrate to more temperate climates such as in the UK or even further south (http://www.vogelbescherming.nl/nl/vogels_beschermen/zenderonderzoeken/roerdomp). In the UK, bittern numbers during winter correlate positively with the annual number of frost days (Bibby 1981), which indicates an influx of bitterns from continental Europe. Moreover, winter distributions with relatively large numbers in south and east England suggest the influx of bitterns from the continent (Bibby 1981, settlement at 'front door'). In central and northern Europe however, bitterns starve rather than emigrate during severe winters, and populations fluctuate considerably and may drop dramatically after a harsh winter. A Swedish study showed a 35-40% decline of bittern numbers after the severe 1978/79 winter (Sveriges Ornitologiska Förening 1990). In contrast, from 1988 to 1990, after a period of mild winters, the number of booming males increased from 70 to 194 in Finland (Hagemeijer & Blair 1997). Most bitterns that breed in the Netherlands are considered to be residential. In severe winters, a part of the population probably migrates to southwest France or the UK (Bibby 1981), and occasionally further (SOVON 2002).

As a result of climate change, the amplitude and frequency of extreme weather events is expected to increase, making the weather more variable (IPCC 2001; IPCC 2007). Increases in variance together with a rising mean temperature will lead to increases in heat wave frequency in summer and fewer frost and cold days in winter. The enlarged variability in weather is expected to have population dynamical consequences, because it will likely lead to increased variation in vital demographic rates (survival, reproduction) in these populations (Verboom et al. 2010). Catastrophic events such as floodings may induce drastic decreases in breeding success. Van de Pol et al. (2010) reported the occurrence of frequent and more catastrophic flooding of nests in Europe's largest estuary, especially around the time when most eggs have just hatched. This increased flooding risks for six saltmarsh nesting bird species, which is expected to worsen in the near future if they do not adapt. Moreover, increasing flooding risks have reduced the reproductive output below stable population levels in at least one species, the Eurasian oystercatcher (*Haematopus ostralegus*). Flooding of wetlands, e.g. along rivers is as well increasing due to changed precipitation patterns (IPCC 2001; Booij 2005), which is similarly detrimental when it happens during the breeding season. In a study of Jovani & Tella (2004) on reproduction success of White storks (*Ciconia*

*ciconia*) in Southwest Spain, nestling mortality and total breeding failure were especially high when rainy periods coincided with the early live of nestlings (between 1 April and 15 May). In the context of climate change, the authors suggest that such rainy springs could have a negative effect on the reproduction of White storks.

Stable populations may conversely be more resilient to environmental change (Oliver et al. 2010). Population dynamics and stability can also be affected by landscape structure. It has been found that in order to perform well and survive under conditions of climate change, populations require larger and more heterogeneous patches. Such patches can support larger populations, to compensate for the effects of increased weather variability (Oliver et al. 2010; Verboom et al. 2010). In case of the Great bitterns in Western Europe, continuous loss of optimal reedbed habitat is occurring due to succession and land use change. This leads to an increased degree of fragmentation of marshland habitats (Foppen 2001). Although the frequency of severe winters is predicted to diminish under climate change (Van den Hurk et al. 2007), it is expected that weather variability especially during the breeding season will increase, which might result in increased population fluctuations. With regard to this habitat loss and the expected increase in weather variability, it is relevant to understand the relation between the effect of weather variability on bittern population dynamics and possible remediating effects of the landscape structure.

We explored the effect of landscape structure characteristics on population resilience. Moreover, we studied the changes in Dutch breeding bittern abundance in relation to winter severity for the period 1984 to 2005 using four variables describing winter weather. We hypothesize that recovery from negative effects of severe winters on bittern population numbers is faster in large, well-connected habitats.

## 4.2   METHODS

### 4.2.1 Deriving bittern monitoring data

Since 1984, monitoring of breeding birds in the Netherlands, organized by SOVON Dutch Centre for Field Ornithology and supported by Statistics Netherlands, has been based on the method of territory mapping in fixed monitoring plots (Bibby et al. 1997; Van Turnhout et al. 2010). Each year, monitoring plots (with an area of

10-500 hectares each) are visited 5-10 times between March and July. The size of the monitoring plots, as well as the number, timing and duration of visits, depend on habitat type and species selection. All birds with behaviour indicative of a territory (e.g. song, pair bond, display, alarm, nests) are recorded on field maps. Species-specific interpretation criteria are used to determine the number of territories at the end of the season. Fieldwork and interpretation methods are highly standardized and are described in detail in manuals (Van Dijk 2004; Van Dijk et al. 2004). Yearly numbers of bittern territories per monitoring plot were obtained for the period 1984-2005. We included only those 28 monitoring plots with at least ten years of data and a total count of more than 20 territories. On average, monitoring plots were counted for a period of 17.6 years, and there are 68 (12%) missing counts.

For each monitoring plot, we determined plot characteristics carrying capacity and spatial cohesion (see below and Table 4.1 for explanation of calculation methods). These were assumed to be constant over time. To determine plot carrying capacity, we used counts from 2003. Bittern numbers were high that year and probably reflected carrying capacity well in monitoring plots. Moreover, in 2003 a special bittern monitoring programme was executed in the Netherlands; all potential habitat sites were monitored over the breeding season. Counts obtained from monitoring plots in 2003 were used as plot carrying capacity. All potential habitat sites (reed marshes) were used to determine plot spatial cohesion. First, counts from the 2003 special monitoring programme were spatially assigned to the accompanying habitat sites with a resolution of 250x250 meter (within a radius of 333 m, Pouwels et al. 2007). Next, densities (in breeding pairs per ha.) were calculated for these sites. The densities comprised the input to the LARCH SCAN module (see e.g. Verboom et al. 2010) to calculate spatial cohesion in ArcView 3.3 (ESRI 2000). The calculation of spatial cohesion involved the densities in the vicinity of a location (250x250 m grid cell), ecologically scaled in relation to the mobility of bitterns (Vos et al. 2001), in this way incorporating the degree of habitat fragmentation. This resulted in a spatial cohesion surface map. See Foppen (2001) for a full description of the spatial cohesion calculation method. The spatial cohesion surface map was overlaid with the monitoring plot map in order to yield plot spatial cohesion. Appendix 4.1 lists the calculated carrying capacities and spatial cohesion values for the 28 monitoring plots. Fig. 4.1 shows the locations of the 28 monitoring plots and the spatial cohesion for bitterns.

**Table 4.1**

Plot characteristics used

| plot characteristic | explanation (both characteristics do not have units) |
|---|---|
| plot carrying capacity | Bittern counts obtained from monitoring plots in 2003, expressed as number of breeding pairs |
| plot spatial cohesion | All potential habitat sites (reed marshes) were used to determine plot spatial cohesion. First, counts from the 2003 special monitoring programme were spatially assigned to the accompanying habitat sites. Next, densities (in breeding pairs per ha.) were calculated for these sites. The densities comprised the input to the LARCH SCAN module to calculate spatial cohesion: densities in the vicinity of a location (250x250 m grid cell) where ecologically scaled in relation to the mobility of a species. This resulted in a spatial cohesion surface map. The spatial cohesion surface map was overlaid with the monitoring plot map in order to yield plot spatial cohesion. |

graphical representation (schematic)



LEGEND

monitoring plot

potential habitat site (reed marsh)

contour line spatial cohesion surface map

location 2003 bittern monitoring programme count
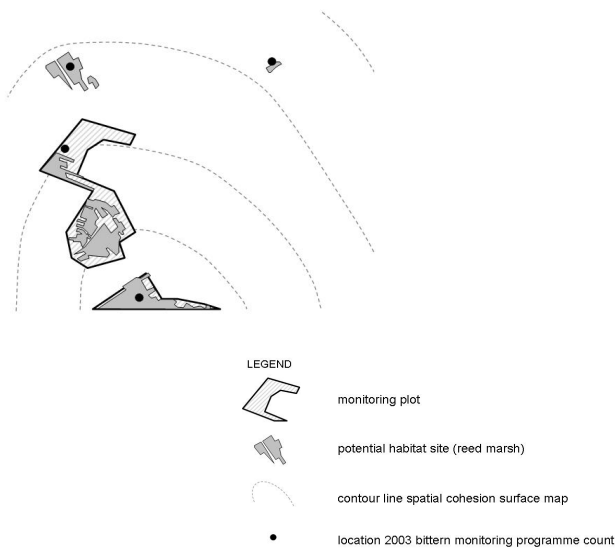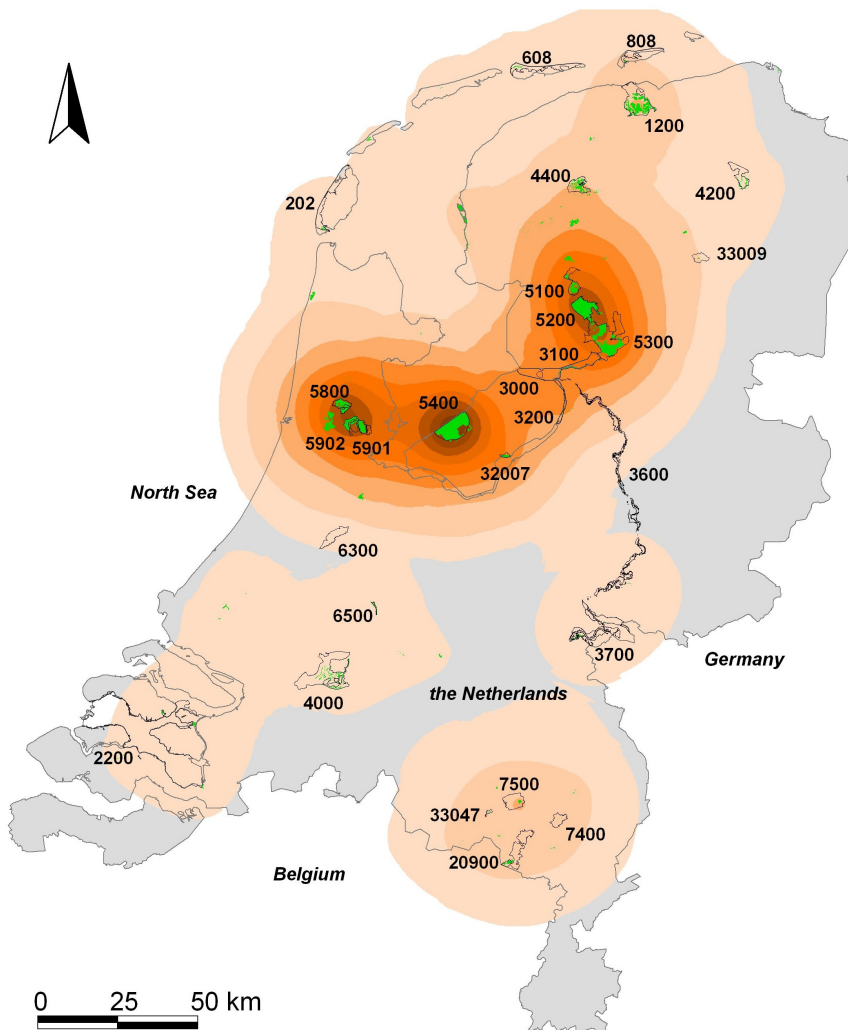
**Figure 4.1**

Locations of 28 monitoring plots (outlined in black) with plot numbers, potential habitat sites (in green), and spatial cohesion for bitterns (reddish contours; the darker the colour, the higher the spatial cohesion)

Carrying capacity and spatial cohesion were heavily skewed and were therefore log-transformed. To avoid taking logs of zero, one was added to the carrying capacity and the spatial cohesion. Plot carrying capacity and spatial cohesion were highly correlated (0.68 after log-transformation), since plots with high carrying capacities are typically clustered.

### 4.2.2 Deriving weather variables

The Royal Netherlands Meteorological Institute (KNMI) acquires weather data according to the standards of the World Meteorological Organization. The KNMI administers 35 weather stations across the Netherlands, of which the station at De Bilt is located in the centre of the country. Weather data acquired from this station are considered to be representative for the mean climate conditions in the Netherlands (Van Oldenborgh & Van Ulden 2003). We obtained data on mean daily temperatures and snowfall from KNMI for the period 1985-2005, accompanied by the longitude and latitude of the stations. From these we calculated four weather variables that describe the weather in the non-breeding seasons (Table 4.2): the IJnsen value (IJnsen 1981), expressing winter severity (further called IJNSEN); mean temperature of the coldest month (TCM); longest duration of consecutive days with frost (FROSTDAYS); and longest duration of consecutive days with snow cover (SNOWDAYS). For IJNSEN and TCM, values were derived from the De Bilt meteorological station. These variables do not vary as much spatially. However, FROSTDAYS and SNOWDAYS were spatially explicit. Each years' maximum number of operational meteorological stations were used to obtain these spatially explicit values for FROSTDAYS and SNOWDAYS for each individual site. The values were obtained by spatial interpolation in ArcView ('linear with sill' or inverse distance weighted kriging), and averaged per monitoring plot. This was done separately for each study year. See Appendix 4.2a for an overview of the yearly weather variables per monitoring plot. IJNSEN, TCM, and FROSTDAYS are highly correlated to each other, but not to SNOWDAYS (Appendix 4.2b), which is achieved by precipitation as well as temperature. Fig. 4.2 shows the values of weather variables for the station of De Bilt over the period 1985-2005. The winters of 1985 (October 1984-March 1985), 1986, 1987, 1991, 1996, and 1997 were relatively severe in the Netherlands.

**Table 4.2**

Weather variables used

| abbreviation | explanation (units) |
|---|---|
| IJNSEN | IJNSEN value (IJnsen 1981) ranging from 0 to 60 (-), expressing winter severity; the higher the value, the more severe the winter. Calculation: ( $v^2$/363) + (2 $y$/3) + (10 $z$/9), where $v$, $y$ and $z$ stand for the number of 24 h periods with a minimum temperature below 0°C, with a maximum temperature below 0°C and with a maximum temperature below - 10°C, respectively, during the period November-March. Data were derived from De Bilt meteorological station. |
| TCM | Mean temperature of the coldest month (°C). For each year, the mean temperature of each month from October to March was calculated and the coldest monthly average was taken. Data were derived from De Bilt meteorological station. |
| FROSTDAYS | Longest duration of consecutive days (-) with daily mean temperature below 0°C. Obtained from each years' maximum number of operational meteorological stations. |
| SNOWDAYS | Longest duration of consecutive days (-) with snow cover more than or equal to 2 cm. Obtained from each years' maximum number of operational meteorological stations. |

*4.2.3 Statistical analyses*

Bird count data observed at various sites in different years are typically analysed by means of a log-linear model using fixed site and year effects (Ter Braak et al. 1994; Thomas 1996; Fewster et al. 2000). Such an analysis takes proper account of missing counts and results in an estimate of the population trend which is generally displayed using annual indices. In this study there are site related covariates such as spatial cohesion, and weather variables which are mostly related to year. Note that although two of the weather variables (FROSTDAYS and SNOWDAYS) are interpolated to sites, making them site specific, the main variation in the
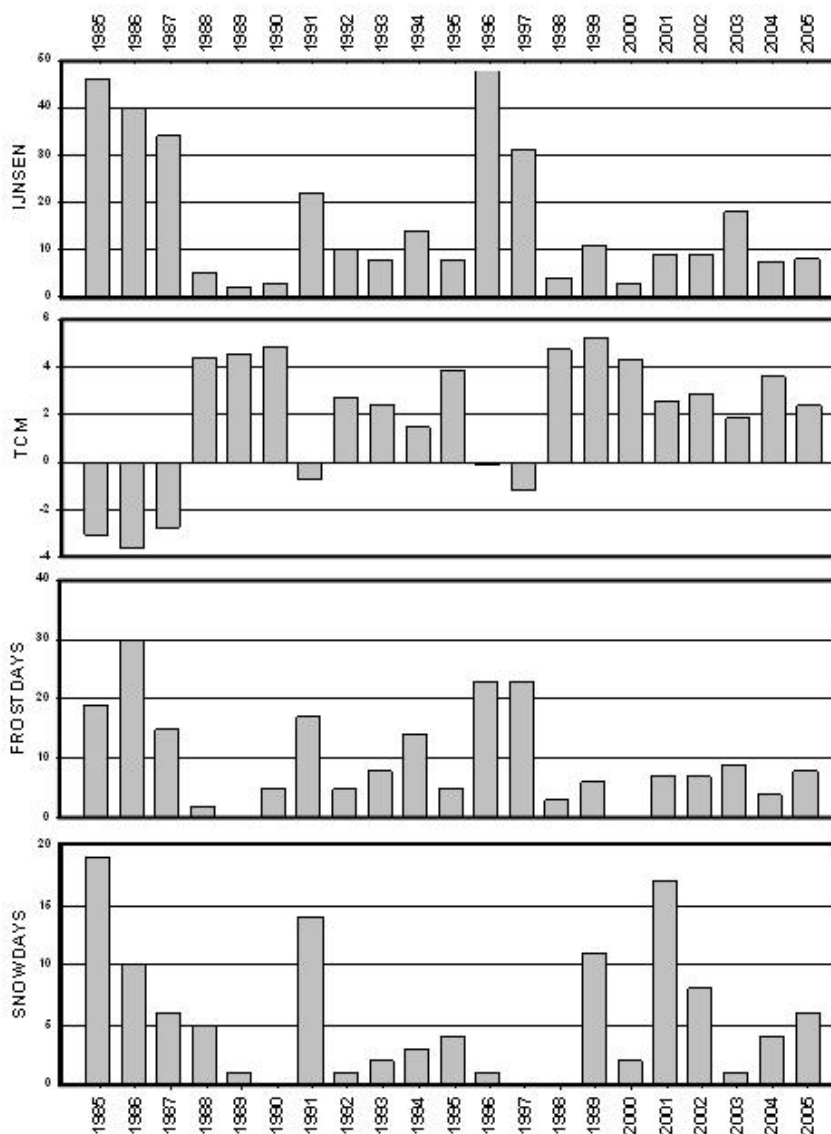
**Figure 4.2**

Values of weather variables in 1985-2005 in De Bilt. For yearly weather variables per monitoring plot see Appendix 4.2

weather variables is between years. A random effects model with random site and random year effects is then more appropriate since the between site variation should be used to test for site related covariates and the between year variation should largely be used for testing the weather variables.

For estimating the effect of weather variables we employed the modelling approach of Freeman & Newson (2008) which is subsequently used by Chamberlain et al. (2009). This approach employs annual growth rates. Suppose that a count $Y_{i,t}$ at site $i$ in year $t$ follows a Poisson distribution with mean $\mu_{i,t}$. Annual changes in the mean parameter can be modelled by

$$\mu_{i,t} = \alpha_{i,t} \, \mu_{i,t-1}$$

This relates means in successive years where $\alpha_{i,t}$ is the annual growth rate from year $t\text{-}1$ to year $t$. Using this relation recursively and taking logarithms, we get

$$\log(\mu_{i,t}) = \log(\mu_{i,0}) + \sum_{k=1}^{t} \log(\alpha_{i,k})$$

The first term in this model, i.e. $\log(\mu_{i,0})$, can be viewed as the site specific starting point, or baseline, of the time series of means. This term is modeled by site related covariates, such as spatial cohesion, and a random site effect, e.g.

$$\log(\mu_{i,0}) = \gamma_0 + \gamma_1 SpatialCohesion_i + Site_i$$

in which $\gamma_0$ and $\gamma_1$ are parameters and $Site_i$ is a random site effect. The second term consists of the sum of the logarithm of annual growth rates. Suppose that the annual growth rate at a site is related to the site specific temperature, i.e.

$$\log(\alpha_{i,k}) = \beta_0 + \beta_1 Temperature_{i,k}$$

in which $\beta_0$ is a baseline growth parameter and $\beta_1$ is a parameter for the temperature effect. Putting these equations together and adding a random year effect $Year_t$ we arrive at the following model

$$\log(\mu_{i,t}) = \gamma_0 + \gamma_1 SpatialCohesion_i + Site_i + \beta_0 t + \beta_1 \sum_{k=1}^{t} Temperature_{i,k} + Year_t$$

So instead of the individual temperatures, the cumulative temperatures are used as covariates in this model. Under this model the temperature, or other weather variables, of each site and year combination must be known, even if the corresponding count is missing. In our case, weather variables are known for each site and year combination, since these are derived from weather stations with com-

plete time series. Also note that a linear time trend $\beta_0 t$ is included in this model, with the possibility to test for interactions between $\beta_0 t$ and spatial plot characteristics. The benefit of this model is that all parameters are linear. The model is a so-called generalized linear mixed model; generalized because the distribution is Poisson and the logarithmic link is used to relate the mean to the covariates, and mixed because random effects enter the model. The model is readily fitted to data using the penalized quasi likelihood approach of Breslow & Clayton (1993). An overdispersion parameter was added to the model to account for extra-Poisson variation.

Missing and zero counts do not pose a problem to this model or to the estimation method since it is the mean of the underlying distribution which is modeled. This is contrary to using observed log ratio counts, i.e. $\log(N_{i,t} / N_{i,t-1})$ which cannot handle zero counts and which is missing when either $N_{i,t}$ or $N_{i,t-1}$ is missing.

Significance of covariates, such as spatial cohesion and TCM, was assessed by means of approximate $F$ statistics using approximate numbers of residual degrees of freedom as implemented in the statistical package GenStat (VSN International 2009). Covariates were selected using a stepwise approach. In the first step spatial plot characteristics were selected. In the second step interactions between spatial plot characteristics and the linear time trend $\beta_0 t$ were selected; this amounts to testing whether the baseline growth parameter $\beta_0$ depends on plot characteristics. In the third and final step weather variables were selected. Note that all models contain a linear time trend as this is required by the model.

## 4.3    RESULTS

Plot means through time, calculated with a log-linear model using fixed plot and year effects, are shown in Fig. 4.3. Monitoring plot means show clear dips in bittern numbers for the years 1985 through 1987, 1991, 1996, and 1997.

In the first step of the covariate selection the spatial plot characteristics carrying capacity and spatial cohesion were found to be significant (P<0.0001), both with a positive effect on plot means. After adding carrying capacity to the model, the additive effect of spatial cohesion is not significant, due to the relatively high correlation between carrying capacity and spatial cohesion (0.67). Subsequently,
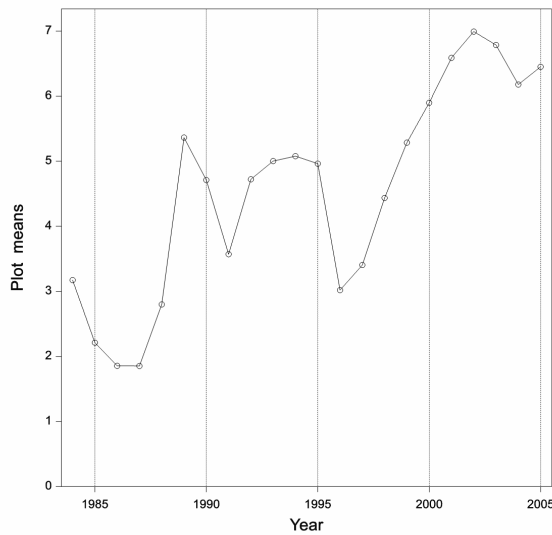
**Figure 4.3**

Plot means through time, with log-linear model corrected for fixed plot and year effects

we explored interactions between the linear time trend $\beta_0 t$ and spatial plot characteristics. We found a significant interaction (P<0.0001) with carrying capacity and spatial cohesion, such that a larger carrying capacity or spatial cohesion leads to a larger mean growth rate $\beta_0$.

In the final step weather variables were added to the model selected so far, i.e. the model which contains a linear time trend, carrying capacity, and the interaction between carrying capacity and the linear time trend. Adding single weather effects leads to significant negative effects of SNOWDAYS (P<0.0001), FROSTDAYS (P<0.0001), and IJNSEN (P=0.006), and to a positive (and almost significant, P=0.054) effect of TCM. Thus, severe winter weather has a significant negative impact on bittern population numbers. Interestingly, the two weather variables that are spatially explicit, SNOWDAYS and FROSTDAYS, are more significant that the other two weather variables. After we added SNOWDAYS to the model (P<0.0001), FROSTDAYS had still additional significant effect (P=0.004). Remain-

ing weather variables were no longer significant (P>0.07). Parameter estimates for the models with single weather variables are given in Table 4.3.

**Table 4.3**

Parameter estimates for the models with weather variables SNOWDAYS and FROSTDAYS, a linear time trend, carrying capacity, and the interaction between $\beta_0 t$ and carrying capacity

| Term | Estimate | S.E. | F value | P value |
|---|---|---|---|---|
| linear time trend $\beta_0 t$ | 0.120 | 0.038 | 9.880 | 0.003 |
| carrying capacity | 0.110 | 0.151 | 0.530 | 0.471 |
| interaction carrying capacity & $\beta_0 t$ | 0.045 | 0.004 | 104.320 | 0.000 |
| SNOWDAYS | -0.017 | 0.006 | 8.510 | 0.004 |
| FROSTDAYS | -0.013 | 0.004 | 9.380 | 0.004 |

## 4.4  DISCUSSION

The results show that severe winter weather has a significant negative impact on bittern population growth rates in the Netherlands. This is in accordance with earlier findings of e.g. Rivière (1930) and Bibby (1981). SNOWDAYS has the strongest effect on bittern numbers, being slightly more significant than FROST-DAYS. The significant effect of SNOWDAYS may be explained by the diet of bitterns. During winter, bitterns feed on fish, amphibians, small mammals, and sporadically on small birds (Day & Wilson 1978). When water bodies are frozen, hunting for fish and amphibians becomes difficult or even impossible. When in addition the land is covered with snow for a significant amount of time, additional food sources such as small mammals become unavailable under the snow cover. This might lead to temporary emigration or even starvation, the latter having direct effect on population numbers.

The two weather variables that are spatially explicit, SNOWDAYS and FROST-DAYS, are more significant that the other two weather variables. This implies that it is meaningful to use spatially explicit weather variables when possible. In 1996 and 1997, especially monitoring plots in the southwestern Netherlands were hardly snow-covered for more than a few days. In these plots, bittern population num-

bers only slightly dropped or remained constant. Monitoring plots in the north-eastern Netherlands were less affected by mild maritime influences. Here, snow cover usually persists as was the case in 1996 and 1997. In these monitoring plots, bittern population numbers did show considerable drops in these years.

This analysis was restricted to data of 28 monitoring plots. Each of these plots has its own history, reflected in differences in e.g. mowing regime and water level management. These factors clearly influence the habitat quality of individual plots (Van der Hut 2001; Gilbert et al. 2005). Hence, carrying capacity and spatial cohesion could have been changed over the years, which we did not take into account in our analysis. Since the values for carrying capacity and spatial cohesion were based on data from 2003, possible over- or underestimations could have been made for few plot means, considering especially the first years of the analysis period. Another monitoring plot characteristic that may have impacted our results is the linear shape of most reedbed vegetations (water edges). When the majority of a grid cell's vegetation consisted of reedbeds, the whole grid cell was assigned as bittern habitat. This might have caused an overestimation of spatial cohesion for some monitoring plots.

Only few small bittern populations are located just across the German and Belgium borders (Vermeersch et al. 2004; Wink et al. 2005). We did not take them into account because of their small size and their hence negligible contribution to the spatial cohesion of Dutch populations. Their absence does therefore not affect the spatial cohesion measures.

We showed that spatial plot characteristics influence recovery rates of populations. This is in accordance with a study of Foppen (1999) who illustrated that breeding populations of Sedge warbler (*Acrocephalus schoenobaenus*) in relatively unfragmented landscape showed a clear recovery after a population drop due to adverse effects in their winter range, as compared to population recovery in heavily fragmented landscapes.

In a study relating life-history traits of marshland species to their response in population growth rate to weather variables (Chapter 3), it was found that waterbirds in general (including bittern) stand out in their negative response to severe winters. It is assumed that climate change will decrease the occurrence of severe winters (IPCC 2001; IPCC 2007), which is beneficial to these species groups. However, climate change might increase the amplitude and frequency of extreme

events (IPCC 2001; IPCC 2007). If this is true, it is expected to have population dynamical consequences (Shaffer 1987). Moreover, climate envelope studies show that Western Europe will no longer be climatically suitable for bitterns by the end of this century (Berry et al. 2007; Huntley et al. 2007). Decreasing suitability might as well lead to increased population dynamics (Anderson et al. 2009; Fraterrigo et al. 2009). Increased variation in vital demographic rates makes species like the bittern susceptible to (local) extinction (Verboom et al. 2010). To compensate for the effects of increased weather variability, growth and recovery rates of populations need to be enhanced. In accordance with the modeling study of Verboom et al. (2010) our results indicate that in plots with large amounts of qualitatively good habitat, growth and recovery rates are relatively high in general. Thus, management authorities of natural areas should aim at maximizing habitat quality for bitterns, enlarging existing areas and increasing wetland density by creating new wetlands, hence preventing further fragmentation.

## ACKNOWLEDGMENTS

## APPENDIX

### Appendix 4.1

Carrying capacity and spatial cohesion value per monitoring plot

| monitoring plot | plot carrying capacity | plot spatial cohesion |
|---|---|---|
| 202 | 4 | 2 |
| 608 | 2 | 3 |
| 808 | 2 | 4 |
| 1200 | 10 | 9 |
| 2200 | 2 | 2 |
| 3000 | 1 | 17 |
| 3100 | 2 | 22 |
| 3200 | 3 | 15 |
| 3600 | 1 | 4 |
| 3700 | 4 | 3 |
| 4000 | 5 | 2 |
| 4200 | 3 | 3 |
| 4400 | 5 | 10 |
| 5100 | 9 | 28 |
| 5200 | 9 | 34 |
| 5300 | 29 | 28 |
| 5400 | 43 | 42 |
| 5800 | 14 | 34 |
| 5901 | 11 | 33 |
| 5902 | 8 | 35 |
| 6300 | 1 | 2 |
| 6500 | 2 | 2 |
| 7400 | 3 | 8 |
| 7500 | 5 | 9 |
| 20900 | 2 | 7 |
| 32007 | 7 | 20 |
| 33009 | 2 | 5 |
| 33047 | 3 | 9 |

**Appendix 4.2**

Yearly weather variables per monitoring plot (a) and correlations after log-transformation (b); grey shading: relatively high correlation

a

| year | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| IJNSEN | 46.0 | 40.0 | 34.0 | 5.0 | 2.0 | 3.0 | 22.0 | 10.0 | 8.0 | 14.0 | 8.0 | 48.0 | 31.0 | 4.0 | 11.0 | 3.0 | 9.0 | 9.0 | 18.0 | 8.0 | 8.0 |
| TCM | -3.0 | -3.6 | -2.7 | 4.4 | 4.5 | 4.8 | -0.8 | 2.7 | 2.4 | 1.5 | 3.8 | -0.1 | -1.2 | 4.7 | 5.2 | 4.3 | 2.6 | 2.9 | 1.8 | 3.6 | 2.4 |

| FROSTDAYS monitoring plot | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 202 | 18.1 | 30.2 | 12.3 | 2.2 | 2.0 | 2.0 | 15.4 | 4.6 | 8.7 | 10.9 | 3.9 | 23.6 | 13.2 | 2.3 | 5.0 | 1.3 | 5.4 | 2.1 | 7.9 | 2.7 | 5.3 |
| 608 | 18.5 | 30.8 | 13.4 | 2.3 | 2.6 | 4.9 | 15.4 | 5.9 | 9.5 | 12.9 | 4.3 | 25.2 | 19.8 | 2.7 | 4.7 | 1.7 | 5.6 | 3.0 | 10.3 | 3.4 | 6.6 |
| 808 | 18.9 | 30.8 | 13.9 | 2.7 | 2.8 | 5.4 | 15.6 | 6.0 | 9.8 | 13.5 | 5.0 | 26.0 | 23.1 | 3.0 | 5.2 | 1.8 | 6.2 | 3.0 | 11.9 | 3.1 | 7.1 |
| 1200 | 19.0 | 30.9 | 13.9 | 2.6 | 2.9 | 5.5 | 15.5 | 6.0 | 9.9 | 13.5 | 5.0 | 25.8 | 24.1 | 2.9 | 5.1 | 1.8 | 6.4 | 3.0 | 12.5 | 3.1 | 7.1 |
| 2200 | 18.0 | 28.4 | 14.2 | 2.6 | 1.1 | 2.9 | 16.5 | 4.9 | 7.7 | 7.0 | 3.2 | 17.6 | 22.1 | 2.2 | 4.9 | 1.5 | 5.8 | 4.0 | 7.3 | 2.4 | 6.3 |
| 3000 | 18.7 | 30.4 | 13.9 | 3.2 | 2.1 | 4.6 | 15.7 | 5.9 | 9.4 | 13.3 | 5.0 | 23.1 | 24.1 | 2.9 | 6.7 | 1.9 | 7.3 | 4.0 | 11.0 | 4.0 | 7.9 |
| 3100 | 18.8 | 30.7 | 14.2 | 3.4 | 2.3 | 4.8 | 15.3 | 6.0 | 9.7 | 13.9 | 5.2 | 23.2 | 24.0 | 3.0 | 6.9 | 2.2 | 7.6 | 3.9 | 11.0 | 4.0 | 8.0 |
| 3200 | 18.8 | 30.5 | 14.2 | 3.5 | 2.1 | 4.7 | 16.0 | 6.0 | 9.5 | 13.7 | 5.4 | 23.2 | 24.0 | 3.2 | 6.7 | 2.1 | 7.5 | 4.2 | 10.8 | 4.1 | 8.0 |
| 3600 | 19.0 | 30.2 | 14.9 | 4.6 | 2.1 | 4.5 | 16.3 | 6.3 | 9.8 | 14.0 | 5.9 | 23.4 | 24.0 | 3.6 | 7.3 | 2.3 | 7.4 | 5.5 | 10.4 | 4.3 | 8.0 |
| 3700 | 19.0 | 29.7 | 15.1 | 5.0 | 1.9 | 4.0 | 17.2 | 6.3 | 9.6 | 14.0 | 5.8 | 22.8 | 23.6 | 3.7 | 7.3 | 2.3 | 7.0 | 7.1 | 9.8 | 4.5 | 8.0 |

**Appendix 4.2 (continued)**

FROSTDAYS

| monitoring plot | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 4000 | 18.9 | 29.1 | 15.0 | 3.0 | 1.1 | 4.2 | 17.0 | 5.4 | 8.4 | 11.0 | 4.6 | 20.9 | 22.7 | 2.6 | 6.1 | 1.6 | 7.2 | 6.2 | 8.7 | 3.8 | 7.9 |
| 4200 | 19.6 | 30.8 | 14.9 | 3.0 | 3.3 | 6.9 | 16.0 | 6.0 | 10.3 | 14.1 | 6.0 | 25.9 | 24.0 | 3.2 | 6.9 | 2.0 | 8.1 | 3.0 | 15.8 | 4.0 | 8.0 |
| 4400 | 18.6 | 31.0 | 13.5 | 2.2 | 2.5 | 5.1 | 15.3 | 6.0 | 9.7 | 13.4 | 4.5 | 24.3 | 24.7 | 2.5 | 5.4 | 1.8 | 6.6 | 3.1 | 12.5 | 3.8 | 7.6 |
| 5100 | 18.7 | 30.7 | 14.0 | 2.9 | 2.4 | 4.9 | 15.4 | 5.9 | 9.7 | 13.4 | 4.8 | 23.7 | 24.6 | 2.7 | 6.6 | 1.9 | 7.1 | 3.5 | 11.7 | 3.9 | 7.8 |
| 5200 | 18.8 | 30.7 | 14.2 | 3.0 | 2.4 | 4.9 | 15.2 | 6.0 | 9.7 | 13.5 | 5.0 | 23.5 | 24.4 | 2.8 | 6.9 | 1.9 | 7.3 | 3.7 | 11.5 | 4.0 | 7.9 |
| 5300 | 18.9 | 30.9 | 14.5 | 3.3 | 2.4 | 4.9 | 15.2 | 6.1 | 9.8 | 13.8 | 5.3 | 23.5 | 24.0 | 3.0 | 7.0 | 2.1 | 7.6 | 3.7 | 11.3 | 4.0 | 8.0 |
| 5400 | 18.5 | 30.0 | 13.5 | 3.0 | 1.7 | 4.7 | 16.8 | 5.8 | 9.0 | 12.6 | 4.9 | 23.0 | 23.5 | 2.8 | 6.1 | 1.7 | 7.1 | 4.4 | 10.6 | 3.9 | 7.8 |
| 5800 | 18.3 | 29.5 | 12.1 | 2.4 | 1.4 | 4.6 | 16.7 | 5.2 | 8.3 | 10.4 | 4.1 | 22.9 | 20.7 | 2.3 | 5.6 | 1.3 | 6.5 | 3.3 | 9.7 | 3.1 | 6.8 |
| 5901 | 18.3 | 29.5 | 12.4 | 2.4 | 1.4 | 4.9 | 16.8 | 5.2 | 8.3 | 10.7 | 4.2 | 23.0 | 21.8 | 2.4 | 5.6 | 1.3 | 6.6 | 3.9 | 9.6 | 3.3 | 7.3 |
| 5902 | 18.3 | 29.5 | 12.2 | 2.3 | 1.4 | 4.9 | 16.8 | 5.2 | 8.3 | 10.5 | 4.2 | 23.0 | 21.5 | 2.4 | 5.6 | 1.3 | 6.5 | 3.6 | 9.5 | 3.2 | 7.1 |
| 6300 | 18.7 | 29.3 | 13.2 | 2.2 | 1.2 | 4.6 | 17.0 | 5.3 | 8.3 | 10.8 | 4.1 | 23.3 | 22.8 | 2.7 | 5.8 | 1.7 | 6.8 | 5.3 | 8.4 | 3.6 | 7.8 |
| 6500 | 19.0 | 29.4 | 14.7 | 1.4 | 1.2 | 3.3 | 17.0 | 5.9 | 8.5 | 12.1 | 4.6 | 23.0 | 23.0 | 2.9 | 6.1 | 1.8 | 7.2 | 7.0 | 9.0 | 4.0 | 8.0 |
| 7400 | 19.0 | 27.5 | 15.3 | 4.6 | 2.0 | 3.4 | 17.4 | 6.6 | 9.6 | 12.4 | 5.3 | 18.4 | 23.0 | 3.5 | 6.7 | 2.2 | 6.5 | 7.5 | 9.3 | 4.6 | 8.0 |
| 7500 | 19.0 | 26.5 | 15.3 | 4.8 | 1.9 | 3.3 | 17.6 | 6.1 | 9.6 | 12.4 | 5.1 | 18.5 | 23.0 | 3.3 | 6.4 | 2.1 | 6.7 | 7.3 | 9.2 | 4.3 | 8.0 |
| 20900 | 19.0 | 27.0 | 15.5 | 4.6 | 1.9 | 3.3 | 17.5 | 6.3 | 9.6 | 11.9 | 5.1 | 17.6 | 23.0 | 3.4 | 6.5 | 2.1 | 6.5 | 7.7 | 9.0 | 4.7 | 8.0 |
| 32007 | 18.7 | 30.2 | 14.2 | 3.5 | 1.8 | 4.7 | 16.8 | 5.9 | 9.4 | 13.5 | 5.4 | 23.0 | 24.0 | 3.1 | 6.3 | 1.9 | 7.3 | 4.8 | 10.5 | 4.0 | 8.0 |
| 33009 | 19.3 | 31.3 | 14.7 | 3.1 | 3.0 | 6.1 | 15.4 | 6.1 | 10.3 | 14.0 | 5.8 | 25.2 | 24.2 | 3.0 | 7.1 | 2.2 | 8.1 | 3.0 | 13.6 | 4.0 | 7.9 |
| 33047 | 19.0 | 25.9 | 15.3 | 4.8 | 1.8 | 3.2 | 17.8 | 6.0 | 9.6 | 12.2 | 5.0 | 17.9 | 23.0 | 3.2 | 6.2 | 2.1 | 6.7 | 7.3 | 9.1 | 4.2 | 8.0 |

**Appendix 4.2 (continued)**

SNOWDAYS monitoring plot

| plot | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 |
|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| 202 | 13.6 | 6.9 | 2.3 | 0.5 | 0.0 | 0.1 | 9.8 | 0.1 | 0.3 | 3.1 | 2.9 | 7.2 | 4.1 | 0.2 | 2.0 | 1.1 | 4.3 | 1.4 | 3.1 | 0.4 | 4.8 |
| 608 | 16.1 | 15.4 | 6.3 | 1.7 | 0.1 | 0.4 | 9.1 | 0.5 | 1.0 | 4.0 | 2.8 | 5.0 | 5.1 | 0.8 | 8.5 | 1.5 | 5.0 | 2.0 | 4.9 | 0.4 | 5.0 |
| 808 | 14.6 | 13.5 | 6.4 | 1.7 | 0.3 | 0.1 | 9.1 | 0.7 | 1.3 | 2.5 | 2.4 | 4.5 | 1.8 | 0.9 | 7.2 | 1.6 | 5.4 | 2.9 | 0.8 | 0.2 | 5.1 |
| 1200 | 15.1 | 14.0 | 6.1 | 1.7 | 0.4 | 0.1 | 8.8 | 0.8 | 1.2 | 2.3 | 2.4 | 4.4 | 1.7 | 0.9 | 7.4 | 1.6 | 5.2 | 2.9 | 1.2 | 0.1 | 5.2 |
| 2200 | 17.0 | 3.9 | 1.6 | 0.1 | 0.0 | 0.0 | 10.8 | 0.0 | 0.9 | 1.7 | 3.0 | 1.1 | -0.1 | 0.0 | 6.3 | 0.4 | 5.3 | 0.3 | 2.8 | 2.2 | 3.4 |
| 3000 | 16.2 | 8.3 | 4.1 | 0.9 | 0.2 | 0.0 | 12.0 | 0.2 | 0.8 | 2.2 | 2.2 | 3.6 | 3.5 | 0.0 | 2.6 | 1.3 | 7.3 | 3.7 | 2.2 | 1.1 | 6.2 |
| 3100 | 16.2 | 8.8 | 4.4 | 1.3 | 0.3 | 0.0 | 11.2 | 0.3 | 0.8 | 2.3 | 2.1 | 3.1 | 5.3 | 0.1 | 2.4 | 1.6 | 9.1 | 2.5 | 3.0 | 1.1 | 6.9 |
| 3200 | 16.8 | 8.1 | 4.8 | 1.0 | 0.3 | 0.0 | 11.7 | 0.2 | 0.9 | 2.3 | 2.0 | 4.3 | 3.7 | 0.1 | 4.4 | 1.5 | 6.8 | 5.4 | 2.4 | 1.2 | 6.5 |
| 3600 | 17.0 | 8.3 | 7.8 | 1.3 | 0.4 | 0.0 | 10.1 | 0.4 | 0.9 | 2.7 | 1.9 | 5.0 | 6.7 | 0.2 | 6.7 | 1.7 | 7.9 | 7.2 | 2.9 | 1.6 | 6.2 |
| 3700 | 16.8 | 8.6 | 11.5 | 1.0 | 0.1 | 0.0 | 10.5 | 0.5 | 0.7 | 2.9 | 2.8 | 3.8 | 11.2 | 0.1 | 7.9 | 1.4 | 6.8 | 6.6 | 1.6 | 2.1 | 5.2 |
| 4000 | 16.9 | 5.8 | 9.6 | 0.6 | 0.1 | 0.1 | 9.3 | 0.1 | 0.5 | 3.2 | 3.3 | 2.1 | 0.1 | 0.2 | 5.3 | 0.8 | 4.0 | 1.2 | 2.2 | 2.2 | 2.8 |
| 4200 | 14.5 | 9.3 | 7.2 | 1.1 | 0.9 | 0.0 | 7.4 | 1.8 | 1.2 | 0.2 | 2.0 | 12.8 | 15.3 | 0.1 | 9.0 | 2.5 | 7.4 | 3.1 | 6.9 | 1.0 | 6.8 |
| 4400 | 16.9 | 19.2 | 4.7 | 2.4 | 0.1 | 0.1 | 8.3 | 0.3 | 1.0 | 2.8 | 2.8 | 4.3 | 3.2 | 0.2 | 7.2 | 1.4 | 4.8 | 1.8 | 6.3 | 0.8 | 5.3 |
| 5100 | 14.1 | 11.1 | 4.6 | 1.5 | 0.2 | 0.1 | 10.8 | 0.4 | 0.8 | 2.4 | 2.5 | 3.8 | 5.2 | 0.1 | 2.8 | 1.4 | 8.8 | 2.3 | 3.2 | 0.9 | 5.7 |
| 5200 | 14.8 | 10.3 | 4.7 | 1.5 | 0.2 | 0.0 | 11.1 | 0.4 | 0.8 | 2.4 | 2.4 | 3.1 | 6.1 | 0.1 | 2.2 | 1.5 | 9.3 | 1.9 | 3.3 | 1.0 | 6.5 |
| 5300 | 15.8 | 9.6 | 5.0 | 1.5 | 0.3 | 0.0 | 11.1 | 0.4 | 0.9 | 2.3 | 2.1 | 3.6 | 6.9 | 0.1 | 2.6 | 1.7 | 9.8 | 2.7 | 3.9 | 1.1 | 7.0 |
| 5400 | 17.4 | 7.1 | 4.0 | 0.4 | 0.1 | 0.0 | 12.8 | 0.1 | 0.9 | 2.2 | 2.3 | 4.2 | 0.5 | 0.0 | 4.6 | 0.9 | 3.2 | 6.1 | 1.6 | 1.2 | 6.1 |
| 5800 | 17.6 | 7.6 | 2.4 | 0.5 | 0.1 | 0.0 | 11.0 | 0.1 | 0.6 | 2.4 | 2.8 | 2.7 | 0.0 | 0.0 | 2.8 | 0.8 | 2.9 | 1.8 | 4.8 | 1.8 | 6.7 |
| 5901 | 17.3 | 6.8 | 2.4 | 0.7 | 0.1 | 0.0 | 10.4 | 0.1 | 0.6 | 2.1 | 2.8 | 2.7 | 0.0 | 0.0 | 3.3 | 0.7 | 3.1 | 2.1 | 5.2 | 1.9 | 6.6 |

SNOWDAYS

| monitoring plot | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 5902 | 17.3 | 6.7 | 2.3 | 0.6 | 0.1 | 0.0 | 10.3 | 0.1 | 0.5 | 2.1 | 2.8 | 2.6 | 0.0 | 0.0 | 3.1 | 0.7 | 3.0 | 2.0 | 5.4 | 2.0 | 6.6 |
| 6300 | 17.0 | 5.3 | 4.9 | 0.8 | 0.1 | 0.1 | 9.4 | 0.1 | 0.5 | 2.2 | 2.9 | 2.5 | 0.4 | 0.2 | 5.1 | 0.9 | 3.9 | 2.0 | 5.1 | 2.0 | 5.1 |
| 6500 | 14.7 | 6.1 | 12.3 | 1.0 | 0.0 | 0.0 | 9.3 | 0.1 | 0.3 | 3.0 | 3.0 | 4.4 | 1.2 | 0.7 | 6.7 | 1.1 | 5.2 | 0.8 | 3.0 | 1.8 | 4.1 |
| 7400 | 18.5 | 7.0 | 14.3 | 0.4 | 0.0 | 0.0 | 12.0 | 0.0 | 0.1 | 5.7 | 3.8 | 2.5 | 15.4 | 0.0 | 5.2 | 1.2 | 2.4 | 2.0 | 2.1 | 2.3 | 1.0 |
| 7500 | 19.3 | 8.0 | 11.6 | 0.4 | 0.0 | 0.0 | 12.1 | 0.0 | 0.1 | 3.5 | 3.9 | 1.3 | 14.0 | 0.0 | 3.9 | 1.1 | 2.5 | 4.4 | 1.4 | 1.8 | 1.2 |
| 20900 | 19.0 | 6.7 | 14.9 | 0.3 | 0.0 | 0.0 | 12.2 | 0.0 | 0.1 | 6.6 | 3.8 | 1.0 | 14.5 | 0.0 | 4.4 | 1.2 | 2.1 | 1.6 | 2.0 | 2.6 | 1.0 |
| 32007 | 17.5 | 7.2 | 4.7 | 0.4 | 0.1 | 0.0 | 13.1 | 0.1 | 1.0 | 2.2 | 2.2 | 4.4 | 2.5 | 0.0 | 5.9 | 1.3 | 3.6 | 6.9 | 1.6 | 1.2 | 6.3 |
| 33009 | 16.0 | 10.5 | 6.4 | 1.6 | 0.4 | 0.0 | 10.9 | 1.1 | 1.2 | 1.6 | 2.4 | 8.4 | 13.7 | 0.6 | 6.4 | 2.3 | 8.9 | 4.7 | 7.2 | 1.3 | 7.5 |
| 33047 | 20.3 | 8.3 | 10.7 | 0.2 | 0.0 | 0.0 | 12.3 | 0.0 | 0.1 | 3.0 | 3.9 | 0.8 | 14.0 | 0.0 | 3.5 | 1.1 | 2.7 | 5.6 | 1.4 | 1.6 | 1.0 |

b

| | TCM | FROSTDAYS | SNOWDAYS |
|---|---|---|---|
| IJNSEN | -0.90 | 0.90 | 0.65 |
| TCM | | -0.89 | -0.69 |
| FROSTDAYS | | | 0.59 |

# 5

# Can phenological shifts compensate for adverse effects of climate change on butterfly metapopulation viability? Explorations with a detailed spatial population model

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Jana Verboom
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Paul Opdam

ABSTRACT

The interaction between climate change and habitat fragmentation has been presented as a deadly anthropogenic cocktail. We cannot stop climate change, but it is within our circle of influence as ecologists to suggest landscape adaptation. Detailed population models that take into account climate change are considerably needed. We explore a detailed individual-based spatially explicit metapopulation model of a univoltine butterfly species where all processes are affected by daily weather, using historical daily weather data and future daily projections as input, in order to examine responses of a butterfly population in landscapes under various states of fragmentation and two climate change scenarios. This tool is used to investigate how landscapes could be adapted to compensate for possible negative impacts of climate change on population performance. We find that our model butterfly metapopulation was not only able to escape adverse conditions in summer by phenological shifts, but even to benefit from climatic warming. Varying either the amount of suitable habitat or patch size revealed a sharp threshold in population viability. In this particular case, however, the threshold was not affected by climate change and climate-dependent landscape adaptation was not required. The model presented here can be adapted for other species and applied to investigate scenarios for landscape adaptation.

## 5.1 INTRODUCTION

Climatic models indicate that increasing atmospheric concentrations of greenhouse gases will result in continued warming as well as in increased changes in daily, seasonal, inter-annual, and decadal weather variability in the next century (IPCC 2001; IPCC 2007). It is suggested that these changes will result in mostly adverse impacts on biophysical systems (IPCC 2007). At a smaller spatial and temporal scale however, climate change is expressed by daily weather that affects populations of individual species. Often, these species are now restricted to isolated patches of habitat that are located within inhospitable area (Hanski & Simberloff 1997). Populations can only survive in these habitat patches if the juxtaposition and sizes of the areas allow a metapopulation network structure (Opdam et al. 2003).

Climate change and habitat fragmentation have been presented as amplifying forces (Warren et al. 2001; Travis 2003; Opdam & Wascher 2004). Warren et al (2001) found that most of the butterfly species considered in their research had not expanded their range, despite the warming climate, because habitat patches were too isolated to colonize. Travis (2003) concluded on the basis of a simple lattice model with a climate-driven shift in suitable habitat that the interaction between climate change and habitat loss might be disastrous: during climate change, decreasing habitat availability becomes critical sooner than habitat loss alone would suggest. Similarly, species suffer more from climate change in a fragmented habitat, because they are unable to keep pace with climate change and patch occupancy quickly declines. If these interactions between climate change and habitat loss are indeed always disastrous, it is important to know which adaptation measures are effective. Except for mitigating greenhouse gas emissions, changing land use to improve habitat configuration would be a main adaptation measure. Increasing sizes and number of habitat areas, connecting habitats, and improving habitat quality (e.g. by making habitats more heterogeneous) have been proposed to be effective adaptation measures (Vos et al. 2008), where increasing the size of habitat patches has proven to be more cost-effective than increasing the number of habitat patches (Shea & Possingham 2000).

The interaction between climate change and habitat fragmentation has several dimensions. Especially increased weather fluctuations have been shown to affect

population dynamics (Morris et al. 2008; Grotan et al. 2009; Piessens et al. 2009). This leads to increased variability in vital demographic rates, especially for meta-populations depending on small patches (Verboom et al. 2010). Moreover, climate change affects habitat quality, either positively or negatively. Thomas et al (2001) found a significant broadening of the range of habitats used by Silver-spotted skipper, *Hesperia comma*, spreading into north-facing hill slope habitats that were previously climatically not suitable. However, WallisDeVries and Van Swaay (2006) showed that climatic warming can lead to a reduction in available habitat due to microclimatic cooling in spring by advancing plant growth, which is particularly unfavourable to thermophilous organisms, such as caterpillars; vegetation has a lower temperature threshold for growth than caterpillars have for activity. At a much larger spatial scale, climatic warming causes shifts in geographical distributions of species (Parmesan & Yohe 2003; Root et al. 2003) and habitat fragmentation may affect these range shifts (Vos et al. 2008; Anderson et al. 2009; Schippers et al. in prep). These large-scale expressions of climate change are the result of changes in population processes at the local and regional scale. These climate-induced demographic changes interact with each other and with landscape characteristics.

Considering the need for measures in the landscape, better understanding of the mechanistics behind the interaction between population dynamics, landscape characteristics and climate change at the local scale is therefore required. However, these interactions have rarely been studied (but see e.g. Zurell et al. 2009).

Empirical studies alone afford insufficient insight into complex interactions and mechanisms. To control underlying processes, models provide tools to study relative impacts of components with mutual dependencies. However, most current models in this field only predict large-scale shifts in species distributions. These envelope models solely consider climate-driven changes in the quantity and location of suitable habitat (Akçakaya et al. 2006) and lack projections of complex dependencies between climate change, population dynamics, and landscape characteristics (Brook et al. 2009). To afford insight into the combined impacts of various weather components and landscape pattern indicators, we developed a novel spatially explicit population model.

In this paper we present a detailed individual-based spatially explicit metapopulation model of a butterfly species developed to study how this butterfly population

performs under different scenarios of climate change and habitat fragmentation. It uses daily weather data as input. We have chosen to model a butterfly species, since butterflies are ectothermic and show a direct response to weather, have a fast turnover, and complete their life cycle on a spatial scale that is comparable to the scale of human land-use interventions (e.g. construction of new industrial or residential areas or abandonment of agricultural land). With model experiments, one can investigate how the landscape pattern could be adapted to compensate for possible negative impacts of climate change on population performance by addressing the following questions:

- What is the effect of current and future weather circumstances, and various climate change scenarios on population dynamics in space and time?
- What is the effect of landscape configuration, especially patch area and habitat density on population viability under current and future weather circumstances?

## 5.2 METHODS

We applied an extended version of the model METAPHOR (Verboom 1996), which is a spatially explicit, individual-based model (programmed in C++) that simulates the dynamics of a population or metapopulation. METAPHOR was used in several theoretical and applied studies (Reijnen et al. 1995; Verboom et al. 2001; Vos et al. 2001; Schippers et al. 2009; Schippers et al. in press). The model was altered by allowing time steps of one day, a stage structured population, and daily weather (past records or future projections) as input, as will be described in detail below following the ODD protocol (Grimm et al. 2006).

### 5.2.1 Purpose

We aimed to investigate the effect of current and future weather circumstances, and various climate change scenarios on butterfly population dynamics in space and time. Moreover, we aimed to study the effect of landscape configuration (patch area and habitat density) on population viability under current and future weather circumstances.

*5.2.2 State variables and scales*

Our population consists of an imaginary butterfly species representing a widespread species in the centre of its range that is moderately mobile and, therefore, potentially affected by habitat fragmentation. Parameter settings were derived from real species data (mostly Meadow brown *Maniola jurtina*) as much as possible. Each individual has 4 or 5 phases: egg, caterpillar, pupa, for female an unfertilized and a fertilized adult phase, and for male only one adult phase. Individuals are characterized by the state variables: identity number, age, sex, identity of the patch where the individual resides, phase, and weight (for caterpillar only). The butterfly species is univoltine and overwinters as half-grown caterpillar.

The experiments were carried out in computer-generated landscapes of 5x5km, with suitable habitat patches that are surrounded by inhospitable area. These dimensions are in proportion to the assumed network size. The left and right sides and the top and bottom sides of the landscapes are merged in a toroidal way (periodic boundary). In these landscapes, all patches have equal quality, and the weather is equal for all patches.

*5.2.3 Process overview and scheduling*

METAPHOR describes the spatial dynamics of a (meta)population in discrete time, and the time step used in the model is one day. Each day, individuals have a chance to change phase (which is evoked by daily growth for caterpillars), to die (mortality), to reproduce (only fertilized female adults) and to move (only adults). Processes development/phase transition, mortality, reproduction, and movement determine the magnitude and structure of subpopulations and, thus, direct population dynamics. The first event in a new day is development, or change to the next phase. Next, reproduction occurs. Then, individuals can move, and finally, mortality takes place.

*5.2.4 Design concepts*

The individual's performance and behaviour are entirely represented by stochastic processes governed by empirical rules, and all affecting factors (mainly weather) are imposed. Thus, individuals make no adaptive decisions. Individuals are assumed to know their own age, sex, position, and phase so that they apply their specific behaviour and performance. Considering interaction among individuals,

the number of eggs produced per female depends on the number of female adults in a patch (density dependence). Also, mating depends on the presence of both a male and an unfertilized female adult within a specified neighbourhood (radius). The model is stochastic for all processes, including both demographic and environmental (variable weather) stochasticity. Indicators for population performance used are total adult numbers and patch occupancy of the landscape, summarized per scenario and over all patches, and date of emergence. The occupancy, or the average fraction of occupied patches during the period the population was extant, was calculated as an ecological measure of fragmentation effects (Hanski 1994). Average population viability in years 1981-2009 (indicated as 1995), 2026-2054 (indicated as 2040), and 2072-2100 (indicated as 2085) were used to present results, as well as population viability continuous through time.

### 5.2.5 Initialization and input

A run starts on January 1 with all patches occupied with 1000 caterpillars and continues for 161 years and, thus, 58765 time steps (no intercalary years). For the first 40 years of each run, the weather of the years 1960-1979, derived from the De Bilt meteorological station (www.knmi.nl), located in the centre of the Netherlands, was used as input, followed by once more the 1960-1979 weather. This resulted in 40 years of pre-climate change weather that were used to burn-in the model, as the pattern of occupancy is presumed to be the result of a quasi equilibrium between species, weather, and landscape characteristics. Subsequently, the weather of the years 1980-2009, derived from the De Bilt meteorological station, was used as input. From KNMI data on future daily average temperatures and precipitation amounts http://www.knmi.nl/research/climate_services/). The KNMI data on future daily average temperatures and precipitation amounts are transformations of historical weather series (1976-2005). Those are available for various baseline years (every tenth year between 2020 and 2100). Hence, weather data for a single day appears in three different, partly overlapping transformation series. The three projections for weather of a single day can be regarded as independent, because of the 10-year interval. We randomly picked daily values from these series, before we supplied them to the model. In this way, we avoid the persistent reoccurrence of extreme weather in consecutive years, as might arise from using the historical weather in their native state. For a detailed description of the transformation series, see http://www.knmi.nl/research/climate_services/. In

Fig. 5.1, we show statistics for daily mean temperature and precipitation surplus for periods 1981-2009, 2026-2054, and 2072-2100 for both the W and W+ scenario.

```
Table 5.1
```

Weather variables used in the model

| Abbreviation | Explanation (units) | Calculation for 2010-2100 |
| --- | --- | --- |
| TAVG | Average daily temperature (˚C) | - [a] |
| TSM7 | Temperature sum (˚C) above 7˚C since 1 January | Sum of temperatures (˚C) for days with TAVG>7˚C since 1 January |
| TSM0 | Temperature sum (˚C) above 0˚C since 1 January | Sum of temperatures (˚C) for days with TAVG>0˚C since 1 January |
| TMAX | Maximum daily temperature (˚C) | Per date: TAVG, summed with average difference TMAX-TAVG for that date over period 1960-2008[a] |
| PDAY | Daily precipitation amount (mm) | - [a] |
| SHWR | Daily precipitation falls in showers (1) or continuously (0) (-) | Per day 50% chance for precipitation in showers, and 50% chance for day with continuous rainfall, based on random number drawn. Chances for rain in showers increase to 100% when TMAX>25˚C |
| HUMI | Average daily air humidity (%) | Linear function of TAVG, PDAY, EVAP[b], and PSPL, based on measured weather 1960-2009 (best GLM)[a] |
| RADI | Average daily radiation (J/m$^2$) | Cosine function, with values for average and standard deviation per date, based on measured weather 1960-2008[a] |
| PSPL | Precipitation surplus since 1 January (mm) | summed difference PDAY-EVAP[b] since 1 January[a] |

**Table 5.1 (continued)**

### 5.2.6 Processes and parameterization

In the processes, we implemented as many weather effect as we found to be relevant from literature and our own field experiments (Chapter 2, Tables 5.1 and 5.2). Egg hatching depends on daily average temperature (˚C), which is summed for the days the individual is in its egg phase until a specified temperature threshold (see Table 5.3 for formulas and parameter values). When the summed daily average temperature exceeds this threshold, the egg has a chance to hatch (cf. Salpiggidis et al. 2004). Egg mortality depends on air humidity (%); with a decreased air humidity, egg mortality increases (Warren 1992). Caterpillar development depends on individual growth in weight (10-4 g), which increases with daily average temperature when this temperature exceeds 7˚C (temperature threshold for caterpillar activity, cf. Kingsolver et al. 2004). This increase in growth is limited when daily average temperatures are more often between 0˚C (temperature threshold for grass growth) and 7˚C than in former, cooler times (1960-1990). In this case, relatively fast grass growth leads to a shady and cool microclimate, limiting caterpillar growth (WallisDeVries & Van Swaay 2006). When individual caterpillar weight exceeds a specified threshold, the caterpillar has a chance to pupate (Jansen unpublished work). Individual caterpillars loose weight when the daily average temperature drops below 7˚C. Reduction in (limited or unlimited) growth occurs in periods of drought, when the precipitation surplus becomes negative. In this case, growth is reduced with a specified factor. Weight loss of more than a third of the maximum individual caterpillar's weight ever reached increases caterpillar mortality. Pupa hatching depends on daily average temperature (˚C), which is summed for the days the individual is in its pupa phase until a specified temperature threshold. When the summed daily average temperature exceeds this threshold, there is a chance for adult emergence from the pupa (cf. Stevens 2004). For adults, reproduction is density dependent; the number of eggs produced per female depends on the number of female adults in the patch. The number of eggs produced per female on a specific day further depends on the age of

the individual as fertilized female (Brakefield 1982). There is a combination of weather that is unfavourable to adult individuals: the daily maximum temperature does not exceed 18˚C (butterflies will not fly/fly less), or the daily precipitation amount exceeds 3mm and falls on a day with almost continuous rainfall (thus not in showers; butterflies will not fly/fly less), or the precipitation surplus is negative (drought can lead to nectar shortage). One such day will limit butterfly movement, will decrease the mating chance (equals 'phase' change from unfertilized to fertilized female, also depending on presence of male adult in neighbourhood), and will decrease reproduction. Three consecutive days of these kinds of weather will increase mortality. When weather is favourable, adult butterflies are able to move in a random walk manner, taking a specified number of steps per day (depending on temperature threshold) of a specified length and tortuosity between the steps. Inside-patch butterfly movement distance increases with radiation and decreases with temperature. Outside-patch movement distance and tortuosity between steps of both inside- and outside-patch movement are not affected by weather (based on Chapter 2). An overview of all parameter values is given in the (Table 5.3). We performed sensitivity analyses for various parameters to study the effect on (meta)population performance.

### 5.2.7 Simulation experiments

The computer-generated landscapes of 5x5km contained suitable habitat amounts of 0.5%, 1%, and 2%, distributed over habitat patches of 0.1, 0.2, 0.4, and 0.8 ha (Table 5.4) that are surrounded by inhospitable area. The number of patches per simulation landscape varied from 11 to 1000 (Table 5.4). The patches were distributed randomly by a landscape generator, keeping a minimal distance between patch edges of 150m. For each of the 11 combinations of habitat amount and patch size, ten landscapes were generated. We generated ten weather series from the KNMI data on future daily average temperatures and precipitation amounts. Hence, ten runs per climate scenario were conducted for each landscape; thus in total 2200 runs were conducted.

**Table 5.2**

Dependencies used in the model
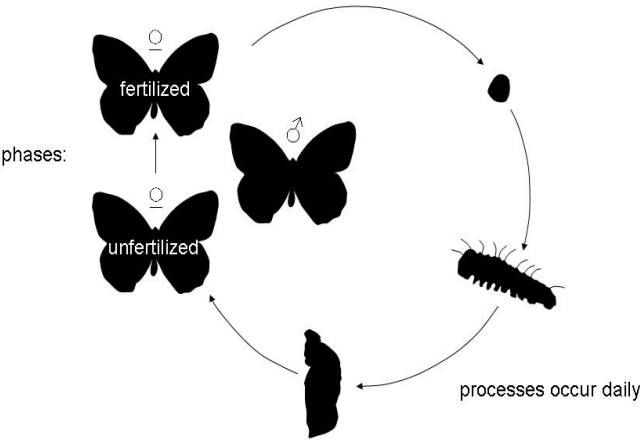


| Phase | Development and/or phase transition | Mortality | Reproduction | Movement |
|---|---|---|---|---|
| | **Process** | | | |
| Egg | [a] TAVG cf. 1 | HUMI 2, 3 | | |
| Caterpillar | TSM7, TSM0, TAVG, PSPL 4, 5 | TAVG, PSPL 2 | | |
| Pupa | TAVG cf. 6 | no dependencies | | |

**Table 5.2 (continued)**

| | | | | |
|---|---|---|---|---|
| Adult female unfertilized | TMAX, PDAY, SHWR, (PSPL) 2 | | male nearby, density females 2 | TMAX, PDAY, SHWR, (PSPL), RADI 2, 8 |
| Adult female fertilized | ▨ | TMAX, PDAY, SHWR, (PSPL) 2 | TMAX, PDAY, SHWR, (PSPL), age 2, 7 | |
| Male | | | ▨ | |

[a] phase transition in this cell is from egg to caterpillar, etc. for other cells;

1 Salpiggidis et al (2004); 2 expert knowledge Dutch Butterfly Conservation; 3 Warren (1992); 4 WallisDeVries and Van Swaay (2006); 5 Jansen (unpublished work); 6 Stevens (2004); 7 Brakefield (1982); 8 Chapter 2; weather variables are abbreviated - for abbreviation of weather variables see Table 5.1; only unshaded cells are relevant in butterfly life-cycle

**Table 5.3**

Parameter values

| Phase | Process | Formula | Parameter | Value (units) |
|---|---|---|---|---|
| egg | development (hatching) | | Threshold for summed TAVG[a] (hatching) | 306.1 (˚C) |
| | | | Standard deviation on threshold for summed TAVG | 51 (˚C) |
| | mortality | $= a \cdot HUMI + b$ | a | 0.07 (-) |
| | | | b | -0.0006 (-) |

Table 5.3 (continued)

| Phase | Process | Formula | Parameter | Value (units) |
|---|---|---|---|---|
| caterpillar | development (growth) | $$= \begin{cases} c \cdot TAVG + d \\ c \cdot TAVG + e \end{cases}$$ | Initial caterpillar weight | 327 ($10^{-4}$g) |
| | | | daily growth (g): | |
| | | | c | 10 ($10^{-4}$g/˚C) |
| | | | d (unlimited growth) | -70 ($10^{-4}$g) |
| | | | e (limited growth) | -80 ($10^{-4}$g) |
| | | | Weight loss for TAVG<7˚C | 1 ($10^{-4}$g) |
| | | | Growth reduction factor for PSPL<0mm | 0.8 (-) |
| | | | Threshold for weight (pupation) | 3500 ($10^{-4}$g) |
| | | | Pupation chance | 0.8 (-) |
| | mortality | | Mortality rate | 0.002 (-) |
| | | | Mortality rate for weight loss to over a third of maximum individual caterpillar's weight ever reached | 0.003 (-) |
| pupa | development (hatching) | | Threshold for summed TAVG (adult emergence) | 355.3 (˚C) |
| | | | Standard deviation on threshold for summed TAVG | 59 (˚C) |
| | mortality | | Mortality rate | 0.03 (-) |

Table 5.3 (continued)

| Phase | Process | Formula | Parameter | Value (units) |
|---|---|---|---|---|
| adult general | development, mortality, reproduction, movement | | Unfavourable weather: (OR/OR/OR) | |
| | | | - TMAX... | <18 (˚C) |
| | | | - SHWR=0; PDAY... | >3 (mm) |
| | | | - PSPL... | <0 (mm) |
| | | | Chance for processes when PSPL<0mm | 0.25 (-) |
| | mortality | | Mortality rate inside patch, favourable weather | 0.14 (-) |
| | | | Mortality rate during dispersal | 0.8 (-) |
| | | | Mortality rate unfavourable weather | 0.8 (-) |
| | movement | | Threshold for TMAX for number of steps per day | 31 (˚C) |
| | | | Number of steps per day when TMAX is above threshold | 647 (-) |
| | | | Number of steps per day when TMAX is below threshold | 510 (-) |
| | | | Chance to stay in patch when encountering patch border (U turn), coming from inside patch | 0.88 (-) |
| | | | step length inside patch (m): | |

Table 5.3 (continued)

| Phase | Process | Formula | Parameter | Value (units) |
|---|---|---|---|---|
| adult general | move-ment | $= \dfrac{f \cdot TMAX +}{g \cdot RADI + h}$ | f | -0.07 (m/˚C) |
| | | | g | $5.3{*}10^{-8}$ $(m/(J/m^2))$ |
| | | | h | 1.54 (m) |
| | | | Tortuosity between steps inside patch | 12.61 (˚) |
| | | | Step length outside patch | 37.2 (m) |
| | | | Tortuosity between steps outside patch | 5.7 (˚) |
| adult female unferti-lized | develop-ment (fertiliza-tion) | | Threshold for radius within which male presence | 100 (m) |
| adult female fertilized | reproduc-tion[b] | $= \dfrac{\dfrac{i}{j + \dfrac{N_{female}{}^c}{k}} \cdot}{\overbrace{\dfrac{l + age^d}{age^d \cdot m}}}$ | i | 100 (-) |
| | | | j | 1 (-) |
| | | | k | 50 (-) |
| | | | l | 60 (-) |
| | | | m | 300 (-) |

[a] For abbreviation of weather variables, see Table 5.1

[b] number of eggs laid per female on specific day (part of formula for daily fraction is indicated below brace)

[c] density of female (unfertilized and fertilized) in patch

[d] age of individual as fertilized female

Table 5.4

Number of patches per simulation landscape

| habitat amount (%) | patch area (ha) | | | |
|---|---|---|---|---|
| | 0.1 | 0.2 | 0.4 | 0.8 |
| 0.5 | 125 | 63 | 31 | 16 |
| 1 | 250 | 125 | 63 | 31 |
| 2 | 500 | 250 | 125 | [a] |

[a] no runs conducted with this landscape

## 5.3   RESULTS

### 5.3.1 Effect of future weather on population viability

Generally, our results do not show any negative impacts of climate change on population viability. If populations are sustainable and survive 160 years, average total adult numbers gradually increase over time for both W and W+ scenarios (Fig. 5.2; graphs at right and bottom). Adult numbers for time slots 2040 are higher than adult numbers for time slots 1995, and adult numbers for time slots 2085 are higher than adult numbers for both time slots 2040 and 1995. There are no significant differences between W and W+ scenarios within time slots. Average occupancy of the landscape remains 1 (all patches occupied) constantly over time (Fig. 5.3).

A phenological shift in the moment of phase change could result in earlier pupation and butterfly emergence and, hence, a lesser vulnerability to drought. For a landscape with 0.5% habitat and patches of 0.8 ha, we investigated the extent to which this phenomenon occurred. Over a period of 130 years, the moment of pupation shifted from mid-June to mid-May for both scenarios (Fig. 5.4). Populations under the W scenario showed a similar phenological shift as populations under the W+ scenario.

The phenological shift in pupation can be caused by several weather components. We varied model dependencies of these components to find out to what compo-

nent(s) the model butterfly is most sensitive. We investigated the effect of drought on caterpillar development by increasing both the growth reduction factor and the mortality rate during weight loss with 10% as well as with 50%. Especially between 1990 and 2030 (years 50 to 90), an increased effect of drought (50% increase in growth reduction and mortality rate) decelerated caterpillar development. After 2030, pupation occurred before summer drought can play a role and caterpillar development is no longer decelerated. Avoiding limited caterpillar growth in the parameter settings leads to an acceleration of caterpillar development. The acceleration is less pronounced after 2040 (year 100). This is caused by the fact that after 2040, caterpillar growth is less limited by grass growth; daily average temperatures usually exceed 7˚C and caterpillar development is not hampered by a shady and cool microclimate.

We indicated the period when butterflies can be encountered on average in Fig. 5.1. This figure illustrates that the species can escape from adverse summer conditions (drought, extreme rainfall, extreme hot weather) by advancing its phenology.

### 5.3.2 Effect of habitat amount and patch size under climate change

By increasing either amount of habitat or patch size, we observe a sudden transition from unviable to viable populations, suggesting a sharp threshold in the physical conditions for population viability. In this particular case, average occupancies of landscapes increase sharply from 0 (all patches empty; graphs at left and top of Fig. 5.2) to 1 (all patches occupied; graphs at right and bottom) while increasing patch size from 0.4 to 0.8 ha with an amount of suitable habitat of 0.5%, while increasing patch size from 0.2 to 0.4 ha with an amount of suitable

**Figure 5.1 (next page)**

Moving averages (30 days) of mean daily temperature (˚C – in black) and precipitation surplus (mm – in grey) and standard deviations (dashed lines). Weather variables are calculated for time slots 1981-2009 (indicated as 1995), 2026-2054 (indicated as 2040), and 2072-2100 (indicated as 2085). Timing of average flight periods resulting from model runs is indicated in the graphs. [a]: Weather variables for time slot 1981-2009 are calculated with historical weather data, which does not concern any climate scenario; hence, the graphs for 1995 are identical.

| time slot | climate scenario | |
|---|---|---|
| | W | W+ |



mean daily temperature (°C – in black) and precipitation surplus (mm – in grey)

1995 [a]

2040

2085

day number    (100 = April 10, etc)        day number
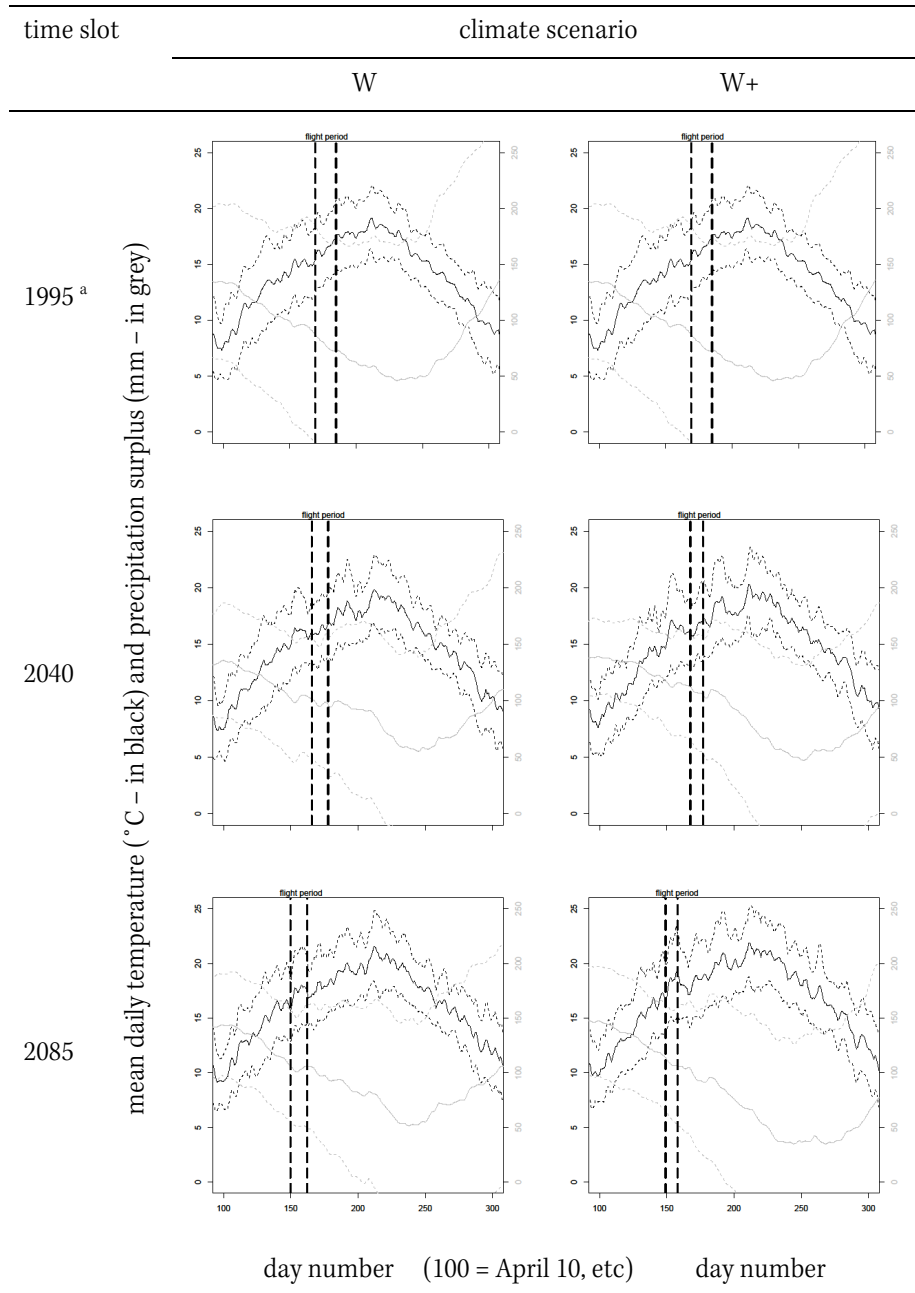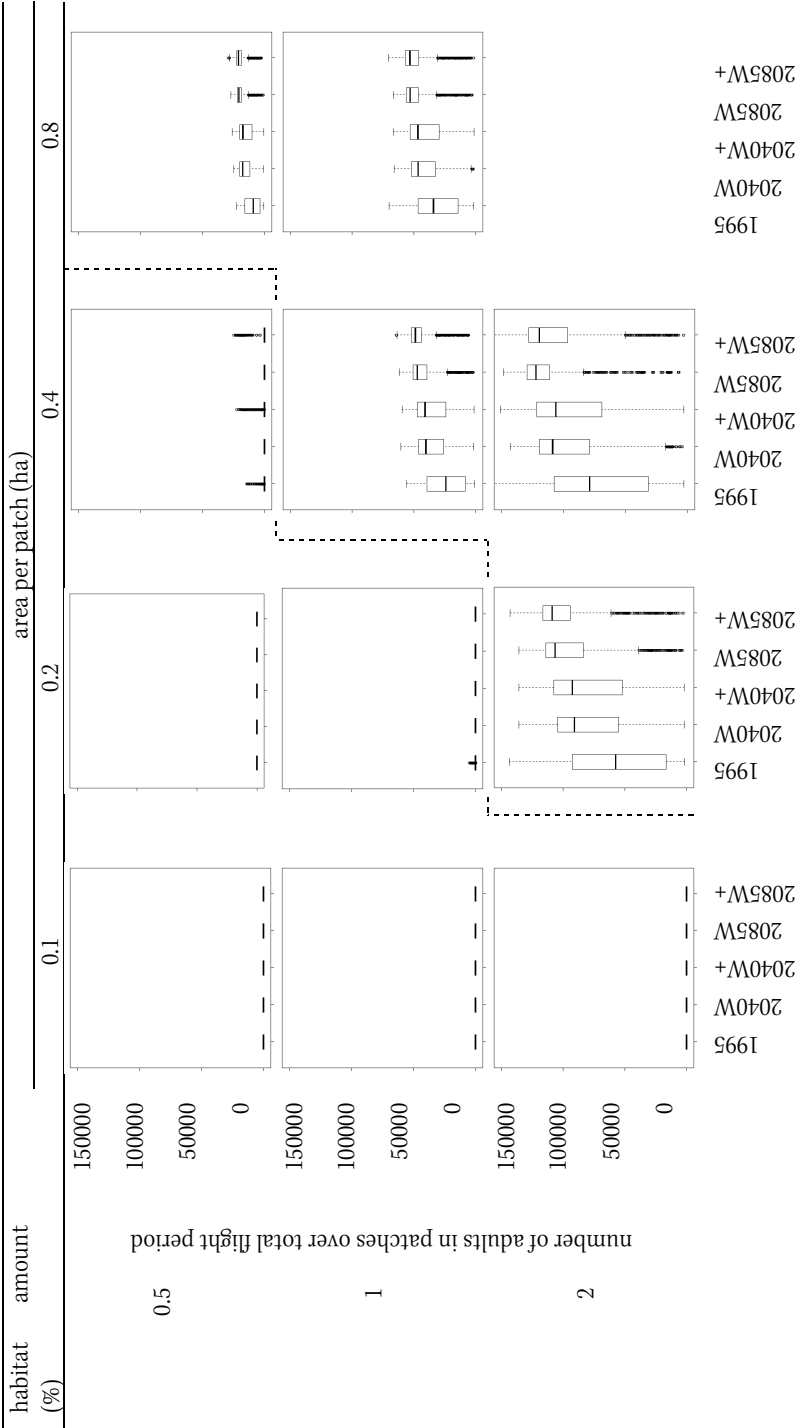
**Figure 5.2** Boxplots for number of adults in patches over total flight period in time slots. Boxplots are shown for different simulation landscapes.
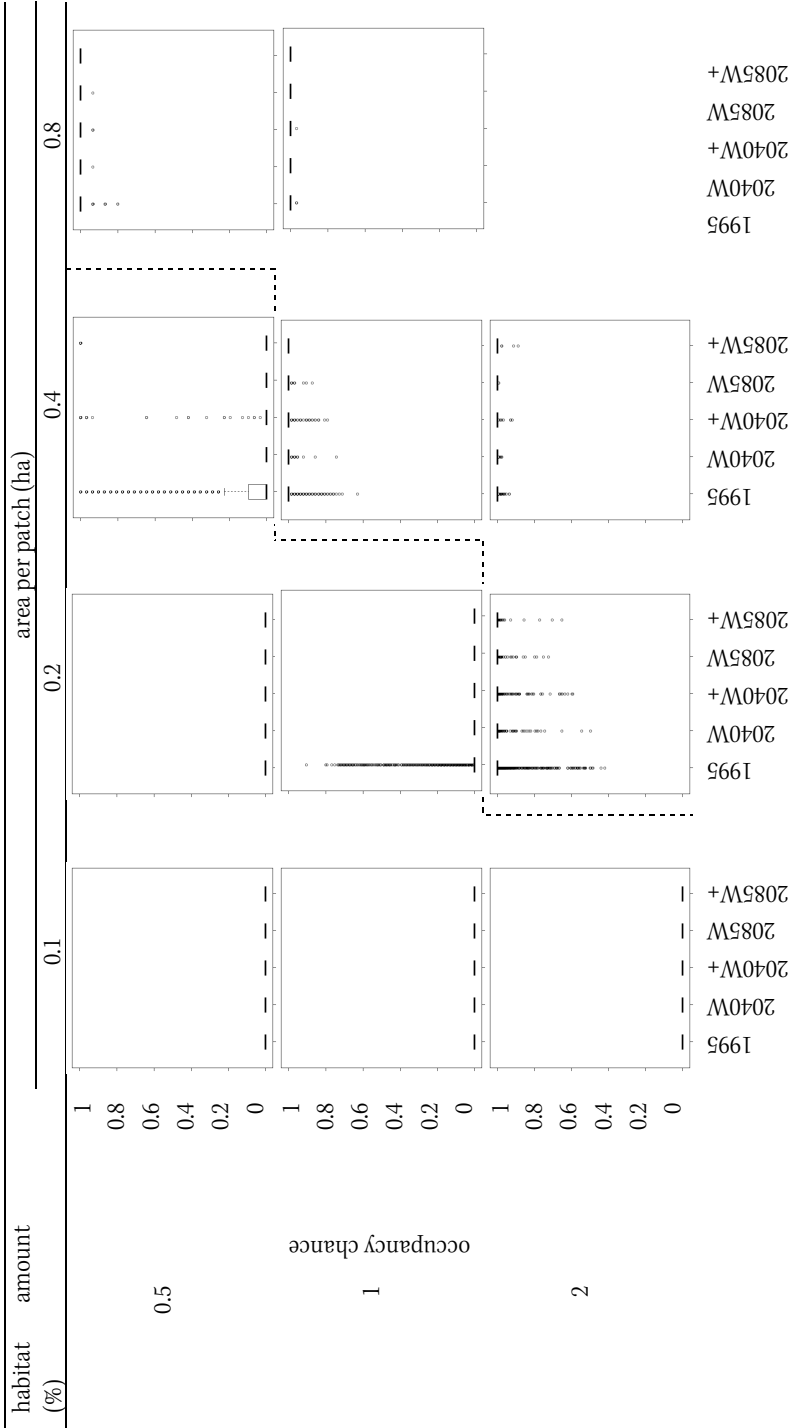
**Figure 5.3** Boxplots for occupancy chance in time slots. Boxplots are shown for different simulation landscapes..

habitat of 1%, and while increasing patch size from 0.1 to 0.2 ha with an amount of suitable habitat of 2%. There are no significant differences between W and W+ scenarios within time slots. Under the same spatial conditions, average adult numbers shift sharply from 0 (or a decrease to 0 within at most the first 70 simulation years) to a gradual increase over time for both W and W+ scenarios (Fig. 5.3). Doubling habitat amounts or patch size on both sides of the threshold sorts similar effects on population viability. In this particular case, the landscape with suitable habitat amounts of 0.5%, distributed over habitat patches of 0.8 ha would be the financially most profitable landscape of the tested landscapes, with the smallest amount of habitat, which is still sustainable to the species.



a                                                                    b
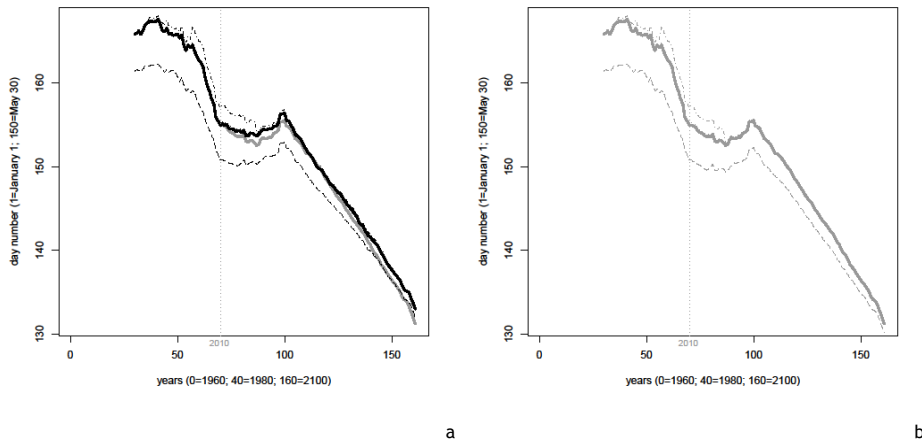
**Figure 5.4**

Sensitivity to parameter settings for landscape with suitable habitat amounts of 0.5, distributed over habitat patches of 0.8 ha, on moving averages (30 years) of day number of start of pupation, which decreased over time under default parameter values (bold solid lines). We increased standard caterpillar mortality rate with 10% (dashed lines), we enlarged the effect of drought on caterpillar development by increasing both growth reduction and caterpillar mortality rate during weight loss with 10% (dotted lines) as well as with both 50% (dotdashed lines), and we avoided limited caterpillar growth (longdashed lines); black lines: W scenario; grey lines: W+ scenario.

## 5.4 DISCUSSION

This paper describes a novel approach to understanding the combined effects of habitat fragmentation and climate change using a detailed individual-based metapopulation model in combination with detailed daily weather data. This model could be used to assess landscape patterns and suggest adaptation options. We cannot stop climate change, but it is within our circle of influence as ecologists to suggest landscape adaptation. Climate change has two aspects important to nature: the global warming and gradual changes in precipitation patterns on the one hand, and the increase in variability of the weather on the other hand. While the global warming is expected to have positive effects on many butterfly species at the northern edge of their range (e.g. Settele et al. 2008), the increasing frequency of weather extremes is expected to have adverse effects (Parmesan et al. 2000; Piessens et al. 2009; Verboom et al. 2010). Explorations with the model revealed that under the current settings the combined effect of augmented weather variability and climate warming resulted in improved conditions for the model butterfly species, illustrated by increased population sizes and habitat occupancy in a fragmented habitat pattern. Our findings indicate that potentially detrimental effects of weather variability did not occur because of a phenological shift in the moment of phase change of caterpillars and pupae. This effect was found in the two climate change scenarios, which both imply an average global temperature rise of 2˚C from 1990 till 2050, and assume an increased occurrence of mild wet winters and warm dry summers for one of the scenarios (W+). The experiments also suggested a sharp viability threshold with a changing landscape pattern: landscape patterns appeared to be either sustainable with all patches occupied, or unsustainable. This all-or-nothing result is due to the large local population sizes (hence, minor contribution of demographic stochasticity) and the fact that all patches were of equal habitat size and quality, and faced equal weather conditions. In real landscape, not only does the weather vary in space (precipitation more than temperature) but also microclimatic heterogeneity will occur, due to slope, vegetation, soil type and other local characteristics.

Varying habitat amount and patch size had a similar impact on population performance. Such a sharp threshold in response to landscape pattern change was found before (e.g. Levins 1970; Lande 1987; Bascompte & Sole 1996) in studies using patch occupancy or spatially explicit metapopulation models. It represents

the metapopulation threshold where colonization rate and local extinction rate are balanced.

### 5.4.1 No negative climate impact due to phenological shift

We show that for the parameter settings used here, average total adult numbers, and hence population viability gradually increase over time for both W and W+ scenarios. This is in agreement with the increase in average global temperature predicted in both scenarios, which has an impact on development and adult activity (see Table 5.2). On the other hand, the increase of dry summer periods expected for the W+ scenario could impede adult activity and caterpillar development, causing negative impacts on population performance. However, we did not find any difference in population viability between scenarios W and W+.

The interruption in the acceleration of caterpillar development between 2010 and 2040 (years 70 to 100; Fig. 5.4) is caused by the shift from historical weather data as model input (up to 2009) to transformation data on future weather (i.e. after 2009) that is derived from transformations of historical weather series, taking the climate around 1990 (1976-2005) as a basis. Changed weather conditions that actually occurred between 1990 and 2010 are therefore not accounted for in the transformation series: the transformed data underestimate the rate of climate change when compared to real change in the period 1990-2010, and especially the record hot years in 2005-2010.

Advanced timing of caterpillar development due to climatic warming can also be inferred from empirical studies showing advancing butterfly emergence (Roy & Sparks 2000; Van Strien et al. 2008). Sparks and Menzel (2002) state that in the UK, most butterfly species have already been affected by climatic warming. Trends to earlier first and peak appearance have been noted, and most of these correlates well with temperature (Roy & Sparks 2000). Data on pupation and emergence dates for Purple Emperor butterfly (*Apatura iris*) shows an advanced emergence of on average 9 (males) to 12 (females) days per decade (Dell et al. 2005). Emergence dates related strongly to spring temperatures, particularly with increasing daily maximum temperatures for the months March to May. The rise in spring temperatures especially influenced late larval instar growth and development. A negative consequence observed with earlier emergence dates is the occurrence of lethal extra broods in typical univoltine species; early instars of

individuals emerging in cold autumn conditions suffer from food shortage due to leaf fall (Dell et al. 2005). However, from empirical studies it is unclear how earlier emergence is related to population abundance (Roy & Sparks 2000). Our simulations suggest a link between population size and emergence date that is of special importance in the light of climate change. Advancing phenology may thus result in an avoidance or reduction of adverse drought conditions during summer.

### 5.4.2 Perspectives for conservation

As advanced timing of development improves conditions for our model butterfly species, climate change does not necessarily sort negative impacts on population performance. It is clear, however, that this applies specifically to a univoltine species with butterflies emerging in late spring or early summer. It is therefore unlikely that this result can be generalized to species with different life-histories. Thus, butterflies emerging later in summer may be expected to suffer more heavily from summer droughts, despite possible phenological shifts.

In any case, viable populations only persist in sufficiently suitable landscapes, concerning juxtaposition and sizes of habitat patches. We have shown that either varying the amount of suitable habitat or patch size revealed a sharp threshold in population viability, and this is consistent with metapopulation theory (e.g. Levins 1970). Hence, further habitat fragmentation will eventually result in regional loss of species. Species requirements on patch carrying capacity and interpatch distance should unabatedly be considered.

### 5.4.3 Perspectives for further research

Developing detailed models is constrained by available knowledge and data necessary for model construction and parameterization (Gallien et al. 2010). Systematic fieldwork and laboratory experiments are necessary to unravel the exact relationship between weather and activity, development and/or survival of the different stages of butterflies.

We suggest that the model can be improved by adding heterogeneity in the landscape, e.g. by varying the weather variables from patch to patch, and possibly also within patches, mimicking different microhabitats with different microclimates. A perspective of our approach would be to apply our model in series of realistic landscapes, including unequal patch sizes and heterogeneous, climate-dependent

habitat quality. Our study can be extended by experiments in which the performances of several taxonomic groups or 'ecoprofiles' (species requirements on patch carrying capacity and interpatch distance, see Opdam et al (2008)) will be compared. We propose to incorporate a greater variation in life-history traits, such as timing of development, that reflects susceptibility to climate change. In these ways, generalizations of landscape adaptation rules will be allowed for.

# 6

# Host plant-mediated effects of climate change on the occurrence of the butterfly Alcon blue *Phengaris alcon*

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Ruut M.A. Wegman

ABSTRACT

Among the expected consequences of climate change are shifts in species' ranges. Most current methods to predict such shifts in distributions consider changes in suitability of climatic conditions for existence. With these models, it is possible to indicate the potential distribution of species that would arise under spatial conditions that cause unlimited accessibility and habitat suitability. At the regional scale however, detailed predictions of changes in species distributions and performance are pivotal for conservation planning. This study aims to predict climate-induced changes in occurrences of species at the regional scale, incorporating demographic processes and dispersal to assess habitat accessibility and suitability in detail. We investigated a system with trophic dependence: the Alcon blue butterfly *Phengaris alcon* is fully dependent on the occurrence of its host plant species. We applied a model chain, consisting of a soil and biomass model, a plant species occurrence and dispersal model and a metapopulation model. We investigated the effect of climate change, both under affected and unaffected habitat conditions as determined by host plant occurrence. Our results show that the modeled butterflies perform best when habitat conditions remain unaffected by climate change. However, when climate change does affect the occurrence of its host plant species, butterfly distribution and performance will be deteriorated. This implies that detailed predictions of changes in species distributions and performance should incorporate dispersal, demographic processes and biotic interactions explicitly. Our approach allows for identification of locations that are potentially suitable for measures increasing network robustness for *P. alcon*.

## 6.1    INTRODUCTION

Climate change is considered to have major effects on ecosystem functioning and biodiversity. Among the expected consequences of the ongoing climate change are shifts in species' geographic ranges (Zurell et al. 2009; Maggini et al. 2011). In geographical space, species can adapt by modifying their distribution, following favourable climatic conditions and habitats. Most current methods to predict such shifts in distributions consider changes in the suitability of climatic conditions for existence (Akçakaya et al. 2006; Settele et al. 2008; Brook et al. 2009). Such climate-envelope models however implicitly assume equilibrium under current conditions, and incorporate neither dispersal, demographic processes nor biotic interactions explicitly (Zurell et al. 2009). With these models, it is possible to indicate the potential distribution of a species that would arise under spatial conditions that cause an unlimited accessibility and habitat suitability. At the regional scale however, detailed predictions of changes in species distributions and performance are pivotal for conservation planning and policy making (Zurell et al. 2009). Studies that investigate species occurrence at this scale and that consider dispersal, demographic processes nor biotic interactions explicitly hardly exist. This study aims to predict climate-induced changes in the occurrences of species with a trophic dependence, incorporating demographic processes and dispersal.

The occurrence of species is controlled by the configuration of the landscape at the regional scale. Dispersal and demographic processes (like reproduction or mortality) often depend on the spatial context (e.g. size, shape, location and number of populations/patches) (Brook et al. 2009). Below a critical threshold in configuration, the expansion of ranges as a result of global temperature rise will be hampered and species may rapidly become extinct (Travis 2003; Opdam & Wascher 2004). Moreover, the increased frequency of extreme weather events will cause overall range contraction, especially in regions with a relatively low spatial cohesion (Opdam & Wascher 2004).

The configuration of the landscape may however change in time as a result of shifting habitat use and suitability (Brook et al. 2009). Thomas et al. (2001) found a significant broadening of the range of habitats used by Silver-spotted skipper, *Hesperia comma*, spreading into north-facing hill slope habitats that were previously climatically not suitable. Hence, at the regional scale spatial cohesion and

habitat suitability interact and change at the same time due to climate change. Yet at this scale detailed predictions considering species occupancy are essential for nature conservation planning – also on the long term. Therefore, a modeling approach is required, that incorporates dispersal and demographic processes. Thus we can track how multiple biotic and abiotic factors interact to affect animal populations through time by applying such models. This involves translating impacts on ecosystem processes resulting from climate change (e.g. changing plant growing conditions) into temporal trends in wildlife habitat, explicitly considering the influence of habitat suitability and availability on population performance (McRae et al. 2008).

In this study we investigated the influence of climate change on habitat suitability and configuration of the Alcon blue butterfly *Phengaris alcon*, a species that is fully dependent on the occurrence of its only host plant species. We investigated the distribution and performance of *P. alcon*, both under affected and unaffected habitat conditions. To simulate affected habitat conditions, we incorporated the impact of climate change on plant growing conditions in terms of pH, nitrate concentration, and mean lowest, spring, and highest groundwater levels. These are the main abiotic soil factors that affect the potential distribution of Common heather *Calluna vulgaris*, Cross-leaved heath *Erica tetralix*, and Marsh gentian *Gentiana pneumonanthe*. The coexistence of these plant species is required for the existence of *P. alcon*. Moreover, *P. alcon* as well as *G. pneumonanthe* show limited dispersal abilities and are hence expected to be negatively impacted by habitat fragmentation. We assessed the actual distribution of the plant species with a plant dispersal model, which supplied the spatial context for *P. alcon*.

## 6.2 METHODS

In the Netherlands, *P. alcon* is an endangered myrmecophilous butterfly. Eggs are deposited on the flowerheads of the host plant *G. pneumonanthe*. The caterpillars depend on *G. pneumonanthe* during the first three larval instars and are then adopted by ant species from the genus *Myrmica*. The butterfly emerges most often between early July and mid-August. The Netherlands harbors a large part of the European lowland populations of *P. alcon* (Wynhoff 1998). These occur mostly on seminatural wet heathland and partly on fen meadows. There has been a steady decline of *P. alcon* since the 1960s under the influence of habitat loss and

degradation (WallisDeVries 2004). To investigate the cascade of effects of climate change on habitat availability and butterfly distribution and performance, we applied a model chain including soil and vegetation processes, plant dispersal, and animal metapopulation models. A schematic overview of the use of the models is given in Fig. 6.1. Below we explain all models briefly.



**Figure 6.1**
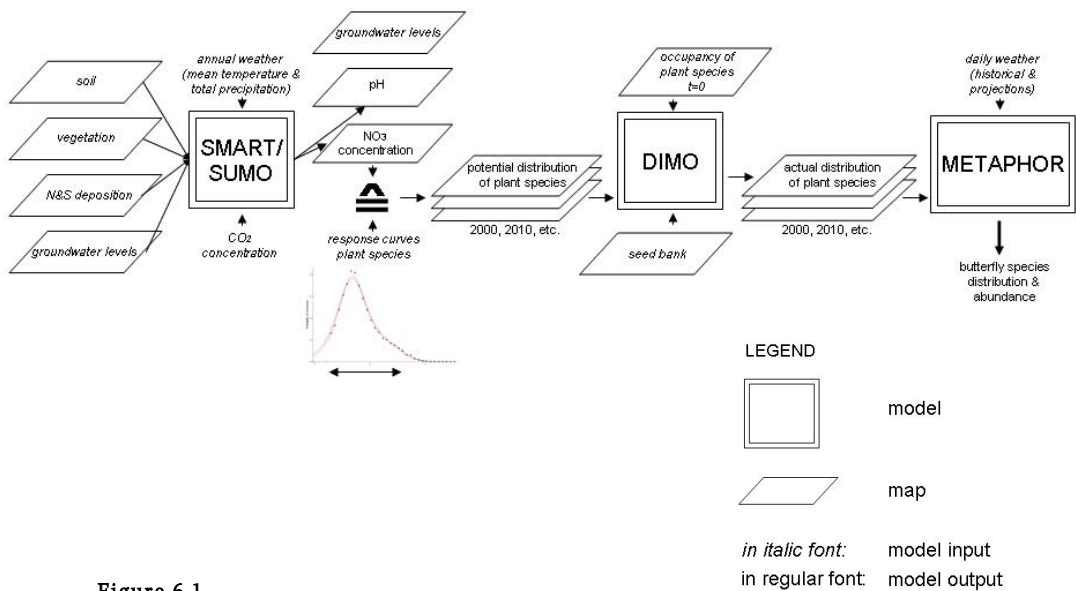
Schematic overview of the cascade of applied models SMART2-SUMO2, DIMO, and METAPHOR, including their main input and output

*6.2.1 SMART2-SUMO2*

The vegetation and soil processes were simulated by applying the models SMART2 (soil) and SUMO2 (vegetation). The models have a time step of one year and exchange information on a yearly basis. The model SMART2 (Kros 2002; Mol-Dijkstra et al. 2009) considers biotic and abiotic processes in the soil solution and the solid phase. It represents the inorganic soil and two organic soil compartments. The model consists of a set of mass balance equations, describing soil processes and input–output relationships. The soil solution chemistry depends on the net element input from the atmosphere and groundwater, canopy interac-

tions, geochemical interactions in the soil ($CO_2$ equilibriums, weathering of carbonates, silicates and/or aluminium hydroxides, $SO_4$ sorption and cation exchange), and nutrient cycling (litterfall, mineralisation, root uptake, nitrification and denitrification). Nutrient uptake by the vegetation and litterfall (including dead roots and dead wood) are provided by SUMO2. SMART2 delivers the nitrogen availability to SUMO2 as the sum of external N input and mineralisation. Solute transport is described by assuming complete mixing of the element input within one homogeneous soil compartment with a constant density and fixed depth.

Like SMART2, SUMO2 (Wamelink et al. 2009; Wamelink et al. 2009) is a process-oriented model that simulates vegetation succession and biomass production. The biomass amount is simulated for five functional types (FT): herbs and grasses, dwarf shrubs, shrubs, and two site specific tree species. The five FT compete with each other for nutrients, light, and moisture. Annual mean temperature and carbon dioxide concentration influence the maximum growth of the FT. Competition for nutrients is based on the relative biomass present in the roots of the FT. Actual biomass growth of each FT is the result of a reduction of the maximum growth by moisture, nutrient and light availability. The biomass can also be reduced as a result of management. Mowing and sod cutting imply the removal of biomass and thus carbon and nutrients from the system. SUMO2 requires information on the initial vegetation type and the management. Management is usually unknown and is therefore based on the vegetation type. In this study grassland is mown once each year, and sod cutting takes place in heathland every 30 years. Since the modeled butterfly does not occur in forest, this vegetation type was not included in the model runs. The model is initialized for 10 years to adjust the biomass and nutrient content to the local circumstances. SMART2 calculates the soil pH and nitrate concentration, which were used to calculate the plant species occurrence. Output was generated every ten years from 1990 till 2100.

### 6.2.2 Selected plant species

Species occurrence was simulated for three species, *Calluna vulgaris*, *Erica tetralix*, and *Gentiana pneumonanthe*. *G. pneumonanthe* serves as a host for both the eggs as well as the caterpillars for *P. alcon*. *C. vulgaris* and *E. tetralix* serve as nec-

tar plants. We assumed that not only the hosts for the butterfly species should be present in the habitat but also the main nectar sources for the adult stage.

### 6.2.3 Plant species abiotic preferences

We used specific ranges of occurrence of the species for soil pH, nitrate concentration, and mean lowest, spring, and highest groundwater levels. Response functions per species abiotic factor combination were estimated from field measurements. Ranges for the species where defined as the interval between the 5 and 95 percentile of the response curve (Table 6.1). For an explanation of the method see Wamelink et al. (2005). Soil pH and nitrate concentration were provided by SMART2. The groundwater levels were derived from a map and influenced by climate scenarios, providing different groundwater levels in time for each scenario. If the simulated abiotic conditions by the SMART2-SUMO2 were below the 5 percentile (pH) or above the 95 percentile (nitrate and groundwater levels) we assumed that the species cannot germinate and/or survive. This resulted in three series of potential species occurrence maps (one per species per output year), which were used as input for the model DIMO.

### 6.2.4 DIMO

DIMO is a spatially explicit model simulating dispersal capacity of plant species including wind dispersal, dispersal via animals (internal and external), vegetative dispersal, and several forms of self-inflicted dispersal (Wamelink et al. 2011). Barriers such as roads and rivers as well as unsuitable vegetation types are reducing the dispersal possibility and speed. Spatially explicit data about the current and past occurrence of plant species is based on extensive surveys in the Netherlands since the 1920s (600.000 records stored in Turboveg, Hennekens & Schaminée 2001). From the inventories the present distribution and the presence of a viable seed bank is derived. A species can (re)appear in a grid cell either by dispersal or from a viable seed bank. The establishment of a species also depends on the biotic and abiotic quality, which is derived from SMART2-SUMO2 and the abiotic

**Table 6.1**

Ecological ranges in terms of probability of occurence for pH, nitrate (NO3; in mg/kg), mean spring groundwater level (msl; in cm below surface) and mean lowest groundwater level (mll) for the plant species. The ranges for the species were defined as the 5 and 95 percentiles of their occurrences in the field. The values in italic were not used for the species model, because they contain no ecological information. As an example, the response curve and ecological range for pH for *C. vulgaris* is given.

| | pH | | $NO_3$ (mg/kg) | | msl (cm bs) | | mll (cm bs) | |
|---|---|---|---|---|---|---|---|---|
| percentile | *5* | *95* | *5* | *95* | *5* | *95* | *5* | *95* |
| species: *Calluna vulgaris* | 4.5 | 5.6 | *7* | 24 | 14 | 67 | *113* | *208* |
| *Erica tetralix* | 4.6 | 5.6 | *7* | 23 | -4 | 48 | 37 | *193* |
| *Gentiana pneumonanthe* | 4.7 | 5.6 | *7* | 21 | -6 | 32 | 50 | *132* |



ranges of the species. Species specific data to parameterize the model were derived from the LEDA-database (www.leda-traitbase.org, Kleyer et al. 2008). The dispersal capacity is corrected with a germination delay to account for fernalization time and the time it takes from germination till seed production. All parameter values are species-specific.

DIMO was used to 'correct' the species potential distribution maps based on the species abiotic preferences. The corrected maps (i.e. dynamic maps of distribution) were subsequently used as input for the METAPHOR model.

*6.2.5 METAPHOR*

METAPHOR (Verboom et al. 2001; Vos et al. 2001; Schippers et al. 2009) is a spatially explicit, individual-based model that simulates the dynamics of an animal (meta-)population. The model was modified by allowing time steps of one day, a stage structured population, and daily weather (past records or future projections) as input, as is described in detail in Appendix 6.1 (see for further explanation Chapter 5).

Here, METAPHOR models population dynamics of a scarce species in the centre of its range that is fairly immobile and, therefore, potentially affected by habitat fragmentation: the Alcon blue. Parameter settings were derived from literature and expert knowledge. Each individual has 4 or 5 life cycle phases: egg, caterpillar, pupa, for female an unfertilized and a fertilized adult phase, and for male only one adult phase. The butterfly species is univoltine and overwinters as half-grown caterpillar. METAPHOR describes the spatial dynamics of a (meta)population in discrete time, with time steps of one day. Each day, individuals have a chance to change phase (e.g. hatch, pupate, become fertilized), to die (mortality), to reproduce (only fertilized female adults) and to move (only adults). Processes development/phase transition, mortality, reproduction, and movement determine the magnitude and structure of subpopulations and, thus, direct population dynamics. The first event in a new day is development, or change to the next phase. Next, reproduction occurs. Then, individuals can move, and finally, mortality takes place. In these processes, we implemented as many weather effect as we found to be relevant from literature and our own field experiments (Table 5.2 and Chapter 2).

In the landscapes of the input maps supplied by DIMO, all habitat grid cells have equal quality, and the weather is equal for all habitat grid cells. The left and right sides and the top and bottom sides of the maps were merged in a toroidal way. A run starts on January 1 with the present landscape (2000), with those habitat grid cells occupied with 1000 caterpillars where *P. alcon* currently occurs (based on km-square resolution distribution data of 1990-2009 from Dutch Butterfly Conservation), and continues for 161 years (58765 time steps; no intercalary years). We performed runs with a 'static' – i.e. the present landscape is continuously used as model input - or a 'dynamic' landscape. In case of a dynamic landscape, every ten years another landscape was used as input to the model from year 2000, based

on the plant species occurrence calculated earlier (and described above). For the years 2010-2019, the 2010 landscape was used as input to the model, etc. For the first 40 years of each run, the weather of the years 1960-1979, derived from the De Bilt meteorological station (www.knmi.nl), located in the centre of the Netherlands, was used as input, followed by once more the 1960-1979 weather. This resulted in 40 years of pre-climate change weather that were used to burn-in the model, as the pattern of occupancy is presumed to be the result of a quasi equilibrium between species, weather, and landscape characteristics. Subsequently, the weather of the years 1980-2009, derived from the De Bilt meteorological station, was used as input. From KNMI data on future daily temperatures and precipitation amounts ([http://climexp.knmi.nl/Scenarios_monthly/](http://climexp.knmi.nl/Scenarios_monthly/)), we calculated future values for weather variables affecting processes in the population for the years 2010-2100. We used KNMI scenarios W and W+, which implies for both scenarios an average global temperature rise of 2˚C from 1990 till 2050, and an increased occurrence of mild wet winters and warm dry summers for the W+ scenario (see [http://www.knmi.nl/research/climate_services/](http://www.knmi.nl/research/climate_services/)). The KNMI data on future daily temperatures and precipitation amounts are transformations of historical weather series (1976-2005). Those are available for various baseline years (every tenth year between 2020 and 2100). Hence, weather data for a single day appears in three different, partly overlapping transformation series. The three projections for weather of a single day can be regarded as independent, because of the 10-year interval. We randomly picked daily values from these series, before we supplied them to the model. In this way, we avoid the persistent reoccurrence of extreme weather in consecutive years, as might arise from using the historical weather in their native state. For a detailed description of the transformation series, see http://www.knmi.nl/research/climate_services/. We generated ten weather series from the KNMI data on future daily temperatures and precipitation amounts. Hence, ten runs per climate scenario were conducted for each landscape; thus in total 2200 runs were conducted.

Indicators for population performance used are total adult numbers and habitat grid cell occupancy of the landscape, summarized per scenario and over all habitat grid cells (10 runs). The occupancy, or the average fraction of occupied habitat grid cells during the period the population was extant, was calculated as an ecological measure of fragmentation effects (Hanski 1994). Average population viability in years 1981-2009 (indicated as 1995), 2026-2054 (indicated as 2040), and

2072-2100 (indicated as 2085) were used to present results, as well as population viability continuous through time, both for the four situations (W_stat, W_dyn, W+_stat, and W+_dyn).
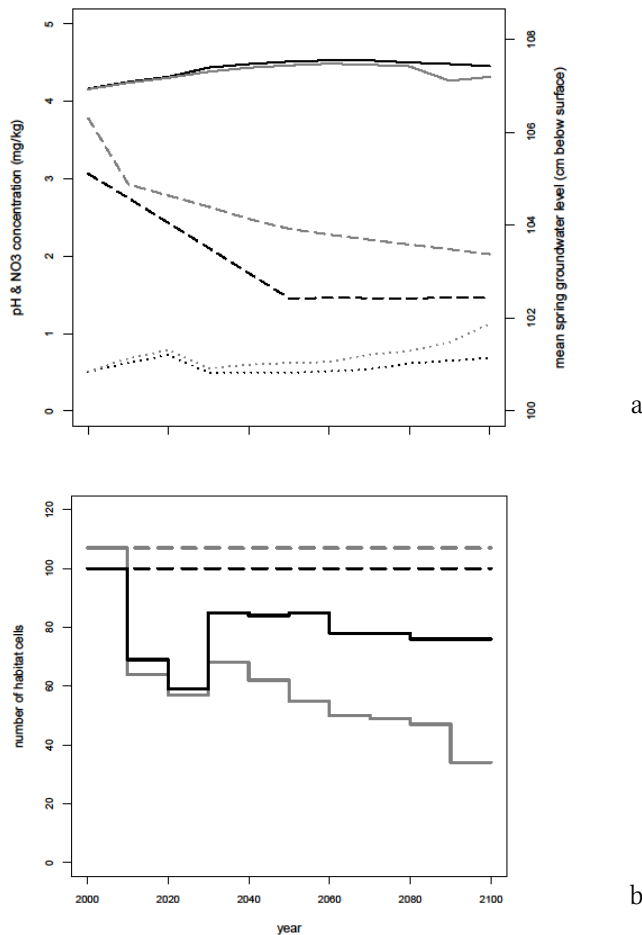


**Figure 6.2**

pH (solid lines), $NO_3$ concentration (in mg/kg, dotted lines), and mean spring groundwater level (in cm below surface, dashed lines) for W (black) and W+ (grey) scenarios through time (a); and number of habitat cells through time, for W (black lines) and W+ (grey) scenarios under static (dashed) and dynamic (solid) landscapes (b)

## 6.3 RESULTS

Climate change is expected to affect habitat conditions mostly by changes in $NO_3$ concentration and groundwater level. In Fig. 6.2a, pH, $NO_3$ concentration (both SUMO output) and mean spring groundwater level is given for 2000-2100 for the two climate scenarios. The pH is fairly constant over time, since weathering (increasing pH) and desiccation due to nitrogen deposition hardly takes place. The $NO_3$ concentration shows a divergence between the two climate scenarios; in 2100 the $NO_3$ concentration under the W+ scenario is almost twice as high as under the W scenario. This is reflected in the number of suitable habitat cells. Under dynamic landscape situations, the number of habitat cells decreases with 24% (W) and 68% (W+) until 2100 (Fig. 6.2b). The mean spring groundwater level decreases under both scenarios, where the level stabilizes at a lower level for the W scenario than for the W+ scenario, where the level continuously decreases (Fig. 6.2a).

The grid cells where *C. vulgaris*, *E. tetralix*, and *G. pneumonanthe* coexist in 2000 according to DIMO are indicated as *P. alcon* habitat in Fig. 6.3. The climate and landscape situations do not show major differences in occupancy pattern, with cells with relatively high occupancy in the southwest and northeast of the landscape. All situations show habitat grid cells that are continuously unoccupied but persisting until 2100. These cells are potentially suitable for measures increasing the robustness of the network for *P. alcon*.

The number of adults that emerge in any of the habitat grid cells during the total flight period highly fluctuates over time due to weather influences (Fig. 6.4). On average, the number of adults increases between 2010 and 2070 for all four situations. The increase is more pronounced for the static landscape situations; especially under the W+ scenario, the number of adults is significantly higher than under the other situations (Fig. 6.5). The factor landscape situation (dynamic/static) sorts more effect on the number of adults ($P_{2040}=0.028$; $P_{2085}=0.020$) than the factor climate scenario (W/W+; $P_{2040}=0.214$; $P_{2085}=0.318$). Table 6.2 shows P-values for the main effects of these factors on the number of adults, and their interaction, resulting from ANOVA.
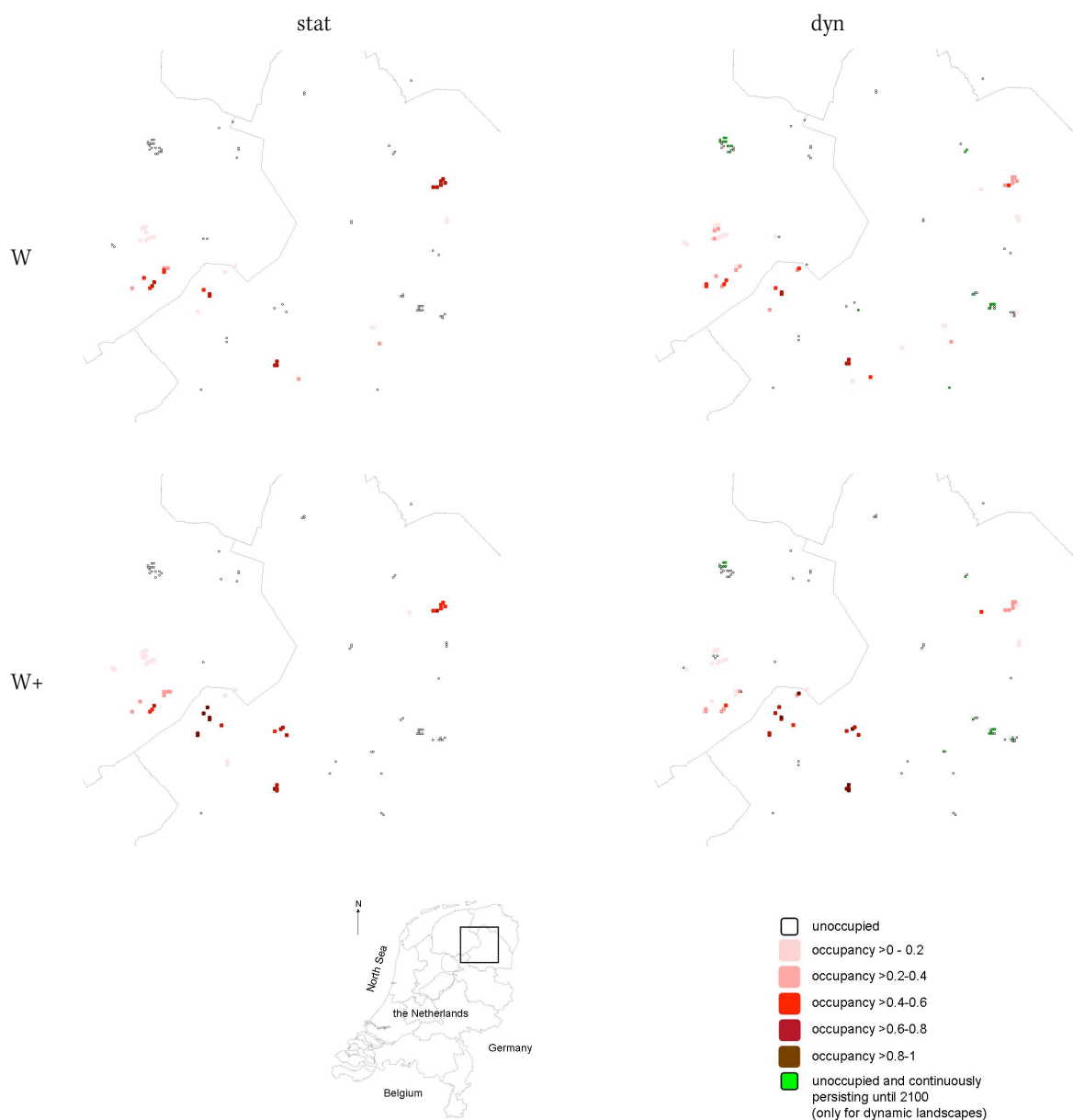
**Figure 6.3**

Occupancy over total run time per habitat grid cell for the four landscape and climate situations; the location of the study area is indicated in map of the Netherlands; grey lines: provincial borders
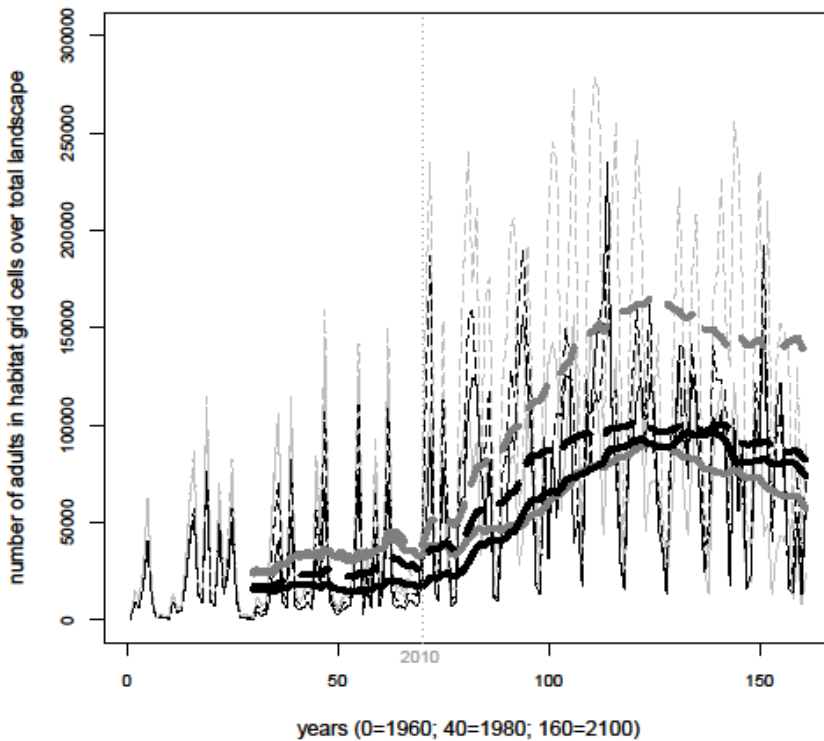
**Figure 6.4**

Number of adults in habitat grid cells over the total landscape through time, for W (black lines) and W+ (grey) scenarios under static (dashed) and dynamic (solid) landscapes, and the 30-year moving averages (bold lines)

## 6.4   DISCUSSION

### 6.4.1 Biotic interactions under climate change

Our results show that the modeled butterflies perform best when habitat conditions remain unaffected by climate change. Especially under the W+ scenario, adult numbers increase over time up to 2070, but seem to decrease afterwards. This means that potentially the W+ scenario would be most beneficial to the butterfly species. However, when this climate scenario also affects the (co-) existence of the required plant species, which happens under the W+_dyn situation,

this climate scenario is no longer most beneficial. In terms of habitat occupancy, the climate and landscape situations showed comparable patterns. All situations show locations with suitable habitat that are continuously unoccupied but persisting until 2100. These locations are potentially suitable for measures increasing the robustness of the network for *P. alcon*.
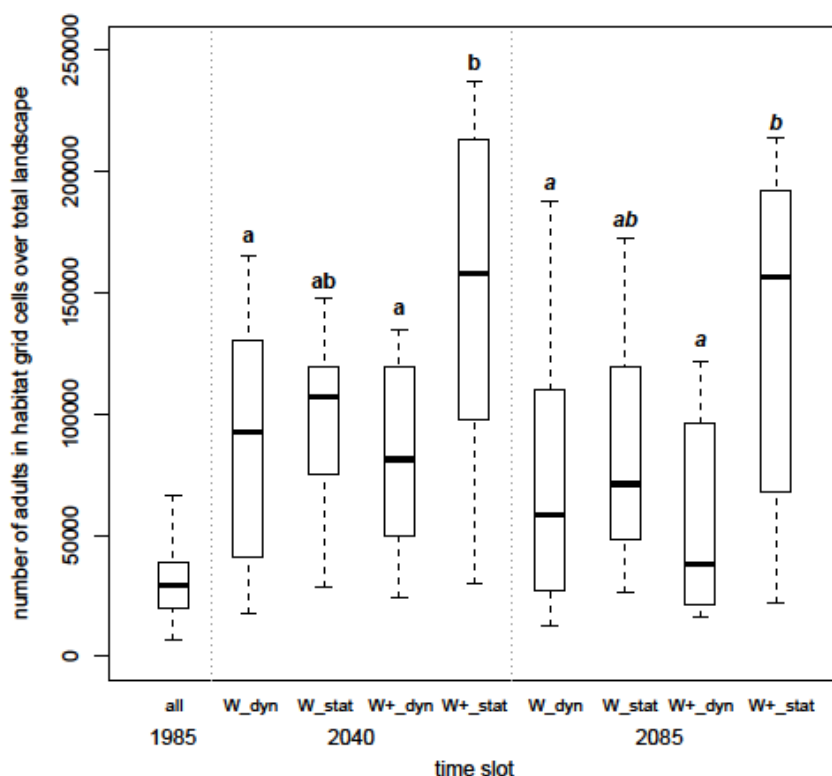


**Figure 6.5**

Boxplots for the number of adults in habitat grid cells over the total landscape for three time slots. For time slot 1995 (1981-2009), climate and landscape scenario are still similar and hence, results are merged. Differences in number of adults per situation are indicated with letters above the boxplots per time slot (P>0.05; regular font for 2040, italic font for 2085).

**Table 6.2**

The importance of factors landscape situation (dynamic/static) and climate scenario (W/W+), and their interaction. Importance results from ANOVA and is expressed by P-values.

| Time slot | P-value effect climate scenario | P-value effect landscape situation | P-value effect interaction |
|---|---|---|---|
| 2040 | 0.214 | 0.028 | 0.135 |
| 2085 | 0.318 | 0.020 | 0.084 |

From our study we conclude that detailed predictions of changes in species distributions and performance should incorporate dispersal, demographic processes and biotic interactions explicitly. Most current methods use present-day climate–species range relationships to infer the impacts of climate change on species distributions at large spatial scales (Akçakaya et al. 2006; Araújo & Luoto 2007; Brook et al. 2009). Araújo and Luoto (2007) incorporated biotic interactions into their study, involving the effects of climate change on host plant and butterfly species (Clouded apollo *Parnassius mnemosyne*) distributions over Europe, using generalized additive models. Their results show that purely climate-based modelling is insufficient to quantify the impacts of climate change on species distributions. By combining climate-envelope models with dispersal models, Vos et al. (2008) already provoked the assumption that the range of climatically suitable conditions is entirely appropriate for colonization and dispersal. In their study, areas where the spatial cohesion of the ecosystem pattern was expected to be insufficient to allow colonization of new climatically suitable space were identified at biogeographical scale.

*6.4.2 Further model development*

Our method is advantageous for application at the regional scale by allowing for the explicit incorporation of dispersal, demographic processes, and biotic interactions. However, for this incorporation we had to make modeling assumptions. We determined e.g. the three main abiotic soil factors that determine the potential host plant distribution. However, other factors that may change with climate change, e.g. phosphorus availability or temperature preferences of the plant species may influence distribution patterns in an unknown way. Another assumption

we made concerned the size of the interval of the response curve that determined the range of occurrence of the host plant and nectar plant species. Defining an interval between the 1 and 99 percentile would broaden the range of occurrence, and hence possibly extend the host plant distribution. Thirdly, our parameterizations of species specific dispersal capacities are most probably underestimated. In reality, rare long-distance dispersal events occur with low frequencies. Such events are not included in the model, which could again result in an underestimation of the host plant distribution (Soons & Ozinga 2005). However, since our butterfly possesses a very low dispersal capacity, we expect this would not significantly affect our results. A fourth assumption encompasses our modeling design. *P. alcon* caterpillars pass their last instar phase in the nests of various *Myrmica* ants, which they parasitize, being fed by the worker ants. They hibernate and pupate in the ant nests (WallisDeVries 2004). The presence of these ants and their nests are not incorporated in the model train explicitly. We assume, that the presence of the various *Myrmica* species is not a limiting factor. If the distribution of the ants in the landscape is less pronounced than assumed here, this would influence the occurrence of the butterfly in a negative way. This would result in an overestimation of the butterflies' occurrence by the model. However, we expect the sustainable occurrence of the butterfly not to be limited by the distribution of the ants.

Measures increasing network cohesion could imply investments in network density and connectivity or habitat suitability (Opdam et al. 2003; Vos et al. 2008). The necessity to implement landscape adaptation seems not to be urgent for *P. alcon*. Nevertheless, with our approach we identify promising locations for the implementation of adaptation measures. By comparison of the maps in Fig. 6.3, we can at least recognize locations for 'no-regret' measures. In the case of *P. alcon*, these are sites where the species exists with a relatively high occupancy chance. To guarantee the regional persistence of the species, it is preferential to prevent for other activities in these locations. On the sites that are continuously unoccupied but persisting until 2100, active reintroduction of *P. alcon* caterpillars could be applied, as was done for other butterflies earlier in North-West Europe (e.g. Lewis et al. 1997). These grid cells are located at too isolated positions to be reached by *P. alcon* adults on dispersal in the current landscape setting. By active reintroduction, stable populations can be created till at least 2100. This is not necessary for the regional persistence of the species, but can be desirable to im-

prove biodiversity standards at these sites. Thus, based on our approach, that allows to incorporate dispersal and demographic processes, scientifically defensible environmental management and conservation planning decisions can be made for the regional scale.

## ACKNOWLEDGMENTS

## APPENDIX

### Appendix 6.1

METAPHOR describes the spatial dynamics of a (meta)population with time steps of one day. Each day, individuals have a chance to change phase (which is evoked by daily growth for caterpillars), to die (mortality), to reproduce (only fertilized female adults) and to move (only adults). In these processes, we implemented as many weather effect as we found to be relevant from literature and our own field experiments (Chapter 2 and Table 5.2). The model is stochastic for all processes. Egg hatching depends on daily temperature (˚C), which is summed for the days the individual is in its egg phase until a specified temperature threshold (see Table 6.2 for formulas and parameter values). When the summed daily temperature exceeds this threshold, the egg has a chance to hatch (cf. Salpiggidis et al. 2004). Egg mortality depends on air humidity (%); with a decreased air humidity, egg mortality increases (Warren 1992). Caterpillar development depends on individual growth in weight (10-4 g), which increases with daily temperature when this temperature exceeds 7˚C (temperature threshold for caterpillar activity, cf. Kingsolver et al. 2004). This increase in growth is limited when daily temperatures are more often between 0˚C (temperature threshold for grass growth) and 7˚C than in former, cooler times (1960-1990). In this case, relatively fast grass growth leads to a shady and cool microclimate, limiting caterpillar growth (WallisDeVries & Van Swaay 2006). When individual caterpillar weight exceeds a specified threshold, the caterpillar has a chance to pupate (Jansen unpublished work). Individual caterpillars loose weight when the daily temperature drops below 7˚C. Reduction in (limited or unlimited) growth occurs in periods of drought, when the precipitation surplus becomes negative. In this case, growth is reduced with a specified factor. Weight loss of more than a third of the maximum individual caterpillar's weight ever reached increases caterpillar mortality. Caterpillar mortality is moreover influenced by inundation (assumed to occur when PSPL exceeds 100mm and rainfall takes place continuously over a day) for caterpillars between 9-18 days old. Mortality rate then increases with the duration of inundation. Pupa hatching depends on daily temperature (˚C), which is summed for the days the individual is in its pupa phase until a specified temperature threshold. When the summed daily temperature exceeds this threshold, there is a

chance for adult emergence from the pupa (cf. Stevens 2004). For adults, repro-duction is density dependent; the number of eggs produced per female depends on the number of female adults in the habitat grid cell. The number of eggs produced per female on a specific day further depends on the age of the individual as fertilized female (Brakefield 1982). There is a combination of weather that is unfavourable to adult individuals: the daily maximum temperature does not exceed 18˚C (butterflies will not fly/fly less), or the daily precipitation amount exceeds 3mm and falls on a day with almost continuous rainfall (thus not in showers; butterflies will not fly/fly less), or the precipitation surplus is negative (thus drought can possibly lead to food shortage), or exceeds 100mm. One such day will limit butterfly movement, will decrease the mating chance (equals 'phase' change from unfertilized to fertilized female, also depending on presence of male adult in neighbourhood), and will decrease reproduction. Three consecutive days of these kinds of weather will increase mortality. When weather is favourable, adult butterflies are able to move in a random walk manner, taking a specified number of steps per day (depending on temperature threshold) of a specified length and tortuosity between the steps. Inside-habitat grid cell butterfly movement distance increases with radiation and decreases with temperature. Outside-habitat grid cell movement distance and tortuosity between steps of both inside- and outside-habitat grid cell movement are not affected by weather (based on Chapter 2). An overview of all parameter values is given in Table 5.3.

# 7

# Synthesis and perspectives

## 7.1 SUMMARY AND REFLECTION

This study was carried out to (1) increase our understanding of the influence of weather and climate change on demographic processes (dispersal, reproduction, survival) in faunal populations, and (2) to disentangle the interaction between the influence of weather and climate change on the one hand, and habitat fragmentation on the other hand, on demographic processes in populations. I took birds and butterflies as study species. Considering species characteristics, I showed that dispersal capacity, migration strategy, and diet type correlate to responses of species to changing weather conditions. These responses can be positive – climate change may diminish the effects of fragmentation by enhancing flight behaviour and dispersal of butterflies – or negative – advanced spring timing may lead to mismatches in food supply of passerine birds. I showed that both positive and negative responses at the individual level can lead to parallel responses at the (meta)population level. At these higher organization levels, (meta)population viability is also affected by the landscape pattern. I showed that increasing spatial cohesion, patch size, and amount of suitable habitat can enhance (meta)population viability and recovery under climate change. Such measures are already known to counteract effects of habitat fragmentation (Opdam et al. 2003), but this study shows their additive usefulness in adapting to effects of climate change.

In the following sections, I will first elaborate on the effect of changing weather conditions on faunal species characteristics considering demographic processes. Subsequently, I will reflect on responses of these species under adaptive landscape characteristics. Trait-based spatial adaptation offers perspectives for nature conservation to mitigate the impact of climate change, which I will discuss in the last section.

### 7.1.1 Species characteristics determine responses to changing weather conditions

In the field study described in Chapter 2, I examined the effect of local weather on butterfly flight behaviour, movement and colonization. I recorded flight behaviour and mobility of four butterfly species: two habitat generalists (Small heath *Coenonympha pamphilus* and Meadow brown *Maniola jurtina*) and two specialists (Heath fritillary *Melitaea athalia* and Silver-studded blue *Plebejus argus*), under different weather conditions. Previous studies have already shown that butterfly

behaviour varies with weather conditions (Clench 1966; Brown 1970; Douwes 1976; Shreeve 1984; Brattstrom et al. 2008). These studies, however, focus on single weather parameters, species or types of behaviour, and do no elucidate the link between weather, behaviour, and dispersal. My results suggest that under weather conditions associated with anticipated climate change, behavioural components of dispersal (flight duration, proportion of time spent flying, net displacement) of butterflies are enhanced. This is consistent with monitoring data, obtained from standardized transect counts over the period 1990-2008, which showed that colonization frequencies increased under the same weather conditions. Increased dispersal propensity at local scale might therefore lower the impact of habitat fragmentation on the distribution at a regional scale. I propose that climate change may diminish the effects of fragmentation by enhancing flight behaviour and dispersal of butterflies. Other ectothermic species may be affected similarly.

Dispersal propensity is a life-history trait that makes species sensitive to or benefit from specific weather events. Investigating which specific combination of life-history traits makes species sensitive to specific weather events is an approach that allows for the generalization of predictions on future performance of species that share the same (combination of) traits (Keddy 1992). In Chapter 3, I investigated how breeding bird species can be grouped, based on their life-history traits and according to weather-correlated variation in their abundances. Most previous studies on life-history traits and weather focused on only one or a few species and weather variables, or on responses from population trend data (Brown & Brown 1998; Both & Visser 2001; Sæther et al. 2004; Both & Visser 2005; Both et al. 2006; Jiguet et al. 2006; Both et al. 2009; Van Turnhout et al. 2010). I used a newly developed statistical method - the linear trait-environment method – to investigate the sensitivity of 77 Dutch breeding bird species to effects of 12 weather variables, based on four of their life-history traits. Despite my focus on single traits, the sensitivity of species to effects of weather can be described by two strategies, combining several traits that relate to demographic processes. If I extrapolate these correlations to the future, assuming that my conclusions are based on causal relationships, and that the way species, weather variables, and the nature of habitat types interact will not alter, I am able to point out species that are expected to show most significant responses to changing weather conditions under climate change. According to their strategies, one group of species (roughly: wa-

terfowl, about 13% of the total number of studied species) will profit from climate change, while the second species group (most passerines, about 17% of the total number of studied species) will be negatively impacted by climate change. Waterfowl are negatively impacted by severe winter weather. Under climate change, severe winters will occur less frequently, which will enhance waterfowl performance. Advanced spring timing in their breeding grounds may lead to mismatches between the timing of reproduction and the food supply to the juveniles of passerine birds. This is in agreement with studies of Both and Visser (2001; 2005) and Both et al. (2006), that show population declines due to population mismatches for a number of passerines. The linear trait-environment method can well be applied to comparable data of other species groups, when only the most important traits are selected that are presumed to be affected by climate change.

### 7.1.2 Landscape characteristics determine responses to changing weather conditions

The interaction between climate change and habitat fragmentation is complex: large-scale climate-driven range shifts are evoked by regional population processes and changes in habitat quality that are in turn affected by augmented weather variability at regional scale. In this study, I address complex interactions between climate change and habitat fragmentation at a small to intermediate spatial and temporal scale. In Chapter 4, I investigated Great bittern (*Botaurus stellaris*) counts from various Dutch marshland sites over the period 1984-2005. Bittern habitat surrounding these sites differed in area, quality, and connectivity. I explored the effect of these landscape structure characteristics on population resilience. Moreover, I studied the changes in Dutch breeding bittern abundance in relation to winter severity. My results show that severe winter weather has a significant negative impact on bittern population growth rates. Severe winters occur less and less - which is probably the main reason that bittern numbers slightly increased between 1997 and 2005 (Van Turnhout et al. 2010) – and this trend is expected to continue in the future. However, bitterns are assumed to become negatively affected by the enlarged weather variability in terms of drought and inundation during the breeding season. I found that an increased carrying capacity and spatial cohesion contributes to an increase in mean growth rates over the years. Thus, recovery from negative effects of weather variability on bittern population numbers could be faster in large, well-connected habitats. Similarly, Fop-

pen (1999) showed that spatial plot characteristics might influence recovery rates of populations. Breeding populations of Sedge warbler (*Acrocephalus schoenobaenus*) in relatively unfragmented Dutch landscapes showed a clear recovery following decline due to drought in African wintering grounds, while those in heavily fragmented landscapes showed no recovery. In contrast to the study of Foppen (1999), I showed declines and subsequent recoveries from weather events related to climate change in the breeding area. Accordingly, marshland birds that are sensitive to extreme weather events, and that breed in highly fragmented habitat sites are more vulnerable than those in more robust habitat sites.

Empirical studies alone afford insufficient insight into complex mechanisms and interactions, such as the synergistic effects of climate change and habitat fragmentation. Alternatively, models provide tools to study relative impacts of factors with mutual interdependencies. Most current methods to predict climate-induced changes in the occurrence and performance of species consider changes in the suitability of climatic conditions for existence. With these models, it is possible to indicate the potential distribution of a species that would arise under spatial conditions that cause an unlimited accessibility and habitat suitability. At the regional scale however, detailed predictions of changes in species distributions and performance are pivotal for conservation planning and policy making. Better understanding of the mechanisms behind the interaction between species and landscape characteristics and climate change at the regional scale is therefore required. However, these interactions have rarely been studied (but see e.g. Zurell et al. 2009). I developed a new approach, including demographic processes at the regional scale, aiming at investigating how the landscape could be adapted to compensate for possible negative impacts of climate change on population performance. To afford insight into the climatic responses of a population in landscapes under various states of fragmentation, I used a spatially explicit population model, which I present in Chapter 5. This individual-based metapopulation model of a univoltine butterfly species is unique in the sense that all processes are affected by daily weather, and subsequently, time steps used in the model are of one day. I showed that increasing patch size and amount of suitable habitat can increase population viability under climate change. Furthermore, I showed that contrary to common belief (e.g. Chapter 3 and 4, and Verboom et al. 2010), populations were not necessarily affected by augmented weather variability during summer and climate warming. The results suggested that species might even

'escape' from unfavourable weather conditions by advancing their life-cycle. Possible consequences of such advancements are mismatches in food chains. Adult butterflies appear earlier in the season, but the question is whether their main nectar sources are then already available. Approaching the food chain from the other site, predators such as passerine birds might face mismatches between the timing of reproduction and the food supply to the juveniles (i.e. caterpillars) when they return relatively late from their wintering grounds.

Moreover, changes in weather circumstances related to climate change may affect habitat quality and suitability, both positively and negatively considering species performance. In Chapter 6, I combined the model described in Chapter 5 with soil and plant development models to allow for the indirect impact of climate change on habitat quality to Alcon blue (*Phengaris alcon*) distribution and performance. Results suggested that the modelled butterflies perform best when habitat conditions remain unaffected by climate change. However, when climate change does affect the occurrence of its host plant species, butterfly distribution and performance will be deteriorated. This implies that detailed predictions of changes in species distributions and performance should incorporate demographic processes and biotic interactions explicitly. Habitat quality is not explicitly taken into account in other chapters, or was kept constant. Chapter 6 makes clear that for future predictions at the regional scale, the indirect impact of climate change on the quality of habitat is highly relevant to include. Moreover, our approach in Chapter 6 allows for the identification of locations that are potentially suitable for measures increasing the robustness of the network for the Alcon blue.

### 7.1.3 Research on different spatial and temporal levels

In this study I have showed for decisions to adept a landscape to climate change, aggregated knowledge is required on various spatial and temporal levels (see top scheme in Fig. 7.1). Studying individual behaviour, I looked at processes at local spatial scale, occurring at a time span of minutes. Processes in metapopulations occur at larger temporal (e.g. years or decades) and spatial (e.g. regional) scales. Studying these large-scale processes within the time span of a doctoral thesis
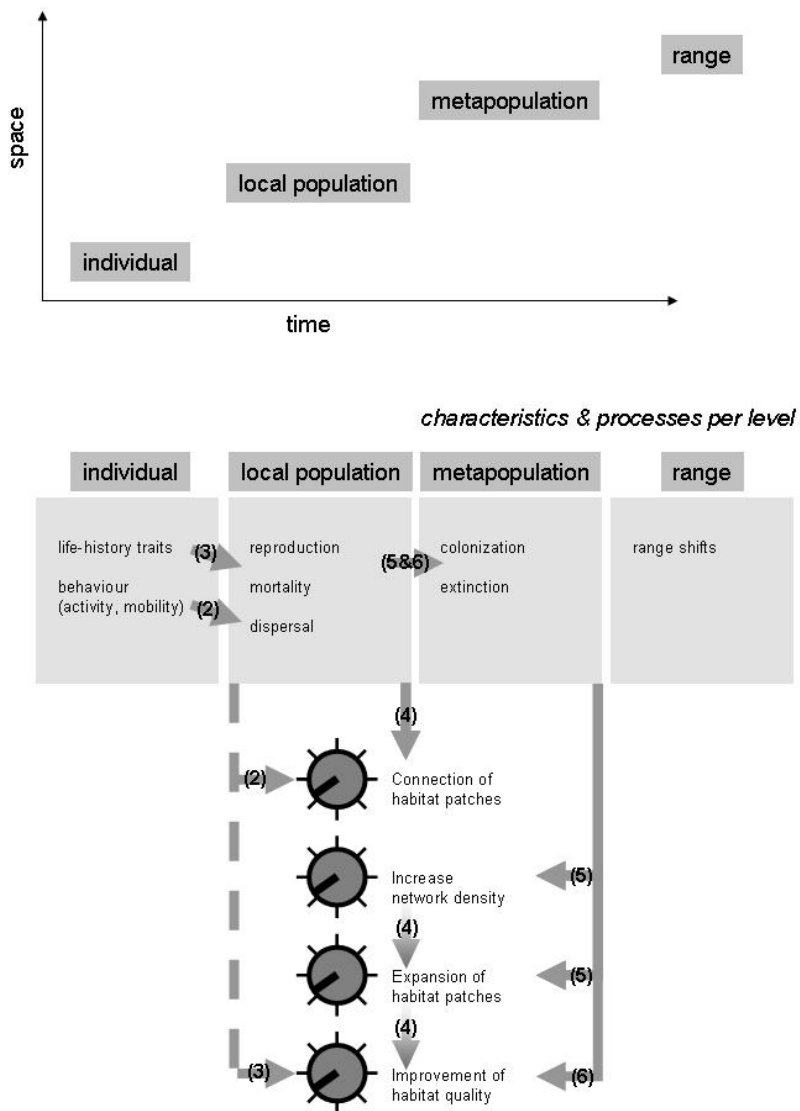
**Figure 7.1**

The coherence in characteristics and processes at different spatial and temporal levels; (2)-(6): chapter number

research requires modeling experiments. Next to data from modeling experiments (Chapter 5 and 6), I used monitoring records to study processes in local populations (Chapter 2, 3, and 4), and experimental data to study processes on the individual level (Chapter 2). Results from these types of analyses and data allow for a coherent overview over various spatial and temporal levels. I showed that enhanced flight behaviour at the individual level can hence be linked to dispersal capacity, which influences population dynamics at the local to regional scale. And as demographic processes (dispersal, reproduction, survival) determine these local population dynamics, species life-history traits determine the extent of the impact of demographic processes. In turn, colonizations and extinctions that define metapopulation dynamics are evoked by demographic processes in local populations. The way this study aggregates characteristics and processes at different spatial and temporal levels is shown in Fig. 7.1.

## 7.2    PERSPECTIVES FOR NATURE CONSERVATION: NEW INSIGHTS

### 7.2.1 Spatial adaptation measures

When designing ecological networks, climate change has rarely been taken into account (e.g. LNV 2000). Nevertheless, these networks were established to preserve biodiversity in a sustainable way. The necessity to adapt the landscape to climate change has become increasingly apparent (see also Brooke 2008; Vos et al. 2008). The influence of weather and climate change on demographic processes on the one hand, and habitat fragmentation on the other hand, changes population vulnerability and persistence, which might then no longer match current biodiversity goals. The divergence from these goals can give rise to spatial adaptation (c.f. Kasperson et al. 2005). Vulnerability and persistence of populations due to alterations in demographic processes is investigated in this study, and here I will further elaborate on adaptation measures that could reduce vulnerability. I follow the adaptation definition of Wilson and Piper (2008), who argue that biodiversity adaptation requires a double focus. The first focus is on adaptation measures that facilitate the ability of species and habitats to move elsewhere into newly suitable areas. The second focus is on adaptation measures that reduce vulnerability on the spot by increasing ecosystem resilience to disturbances and by accommodating change.

To facilitate the ability of species to move into newly suitable areas, networks can be made denser by fitting new patches into the network, providing more habitat and refuges. Moreover, the added areas can act as stepping-stones for dispersal, and form likewise connections between the older patches. Other species prefer continuous, line-shaped connections or corridors. Vos et al. (2008; 2010) analyzed Dutch and European ecological networks for locations where the effectiveness of the networks might be weakened because of climate change. In these studies, several adaptation strategies were proposed. The ability of species to move elsewhere into newly suitable areas were suggested to be facilitated by (1) linking isolated habitat and networks that are within a new suitable climatic zone to the nearest climate-proof network, and by (2) increasing the colonization capacities in the part of the network that remains suitable in successive time frames. Although these measures are mainly developed for the level of species ranges, my results contribute to understanding how these measures support local and regional processes and thereby contribute to facilitating shifts at the biogeographical scale level. Increasing habitat density and connectivity by appending existing (protected) nature areas with new patches in the network is beneficial for species with a relatively low dispersal capacity, that should be guided through the landscape. Based on my results from Chapter 2, I state that increased dispersal propensity at local scale might lower the impact of habitat fragmentation on the distribution at a regional scale. I propose that climate change may diminish the effects of fragmentation by enhancing flight behaviour and dispersal of butterflies, and presumably also other ectothermic species. However, the probability to encounter unsuitable conditions or hostile environments during dispersal might prevent the enhanced flight activity to lead to higher dispersal and colonization success. In hostile environment, dispersal is expected to be less successful as dispersing individuals will take longer to reach a next patch of suitable habitat, with reduced chances of survival. Moreover, the density of dispersing individuals decreases with distance from the source patch (e.g. Baguette 2003). I therefore propose to guide dispersers through the landscape. This can be done by adding more suitable habitat, which should lead to more efficient and more successful dispersal at an increased survival rate. In butterflies, adopting straight movements for dispersal reduces its costs in fragmented landscapes (Schtickzelle et al. 2007). Butterflies might therefore prefer continuous, line-shaped connections or corridors (cf. Adriaensen et al. 2003; Noordijk et al. 2008). Grashof-Bokdam et al.

(2009) shows that combining nature areas with these smaller-scaled corridors (green-blue veining) may improve the persistence of plant and animal species in fragmented landscapes, especially of species with a low dispersal capacity. In Chapter 5 I found that providing more habitat and refuges by fitting new patches into the network revealed an increase in population viability above a viability threshold (cf. Vos et al. 2001). Hence, the ability of species and habitats to move into newly suitable areas could also be facilitated by increasing network density.

Moreover, species that are vulnerable to extreme weather events may be facilitated by a well-connected landscape in their recovery. Based on my results from Chapter 4, I can say that populations in areas that contain a relatively large share of qualitatively good, well-connected habitat show relatively high numbers. These populations tend to recover sooner after a reduction in numbers due to for instance an extreme weather event. This as well shows that an increased connectivity can reduce species vulnerability.

To reduce the vulnerability on the spot, Vos et al. (2008; 2010) propose (1) to enlarge the carrying capacity of nature areas by either enlarging the size or by improving habitat quality, especially in parts of a species' range where the climate remains stable, and/or (2) to increase the heterogeneity of natural areas. In Chapter 4 I found that, next to spatial cohesion, carrying capacity influences recovery rates in bittern populations. Therefore, my results support measures to enlarge carrying capacities to shorten population recovery after disturbances. Moreover, in Chapter 5 I found that expanding the size of habitat patches within a network revealed an increase in population viability above a viability threshold. In this way, the vulnerability of populations due to alterations in demographic processes could be reduced. In Chapter 6, I found a reduction of habitat quality due to climate change. This reduction was here directly coupled to a decrease in habitat availability, which led to a reduction in population viability. Abiotic constrains (e.g. eutrophication and desiccation) may be amplified by climate change. When extreme events such as drought or flooding occur (Kindvall 1996; Sutcliffe et al. 1997; Piha et al. 2007; Wu 2008), population stability may be harmed even more. Increasing heterogeneity of patches and landscapes could on the other hand enhance resilience, dampen fluctuations and avoid large synchronized extinctions, which may increase population stability (Oliver et al. 2010; Verboom et al. 2010). It can be argued that heterogeneity, causing spatial variation in resource availability, might as well reduce effects of mismatches in food supply to passerines

(Chapter 3). As Hunter and Price (1992) suggest, habitat heterogeneity plays a dominant role in insect population dynamics and community structure. Blondel (2007) shows that reproduction in Mediterranean blue tit (*Cyanistes caeruleus*) is indeed optimized in heterogeneous landscapes where there is a good synchronism between the development of leaves, caterpillar availability and the fledgling period. The spatial variation in resource availability introduced by increasing heterogeneity can therefore be a crucial element of successful reproduction (Durant et al. 2007), especially for species limited to one resource (Chapter 6) or when the resource is limited to a specific period (Chapter 3). With the model used in Chapters 5 and 6 I could explore the impact of spatial variation in resource availability, e.g. by adding local differences in weather circumstances. Thus, the model could be used as a research tool to compare the performance of metapopulations during weather extremes under homogenous and heterogeneous habitat configurations. Such modeling experiments should be built on field data from heterogeneous landscapes, that is still hardly available.

Implementation of adaptation measures to accommodate ecological networks for increased weather variability and temperature rise asks for a quantification of previously mend adaptation measures. Deriving new specific design criteria is crucial to design optimal configurations of habitat areas. The research described in this thesis shows the importance of traits in profiling species and the subsequent selection of specific adaptation measures for implementation, and I elaborate on possible consequences for nature management approaches in the following section.

### 7.2.2 Nature management, target species and traits

In addition to other recent research, this study shows that while climate change will be beneficial to some species, other species will be negatively impacted. Moreover, some species may be expected to respond positively to climate change based on projections of their population trends – their direct responses -, but may be negatively impacted by e.g. mismatches in food supply in an indirect way. In the hypothetical case that all target species in a conservation network that are sensitive to habitat fragmentation respond positively to climate change – both directly and indirectly -, spatial adaptation would not be necessary. However, the broad variety (between species) and variability (within species) of responses to

climate change (Parmesan & Yohe 2003; Van Turnhout et al. 2010), also shown in Chapter 3 of this thesis, suggests that there is little chance that this situation will occur. This calls for research on optimized combinations of adaptation measures, which searches for measures that accommodate the response of most of the species.

Impacts of climate change on species dynamics may interfere with aims set in nature conservation programmes. These are often defined in terms of the presence and abundance of target species in protected areas. Target species are on the one hand used for monitoring, as indicators for abiotic constrains (e.g. eutrophication, nitrification, desiccation). In the practice of conservation, target species are on the other hand used as assessment mechanism for conservation management success; nature managers are judged by the presence and abundance of target species in their protected area. One option to cope with changing presence and abundance of target species is to adjust the set of target species to changing climate conditions, based on current understanding of e.g. large-scale range shifts. This would however involve a loss of continuity in monitoring series. Turner et al. (2007) proposed another option by arguing that future nature conservation programmes should emphasize the functioning of ecosystems and the distribution of functional groups of species over ecosystems, rather than target species. Species traits play an important role in constructing functional groups. For some systems a decline in biodiversity might not necessarily lead to a loss in functional trait diversity (Mayfield et al. 2010). An indicator system that takes the responses of functional traits into account will improve our ability to develop conservation policy frameworks that are more adaptive to the dynamics in species assemblages caused by climate change.

The approach applied in Chapter 2 and 3 allows to incorporate the vulnerability of species traits to climate change into a functional approach. The traits used here can be addressed as response traits (cf. Lavorel & Garnier 2002): characteristics that define reproduction and mortality rates and dispersal capacity, possessed by species that respond comparably to climatic factors. A complementary approach is to investigate so-called effect traits, that can group species according to their characteristics that sort important effects on ecosystem functioning. Ecosystem functioning can thereby refer to an intrinsic value, as well as to a user value (e.g. pollination, water retention and purification, recreational value). A shift in species composition in response to climate change can occur while ecosystem function-

ing is maintained. Such a resilient ecosystem can exist only when sufficient response diversity is present within a group of species possessing a similar effect trait. This calls for the implementation of effect traits in the methodology applied in Chapter 2 and 3, which would involve an important new research step. Extracting 'target traits' in this way would facilitate the adequate prioritising of the spatial adaptation measures, to be implemented to compensate for possible negative impacts of climate change.

# 8

# Samenvatting

Er was eens een keizer die, ergens in de negende eeuw na Christus, leefde in Kyoto – in die tijd de hoofdstad van Japan. De keizer besloot een feestje te geven onder de kersenbomen op zijn landgoed, dat zou plaatsvinden precies op het moment dat de bomen in volle bloei stonden. Vanaf dat moment werden de feestjes onder de bloeiende kersenbomen een traditie, die ook onder het bewind van de volgende keizers gehandhaafd werd. Het moment van die feestjes, en dus ook het moment van bloei van de kersenbomen, is sindsdien bijgehouden. Vandaar dat er vandaag de dag een fenologische database van momenten van bloei van de kersenbomen bestaat. De momenten van bloei geven een goede afspiegeling van de voorjaarstemperaturen in de omgeving van Kyoto vanaf de negende eeuw, waar periodes van klimatologische veranderingen uit afgeleid kunnen worden.

Zulke databases maken duidelijk dat vanaf de laatste decennia het klimaat mondiaal behoorlijk aan het veranderen is. Klimaat is de drijvende kracht achter veel ecologische processen. Mensen ondervinden de invloed van het klimaat op hun directe leefomgeving door de timing van natuurlijke processen, zoals bloei. De stijging van de mondiale temperatuur lijdt, naast de toename in atmosferische broeikasgasconcentraties, tot een directe versterking van fysiologische processen, zoals fotosynthese, groei en decompositie. Op de langere termijn kunnen populaties zich lokaal evolutionair aanpassen aan de nieuwe klimatologische omstandigheden.

Omdat klimatologische condities bepalen wat geschikt habitat is voor soorten, kan klimaatverandering in de zin van temperatuursstijging ook leiden tot verschuivingen in de verspreiding van soorten. De mogelijkheid van soorten om zich ook daadwerkelijk te vestigen in de nieuwe geschikte habitatgebieden, is afhankelijk van hun reproductiesnelheid en dispersiecapaciteit. Soorten die weinig mobiel zijn, hebben een langere periode nodig om zich te verplaatsen naar locaties met nieuw ontstaan habitat, en óf die soorten deze locaties daadwerkelijk zullen bereiken, hangt af van de mate van habitatfragmentatie en de mate waarin de soorten daar last van hebben.

Klimaatverandering uit zich ook in een toename in het optreden van weersextremen (weersvariabiliteit), dat zorgt voor grotere fluctuaties in aantallen individuen van soorten binnen populaties. Net als bij verschuivingen in de verspreiding van soorten, interfereren fluctuaties in weer en in aantallen individuen met het landschapspatroon: de aanwezigheid van grote habitatplekken en uitwisseling tussen

individuen kan de stabiliteit van populaties versterken en het herstelvermogen na een catastrofe (bijv. weersextreem) vergroten. De mate waarin populatieaantallen afnemen na het optreden een weersextreem hangt, net als de tijd die nodig is voor herstel van de aantallen, af van de groei van een populatie. Een populatie groeit, wanneer geboortes en immigraties compenseren voor het verlies aan individuen als gevolg van sterfte en emigratie. De groeisnelheid, en daarmee de tijd die nodig is voor herstel, is soortspecifiek.

Een voortschrijdende stijging van de temperatuur vereist het vermogen van soorten om te kunnen dispergeren en populaties te kunnen opbouwen in nieuw ontstane habitatgebieden, terwijl een toename in weersvariabiliteit het vermogen om achteruitgang in aantallen tegen te gaan en om snel te herstellen vereist. Demografische processen – reproductie, overleving en dispersie – zijn daarom belangrijker dan ooit. De balans tussen deze processen bepaalt de dynamiek van populatieaantallen en is soortspecifiek – het hangt af van de eigenschappen van soorten. Dus terwijl de respons op veranderende weersomstandigheden effect heeft op processen die spelen op het niveau van individuen, uit de som van deze responsen zich in fluctuaties in aantallen van complete populaties en metapopulaties, terwijl de som van responsen op metapopulatieniveau zich manifesteert in verschuivingen in de verspreiding van soorten. Om de respons van soorten op het gecombineerde effect van klimaatverandering en habitatfragmentatie te begrijpen, moet worden uitgegaan van het individuele niveau. Adaptatiemaatregelen worden echter toegepast op het niveau van metapopulaties en beïnvloeden uiteindelijk het totale verspreidingspatroon van soorten.

Wanneer (meta)populaties reageren op veranderende weersomstandigheden door een afname in aantallen individuen, zouden landschapskarakteristieken dit effect kunnen verminderen. Ter illustratie: in netwerken met een grote ruimtelijke samenhang kunnen soorten dispergeren om te ontsnappen aan ongunstige weersomstandigheden, of kan de tijd voor herstel verkorten. Wanneer de ruimtelijke condities echter ontoereikend zijn, kunnen we het landschapspatroon aanpassen. Ruimtelijke adaptatiemaatregelen kunnen bijdragen aan de ontwikkeling van duurzame ecologische netwerken. Om de meest effectieve adaptatiemaatregel te kunnen identificeren is het noodzakelijk om uit te zoeken hoe landschapskarakteristieken de populatiegroei en uitbreiding van het verspreidingsgebied – en daarmee het voortbestaan van (meta)populaties - kunnen beïnvloeden bij klimaatverandering.

## 8.1 SOORTSEIGENSCHAPPEN EN RESPONS OP WEER

Met de veldstudie zoals beschreven in hoofdstuk 2 heb ik het effect van lokaal weer op vlindervlieggedrag, verplaatsing en kolonisatie bestudeerd. Ik bestudeerde het vlieggedrag en de mobiliteit van vier vlindersoorten - twee habitatgeneralisten (Hooibeestje *Coenonympha pamphilus* en Bruin zandoogje *Maniola jurtina*) en twee habitatspecialisten (Bosparelmoervlinder *Melitaea athalia* en Heideblauwtje *Plebejus argus*) – onder verschillende weersomstandigheden. Eerdere studies hebben al laten zien dat vlindergedrag afhankelijk is van weersomstandigheden. In deze studies gaat de aandacht echter uit naar het effect van slechts een enkele weersparameter, soort of type gedrag en belichten niet het verband tussen weer, gedrag en dispersie. Mijn resultaten suggereren dat onder weersomstandigheden die vaker zullen optreden bij klimaatverandering, gedrag dat hoort bij dispersie (vliegduur, aandeel van de tijd dat aan vliegen besteed wordt, netto verplaatsing) wordt versterkt. Dit komt overeen met monitoringsdata, verkregen uit gestandaardiseerde transecttellingen uit de periode 1990-2008, die laat zien dat kolonisaties vaker optraden onder dergelijke weersomstandigheden. Een toename in mogelijkheid tot dispersie op lokale schaal kan daarom de invloed van habitatfragmentatie op de verspreiding van de soort op regionale schaal doen afnemen. Klimaatverandering zou daarmee de negatieve effecten van fragmentatie op vlinders kunnen verkleinen door vlieggedrag en dispersie te bevorderen. Andere koudbloedige soorten zouden op dezelfde manier beïnvloed kunnen worden.

De dispersiecapaciteit is een soortseigenschap die soorten gevoelig maakt of soorten laat profiteren van bepaalde (extreme) weersomstandigheden. Door na te gaan welke specifieke combinatie van eigenschappen soorten gevoelig maakt voor bepaalde weersomstandigheden, kunnen voorspellingen wat betreft de toekomstige toestand van soorten gegeneraliseerd worden voor soorten met overeenkomstige eigenschappen. In hoofdstuk 3 heb ik onderzocht hoe broedvogelsoorten gegroepeerd kunnen worden, gebaseerd op hun eigenschappen en aan de hand van variaties in abundanties die gecorreleerd kunnen worden aan weer. De meeste eerdere studies naar soortseigenschappen en weer belichten slechts één of een aantal soorten en weersvariabelen, of bestuderen responsies aan de hand van populatietrenddata. Ik heb een nieuw ontwikkelde statistische methode gebruikt - de 'linear trait-environment' methode – om de gevoeligheid van 77 Nederlandse

broedvogels voor 12 weersvariabelen op basis van vier soortseigenschappen te onderzoeken. Ondanks het feit dat ik het effect van elke eigenschap afzonderlijk bestudeerde, bleek dat de gevoeligheid van soorten toegeschreven kan worden aan twee strategieën, die verschillende eigenschappen in zich combineerden. Wanneer ik de gevonden correlaties extrapoleer naar de toekomst – er van uitgaande dat mijn conclusies gebaseerd zijn op causale relaties en dat de manier waarop soorten, weersvariabelen en habitat op elkaar inwerken, niet zal veranderen – kan ik soorten aanwijzen die naar verwachting significante effecten zullen ondervinden van veranderende weersomstandigheden. Op basis van hun eigenschappen blijkt dat één groep soorten zal profiteren van klimaatverandering. Dit zijn kortgezegd de watervogels (13% van het totaal aantal onderzochte soorten). Een tweede groep – de meeste zangvogels (17% het totaal aantal onderzochte soorten) zal negatief beïnvloed worden door klimaatverandering. Vervroeging van het voorjaar in hun broedgebied kan ertoe leiden dat deze soorten de piek in het voedselaanbod van hun jongen mislopen. Daarmee komen ze te laat terug uit hun overwinteringsgebied. De 'linear trait-environment' methode is geschikt om te worden toegepast op vergelijkbare data van andere soortsgroepen, wanneer slechts de belangrijkste soortseigenschappen die door klimaatverandering beïnvloed worden, worden meegenomen.

## 8.2    LANDSCHAPSKARAKTERISTIEKEN EN RESPONS OP WEER

De interactie tussen klimaatverandering en habitatfragmentatie is complex: de grootschalige klimaatgedreven verschuivingen in verspreidingsgebieden van soorten worden mede bepaald door populatieprocessen en veranderingen in habitatkwaliteit die op hun beurt door toename in weersvariabiliteit op kleinere ruimtelijke schaal beïnvloed worden. In deze studie beschouw ik de complexe interacties tussen klimaatverandering en habitatfragmentatie op kleine tot intermediaire ruimtelijke en temporele schaal. In hoofdstuk 4 onderzoek ik tellingen van in Nederland broedende Roerdompen (*Botaurus stellaris*), afkomstig uit telplots in verschillende moerasgebieden uit de periode 1984-2005. Roerdomphabitat rondom deze telplots varieert in grootte, kwaliteit en connectiviteit. Ik onderzocht het effect van deze landschapskarakteristieken op veerkracht van Roerdomppopulaties. Daarnaast bestudeerde ik de veranderingen in aantallen Roerdompen in relatie tot de strengheid van de winters. De resultaten laten zien dat streng win-

terweer een significant negatieve invloed heeft op de populatiegroei. Strenge winters zullen echter steeds minder vaak optreden – wat er waarschijnlijk voor zorgt dat de aantallen Roerdompen weer licht zijn gestegen tussen 1997 en 2005 en deze trend zal zich naar verwachting in de toekomst voortzetten. Desondanks zullen Roerdompen negatief beïnvloed worden door de toename in weersvariabiliteit, met name door het voorkomen van meer droogtes en overstromingen tijdens het broedseizoen. Ik vond dat een hogere ruimtelijke samenhang in habitat bijdraagt aan een toename in populatiegroei over de jaren. Daarom zal het herstel van negatieve effecten van weersvariabiliteit op populatieaantallen van Roerdompen sneller kunnen verlopen in grote, goed verbonden habitatplekken.

Enkel empirische studies verschaffen onvoldoende inzicht in complexe mechanismes en interacties, zoals het gecombineerde effect van klimaatverandering en habitatfragmentatie. Werken met modellen heeft toegevoegde waarde, omdat hiermee het relatieve belang van factoren die van elkaar afhankelijk zijn bestudeerd kunnen worden. De meeste huidige modellen die klimaatgedreven veranderingen in de verspreiding en het voortbestaan van populaties voorspellen, doen dit aan de hand van verschuivingen van de voor de soort geschikte klimaatzones. Met deze modellen is het mogelijk een indicatie te geven van de potentiële verspreiding van een soort, die gerealiseerd zou kunnen worden bij ruimtelijke condities waarbij de soort ongehinderd zijn geschikte habitat kan bereiken. Echter, op regionale schaalniveau is het noodzakelijk gedetailleerde voorspellingen te doen wat betreft verschuiving en toestand van populaties, voor een juiste planvorming omtrent bescherming en beheer. Gezien de behoefte aan inzicht in ruimtelijke adaptatiemaatregelen is een beter begrip van de mechanismen achter de interactie tussen landschapskarakteristieken en klimaatverandering op regionale schaal nodig. Toch zijn deze interacties nauwelijks bestudeerd. Ik gebruikte een nieuwe benadering waarbij demografische processen op de regionale schaal worden meegenomen, en die tot doel heeft te onderzoeken hoe het landschap aangepast kan worden om te compenseren voor mogelijke negatieve effecten van klimaatverandering op populaties. Om inzicht te krijgen in het effect van klimaatverandering op een populatie in landschappen in verschillende gradaties van fragmentatie heb ik een nieuw ruimtelijk expliciet populatiemodel ontwikkeld, dat wordt gepresenteerd in hoofdstuk 5. Dit individugebaseerde metapopulatiemodel van een vlindersoort met één vliegperiode is uniek in de zin dat alle processen beïnvloed worden door dagelijks weer. Daarom wordt gesimuleerd met tijdstappen van een dag.

Resultaten laten zien dat zowel grotere leefgebieden als een grotere hoeveelheid geschikte leefgebieden zorgt voor een toename in populatielevensvatbaarheid bij klimaatverandering. Verder toonde ik aan dat, in tegenstelling tot wat vaak wordt beweerd, populaties niet noodzakelijkerwijs negatief beïnvloed worden door een stijging in de temperatuur en een toename in weersvariabiliteit tijdens de zomer. Resultaten laten zien dat vlindersoorten zelfs zouden kunnen 'ontsnappen' aan ongunstige weersomstandigheden door hun levenscyclus te vervroegen. Mogelijk ontstaan als gevolg van deze vervroeging gebreken in voedselketens. Vlinders verschijnen mogelijk vroeger in het seizoen, maar de vraag is of hun belangrijkste nectarbronnen dan al beschikbaar zijn. En bekijken we de voedselketen van de andere kant, dan kunnen predatoren zoals zangvogels zich voor een tekort aan voedsel (rupsen) gesteld zien, wanneer ze relatief laat uit hun overwinteringsgebied terugkeren.

Klimaatverandering kan bovendien effect hebben op de kwaliteit en geschiktheid van habitat en de toestand van soorten zowel positief als negatief beïnvloeden. In hoofdstuk 6 combineerde ik het vlinderpopulatiemodel, zoals beschreven in hoofdstuk 5, met bodem- en plantontwikkelingsmodellen. Op deze manier bestudeerde ik de indirecte invloed van klimaatverandering op de habitatkwaliteit en daarmee op de verspreiding van Gentiaanblauwtje (*Phengaris alcon*). Resultaten suggereren dat de gemodelleerde vlindersoort het best gedijt wanneer de toestand van het habitat niet verandert als gevolg van klimaatverandering. Echter, wanneer klimaatverandering wel invloed heeft op het voorkomen van de waardplant van Gentiaanblauwtje, dan verkleint dit de verspreiding van de vlindersoort. Dit betekent, dat de invloed van klimaatverandering op geschiktheid en aanwezigheid van habitat moet worden meegenomen in studies die bedoeld zijn om richtlijnen te geven voor natuurbeheer en –beleid. De kwaliteit van het habitat is niet expliciet meegenomen in de andere hoofdstukken of was als constant verondersteld. De resultaten van hoofdstuk 6 laten zien dat de indirecte invloed van klimaatverandering wel relevant is om mee te nemen in toekomstvoorspellingen. Verder kunnen met de methode zoals gebruikt in hoofdstuk 6 gebieden aangewezen worden die potentieel geschikt zijn om maatregelen uit te voeren die het voorkomen van soorten in een gebied bevorderen. Bij dergelijke maatregelen kan gedacht worden aan het creëren of verbinden van leefgebieden, bijvoorbeeld door habitatcondities te verbeteren, maar ook aan het uitzetten van soorten in doorlopend kwalitatief geschikte leefgebieden.

## 8.3    ADAPTATIEMAATREGELEN EN NATUURBELEID

Ruimtelijke adaptatiemaatregelen die in dit proefschrift naar voren komen – het vergroten van habitatplekken, het vergroten van de draagkracht van de plekken, het verdichten en verbinden van netwerken – komen overeen met adaptatiemaatregelen die al eerder zijn voorgesteld om negatieve effecten van habitatfragmentatie tegen te gaan, ook bij klimaatverandering. Het vergroten van de dichtheid en connectiviteit van netwerken, bijvoorbeeld door nieuwe habitatplekken of lijnvormige elementen binnen het netwerk te creëren, is voordelig voor soorten met een relatief lage dispersiecapaciteit (hoofdstuk 2). Het vermogen om nieuwe geschikte leefgebieden te bereiken wordt hierdoor gefaciliteerd. Bovendien kan het vergroten van de connectiviteit de gevoeligheid van soorten voor weersextremen onderdrukken door de uitwisseling van individuen en daarmee het herstelvermogen van populaties te bevorderen (hoofdstuk 4). Hersteltijden van populaties van soorten die gevoelig zijn voor weersextremen kunnen daarnaast ook verkort worden door het vergroten van de draagkracht van leefgebieden, door de omvang van habitatplekken te vergroten, of door de kwaliteit van de leefgebieden te verbeteren (hoofdstuk 4, 5 en 6). Een toename in de heterogeniteit van habitatplekken kan zorgen voor risicospreiding: populatieaantallen zullen minder snel en niet overal tegelijkertijd afnemen, en daarmee zal de stabiliteit van populaties worden versterkt. Bovendien kan heterogeniteit zorgen voor een ruimtelijke verspreiding in voedselaanbod. Dit is van cruciaal belang voor soorten die afhankelijk zijn van één voedselbron (hoofdstuk 6), of waarvan het voedsel slechts over een korte periode beschikbaar is (hoofdstuk 3).

Om de meest effectieve ruimtelijke adaptatiemaatregel te kunnen identificeren, is het daarom noodzakelijk inzicht te hebben in de eigenschappen die soorten gevoelig maken voor klimaatverandering. Met het onderzoek dat beschreven is in de hoofdstukken 2 en 3 heb ik hier inzicht in gekregen. Aanvullend is het waardevol inzicht te krijgen in de rol die eigenschappen van soorten spelen in het functioneren van ecosystemen (bijv. bestuiving, waterzuivering, recreatieve waarde). Een verschuiving in soortensamenstelling – en daarmee de samenstelling van soortseigenschappen in een systeem – als gevolg van klimaatverandering kan gevolgen hebben voor het functioneren van ecosystemen. In een veerkrachtig ecosysteem is voldoende diversiteit in soortseigenschappen aanwezig om het functioneren te waarborgen, ook wanneer een verschuiving in samenstelling optreedt door bij-

voorbeeld klimaatverandering. Sturing en monitoring van beleidsdoelen aan de hand van doel*soorten* zou daarom uitgebreid moeten worden met doel*eigenschappen*, aan de hand waarvan adequaat ruimtelijke adaptatiemaatregelen geïmplementeerd kunnen worden.

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**!**

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Anouk
voorjaar 2011

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# Curriculum vitae and publications

## CURRICULUM VITAE

On 13 July 1980 I was born in Delft. In Zoetermeer, where I grew up, I went to the Alfrink College for secundairy education (VWO). After I passed my exam in 1998, I went to study Physical Geography at Utrecht University, where I chose to specialize myself into coast and river systems. My Master thesis was based on a field study (2001) on the effect of morphodynamics on vegetation succession along the Allier River (France) and the Lower Volga River (Russia). This was a reference study for the Dutch Rhine branches, commissioned by the Dutch Institute for Inland Water Management and Waste Water Treatment (RIZA). I ended my Physical Geography study in Denmark in 2003, where I participated in the Erasmus programme at the Geography Department of Roskilde Universitetscenter. Here, I worked on a project on landscape structure metrics and population dynamics.

I gave my education a 'green' impulse by taking an additional MSc in Biology (Natural Resources Management, Utrecht University). I did an internship at the Department of Environmental Sciences, where I studied the influence of the age of the present Dutch landscape on the distribution of species. Additionally, I performed a modelling study on the effect of foraging strategies on contamination risks in food webs at Alterra, Wageningen UR. This project was part of the INTERREG IIIB North West Europe Programme.

During my secondary school and university years, I worked as a waiter in a restaurant and as a housekeeper in homes for the elderly. I have also assisted during fruit harvest on a Norwegian farm. In January 2006, I started to work as a PhD student at the Land Use Planning group of Wageningen University. I had my workplace at the Ecological Networks team of Alterra. My PhD project was funded by the Dutch national research programme 'Climate Changes Spatial Planning' (project A02: Adaptation of the Dutch Ecological Network) and was part of the strategic research programme 'Sustainable spatial development of ecosystems, landscapes, seas and regions' (Ecological Resilience Project) funded by the Dutch Ministry of Agriculture, Nature Conservation and Food Quality, and carried out by Wageningen University and Research centre. The work resulted in this thesis.

In my spare time, I like to play the oboe. I am a member of orchestra 'Sonante', and secretary of its board. Moreover, I enjoy to hike and cycle, enjoying the landscape at the same time.

## LIST OF PUBLICATIONS

*Articles in refereed journals:*

**Cormont, A., C. C. Vos, C. A. M. van Turnhout, R. P. B. Foppen & C. J. F. ter Braak (2011).** Using life-history traits to explain bird population responses to increasing weather variability. Climate Research (in press)

**Cormont, A., A. H. Malinowska, O. Kostenko, V. Radchuk, L. Hemerik, M. F. WallisDeVries, J. Verboom (2011).** Effect of local weather on butterfly flight behaviour, movement, and colonization: significance for dispersal under climate change. Biodiversity and Conservation 20, 483–503.

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*Article in non-refereed journal:*

**Cormont, A. (2006).** Versnippering en klimaatverandering – Hoe maken we de EHS climate change-proof? TOPOS 2, pp. 46-49.

*Reports:*

**Cormont, A., J. M. Baveco & N. W. van den Brink (2006).** Effects of spatial foraging behaviour on risks of contaminants for wildlife. Breaking Ecotoxicological Restraints in Spatial Planning (BERISP): the development of a spatially explicit risk assessment, rep. no. 1369. Alterra, Wageningen UR, Wageningen, the Netherlands.

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**Cormont, A., C. J. F. ter Braak & M. F. WallisDeVries (2008).** Climate change and habitat fragmentation: range shifts for Dutch butterfly species. 2nd

Ann. Int. Symp. Future of Butterflies in Europe II, 17-19 April 2008, Wageningen, the Netherlands.

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**Malinowska, A.H., A. Cormont & J. Verboom (2007).** The influence of weather on behaviour and dispersal of butterflies in De Hoge Veluwe National Park. IALE World Congress, 8-12 July 2007, Ede, the Netherlands.

**Cormont, A. (2006).** Towards a Climate Change Proof National Ecological Network: the use of (mechanistic) models, Alternet workshop, 20-23 March 2006, Aberdeen, UK.

**Netherlands Research School for the
Socio-Economic and Natural Sciences of the Environment**

# C E R T I F I C A T E

The Netherlands Research School for the
Socio-Economic and Natural Sciences of the Environment (SENSE),
declares that

## *Anouk Cormont*

born on 13 July 1980 in Delft, The Netherlands

has successfully fulfilled all requirements of the
Educational Programme of SENSE.

Wageningen, 21 September 2011

the Chairman of the SENSE board

Prof. dr. Rik Leemans

the SENSE Director of Education

Dr. Ad van Dommelen

The SENSE Research School has been accredited by the Royal Netherlands Academy of Arts and Sciences (KNAW)



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The SENSE Research School declares that **Ms. Anouk Cormont** has successfully fulfilled all requirements of the Educational PhD Programme of SENSE with a work load of 45 ECTS, including the following activities:

**SENSE PhD courses**
- Environmental Research in Context
- Research Context Activity: Co-organizing course on Planning and design with ecological networks in multifunctional space (January-February 2007and 2008).
- The Art of Modelling
- Survival analysis

**Other PhD and MSc courses**
- Toegepaste Statistiek
- Landscape ecology: understanding processes from patterns
- Biodiversity and ecosystem services
- Planning en ontwerp met ecologische netwerken in de multifunctionele ruimte
- Personal efficacy
- Techniques for writing and presenting scientific papers
- Career perspectives

**Oral Presentations**
- Towards a Climate Change Proof National Ecological Network: the use of (mechanistic) models, Alternet workshop, 20 – 23 March 2006, Aberdeen, UK
- Climate change and habitat fragmentation: range shifts for Dutch butterfly species, 2nd Ann. International. Symposium Future of Butterflies in Europe II, 17 – 19 April 2008, Wageningen, The Netherlands

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