

Is green infrastructure an effective climate adaptation strategy for conserving biodiversity? A case study with the great crested newt

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Abstract

Context Increasing the amount of green infrastructure, defined as small-scale natural landscape elements, has been named as a climate adaptation measure for biodiversity. While green infrastructure strengthened ecological networks in some studies, it is not known whether this effect also holds under climate change, and how it compares to other landscape adaptation options.

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Objectives We assessed landscape adaptation options under scenarios of climate change for a dispersal-limited and climate-sensitive species: great crested newt, *Triturus cristatus*.

Methods A spatially-explicit modelling framework was used to simulate newt metapopulation dynamics in a case study area in the Netherlands, under alternative spatial configurations of 500 ha to-be-restored habitat. The framework incorporated weather-related effects on newt recruitment, following current and changing climate conditions.

Results Mild climate change resulted in slightly higher metapopulation viability, while more severe climate change (i.e. more frequent mild winters and summer droughts) had detrimental effects on metapopulation viability. The modelling framework revealed interactions between climate and landscape configuration on newt viability. Restoration of ponds and terrestrial habitat may reduce the negative effects of climate change, but only when certain spatial requirements (habitat density, connectivity) as well as abiotic requirements (high ground water level) are met.

Conclusions Landscape scenarios where habitat was added in the form of green infrastructure were not able to meet these multiple conditions, as was the case for a scenario that enlarged core areas. The approach allowed a deduction of landscape design rules that incorporated both spatial and abiotic requirements resulting in more effective climate adaptation options.

Keywords Dispersal · Environmental stochasticity · Extreme weather events · Habitat restoration · Landscape-climate interactions · Metapopulation model

Introduction

That climate change is likely to pose a major challenge for biodiversity conservation is beyond doubt (Thomas et al. 2004; Bellard et al. 2012). While there is relative consensus on the key effects of climate change at large scales, e.g. shifts in suitable climate zones, more frequent and more extreme weather events like heavy rainfall, and periods of droughts (Stocker et al. 2013), the effects of climate change at finer spatial scales and how these will play out for individual species and habitat types are difficult to predict. Despite these uncertainties, climate change adaptation measures need to be implemented locally and in the near future, as recreated or restored habitat needs time to mature before species are able to benefit from these measures in terms of adaptation or resilience to climatic change. The list of recommendations on climate change adaptation for biodiversity is long (e.g. Heller and Zavaleta 2009; Mawdsley et al. 2009; Mooney et al. 2009), but the recommendations are typically generic. Which adaptation measures are most effectively applied in a local planning context, depends on (i) the specifics of the planning location (e.g. the size and spatial configuration of the ecosystem network within and around the planning area, the intensity of land use in which the network is embedded), (ii) the state of the ecosystems (e.g. level of pollution, nutrient load, desiccation), (iii) the viability of the species of concern, and (iv) the expected effects of climate change, including the vulnerability of the ecosystem and the species thereto.

Several impacts of climate change particularly influence species survival in ecosystem networks. Shifting suitable climate zones are an important factor driving shifts in species geographical distributions (Root et al. 2003; Gaston 2006), provided that the spatial cohesion within ecosystem networks is sufficient to facilitate these range shifts (Vos et al. 2008). More frequent weather extremes cause larger population fluctuations, increasing local extinction probabilities (Verboom et al. 2010). A number of adaptation measures have been suggested to strengthen the

adaptive capacity of ecosystem networks to cope with these impacts, e.g. increase the connectivity within and between ecosystem networks to facilitate range shifts, enlarge the carrying capacity of the network by adding new habitats or enlarging existing habitat patches and improve the abiotic conditions to dampen the impacts of weather extremes and changing conditions (e.g. Heller and Zavaleta 2009; Mawdsley et al. 2009; Mooney et al. 2009; European Commission 2013).

In intensively-used landscapes, where areas of natural habitat are typically small and fragmented, green infrastructure has been suggested as a measure to reduce fragmentation in ecosystem networks (Benedict and McMahon 2006). Green infrastructure, which is here defined as small, natural elements within the agricultural landscape (such as hedgerows, natural water verges, ponds and small woods or semi-natural grassland), could improve landscape permeability and might function as reproduction habitat to certain species (Jongman and Pungetti 2004). Green infrastructure has been frequently applied in landscape planning as it provides many other ecosystem services to society, and it can be combined with agricultural practice (Benedict and McMahon 2002, 2006; Fischer et al. 2006). The question is however whether adding green infrastructure to ecosystem networks will also allow species to cope with the multiple impacts of climate change: weather extremes, changing abiotic conditions and shifting suitable climate zones?

To shed some light on this question we developed scenarios with different landscape configurations, and evaluated these using a spatially-explicit metapopulation model that incorporates the impacts of changing weather conditions on population dynamics, under different climate change scenarios. We specifically assessed the effectiveness of green infrastructure as a climate adaptation measure for great crested newt (*Triturus cristatus*) in a case study area in the Netherlands, the Baakse Beek stream valley (see “Study area” section for details). This region is currently going through a planning process to make the region climate proof, and one of the challenges identified by stakeholders is the adaptation of the ecosystem network. Given the multiple land use planning challenges (agriculture, water, nature), there is an explicit interest to test the effectiveness of green infrastructure being an adaptation measure with multiple potential benefits. Hence, two landscapes scenarios were developed where habitat was added in the

form of green infrastructure, in low density (“*Broad-Zone*” scenario) and high density (“*NarrowZone*” scenario). As enlarging existing natural areas or increasing the amount of green infrastructure between nature areas are often mentioned as alternate strategies (Van Langevelde et al. 2002; Falcy and Estades 2007; Schippers et al. 2009a), an “*EnlargeArea*” scenario was added to the set of scenarios. Finally, based on the insights gained from these scenarios, a scenario was developed that would be expected to meet the multiple challenges from climate change and landscape configuration for great crested newt in this specific region (“*Optimal*” scenario), to illustrate a set of landscape design rules for spatial planning.

The great crested newt was selected as a model species, because (i) it is a characteristic species for the Baakse Beek area; (ii) it is a species of conservation concern in the Netherlands, listed as ‘vulnerable’ on the national red list, and a species for which the Netherlands has international responsibility (Habitats Directive, listed at Annex II and Annex IV); (iii) great crested newts depend on both terrestrial and aquatic habitat throughout their life span, and are considered sensitive to landscape configuration upon dispersal (Jehle and Arntzen 2000); and (iv) amphibians are considered sensitive to climate change as they are sensitive to environmental stochasticity and depend on small waters that are vulnerable to droughts (Blaustein et al. 2010). Studying the effects of climate change on the viability of a species like the great crested newt, and the effectiveness of landscape adaptation measures, could therefore bring broader understanding of the conservation needs of a larger group of terrestrial species with limited dispersal capacity.

Methods

Study area

The Baakse Beek stream valley in the east of the Netherlands (hereafter indicated as “Baakse Beek”) is a region of 30,000 ha dominated by dairy farming and rural villages (Fig. 1). The western section is characterized by several historic estates. A stream flows through the region from east to west, which has been fully adjusted in the past to allow for agriculture in the formerly bog-dominated region. This region is currently going through a planning process to make the region climate

proof. The process involves local land owners, government bodies (local and regional) and NGOs (farmers associations and nature management organizations).

Land cover data from the year 2009 were available at a 25×25 m grid resolution from VIRIS 2006 (<http://www.wageningenur.nl/nl/show/VIRIS.htm>) and LGN6 raster (Hazeu et al. 2010). In LGN6 each grid cell is assigned to the dominant land cover type in that grid cell, while in VIRIS data each grid cell can consist of multiple land cover types, in proportion to the fraction present. Reproduction water point data (pond map) was provided by the Province of Gelderland (2005), as most small ponds are not included in the land cover data. From these data sets we created habitat suitability maps for reproduction and dispersal. A landscape buffer of five km around the Baakse Beek region was used in habitat classifications, to account for habitat clusters just beyond the region that are relevant from a population dynamic perspective. While newts reproduce in ponds, the surrounding terrestrial habitat is critical during the post-breeding period for feeding, shelter from predation and hibernation of the juvenile and adult population (Griffiths 1996; Müllner 2001). Land cover types that are considered suitable terrestrial habitat are deciduous forests, natural or old pastures and hedgerows (Cooke 1986; Griffiths 1996; Jehle and Arntzen 2000; Langton et al. 2001). For each grid cell of 25×25 m the total area of land cover that was classified as terrestrial habitat was summed, to a maximum of 625 m^2 . For the dispersal habitat map land cover types that can be assumed to be preferred by newts for dispersal were classified as ‘dispersal habitat’, such as deciduous forests, shrubs, hedgerows, tree lines and pastures (Table 1), while open fields with sparse vegetation are actively avoided during movements through agricultural landscapes (Cooke 1986; Jehle and Arntzen 2000; Müllner 2001; Malmgren 2002). Hence, the intensively-managed grasslands for dairy farming and arable land were considered as unsuitable habitat for dispersal. For each grid cell of 25×25 m the total area of land cover that was classified as dispersal habitat was summed, to a maximum of 625 m^2 .

From all ponds in the pond map, only ponds that have a carrying capacity >0 were considered as patches in the population dynamics simulations. The carrying capacity of a pond is likely to depend on pond size, pond quality, and terrestrial habitat quality in the vicinity of the pond (Oldham et al. 2000). As data on

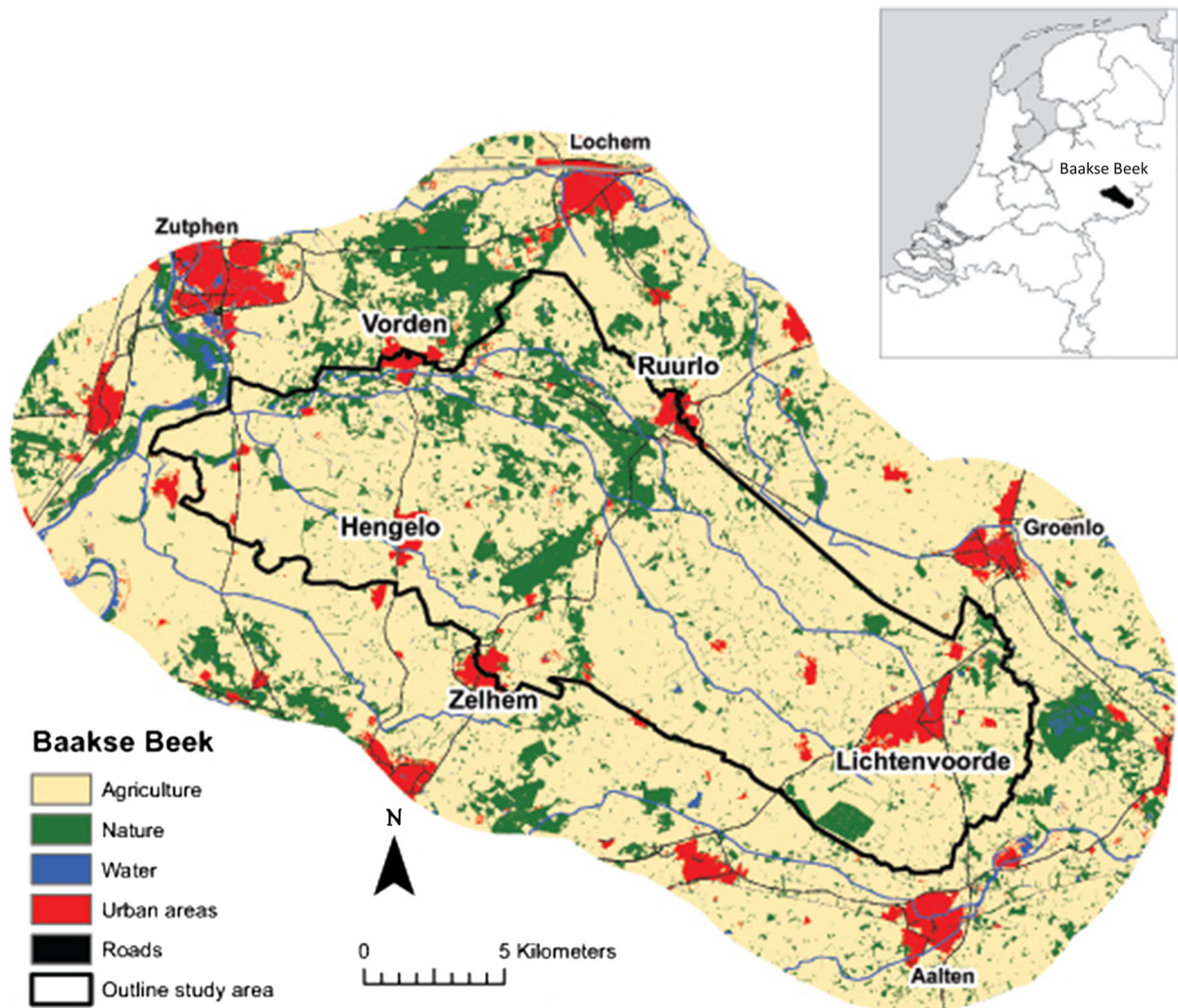


Fig. 1 The Baakse Beek study area. *Top right map*: the location of the study area in the Netherlands. *Large map*: the main land use types, water courses and roads in the study area

pond size and quality were not available, we assumed the carrying capacity to be positively related to the amount of suitable terrestrial habitat in a 250 m radius around the pond (Table 1, terrestrial habitat). Gustafson et al. (2011) indeed showed that the amount of suitable terrestrial habitat within a few hundred meters from the pond explained the presence of great crested newt in agricultural landscapes. Ponds with less than 2.5 ha of terrestrial habitat within the 250 m buffer zone were considered unsuitable for great crested newt. Beyond 2.5 ha of terrestrial habitat, pond quality was assumed to increase linearly with the amount of terrestrial habitat, reaching maximum carrying

capacity when at least 52 % (10.0 ha) of the buffer zone around a pond was covered by suitable terrestrial habitat. The carrying capacity for ponds with optimal quality was set to 75 adult females, corresponding to densities that have been reported for great crested newts in comparable landscapes (Rannap et al. 2008; Table 1). However, as newt density varies considerably in the field (about 100–300 adults depending on both pond and terrestrial habitat quality; Arntzen and Teunis 1993; Halley et al. 1996; Karlsson et al. 2007; Rannap et al. 2008; Griffiths et al. 2010), we conducted a sensitivity analysis with a minimum and maximum value for carrying capacity that can be

Table 1 Land cover types considered in the determination of patch carrying capacity and dispersal habitat

Land cover type	Terrestrial habitat determining patch carrying capacity	Dispersal Habitat	Data sources: LGN6 (2007–2008 Hazeu et al. 2010) VIRIS 2006: Alterra, http://www.wageningenur.nl/nl/show/VIRIS.htm
Deciduous forest	✓	✓	VIRIS 2006 LGN6
Mixed forest	✓	✓	VIRIS 2006
Coppice wood	✓	✓	VIRIS 2006
Alluvial forests	✓	✓	LGN6
Aspen tree stands	✓	✓	VIRIS 2006
Hedgerows (a width of 10 m was assumed for area calculations)	✓	✓	VIRIS 2006
Tree lines (a width of 10 m was assumed for area calculations)	–	✓	VIRIS 2006
Natural grasslands (area × 0.5 as being suboptimal habitat for great crested newt)	✓	✓	LGN6

considered realistic in the context of the Baakse Beek: 50 and 125 adult female newts per pond, respectively. Results of the sensitivity analysis are reported in the supplementary material (Tables S3 and S4), all other results are based on a carrying capacity of 75.

Landscape scenarios

The Province's nature conservation target foresees in the re-creation of 500 ha habitat. To identify in what spatial configuration additional habitat would be effective as a climate adaptation strategy, we tested four different landscape scenarios. The Province identified three different zones where the additional habitat could be created (Fig. 2a–c, scenarios *BroadZone*, *NarrowZone*, *EnlargeAreas*). In addition we identified a zone that would be more optimal from the perspective of a species like the great crested newt, given its dispersal capacity and habitat requirements (Fig. 2d, *Optimal*). For scenarios *Narrow Zone* and *Broad Zone* 500 ha of terrestrial habitat for newt (Table 1, terrestrial habitat) was added to the current landscape in the form of green infrastructure (GI), being a combination of linear natural landscape elements along fields margins, and small nature parcels. A landscape generator was developed which assigned GI randomly over the available field margins within the respective zone. Agricultural parcel data was available in vector format and overlaid with the 25 × 25 m grid from the LGN6 and VIRIS data sets. All grid cells in the present landscape that contained a

field margin and where less than 250 m² of newt habitat (Table 1, terrestrial habitat) was present, were upgraded to 250 m² newt terrestrial habitat per grid cell. This amount corresponds to a linear natural element along the field margin of approximately 10 m wide. In addition, small fields were randomly transformed into nature parcels with woody vegetation, in order to be able to reach the 500 ha habitat restoration target. A field was considered small if 70 % or more of the grid cells of a particular field contained a field margin. In addition, a grid with 1 × 1 km cell size was placed over the broad and the narrow zone respectively. For those 1 km² grid cells within the zone that did not contain at least two ponds, one or two additional ponds were added in a random manner, to ensure that in every square kilometre of the zone a minimum of two potential reproduction sites was present. Of all scenarios, *BroadZone* received the largest number of ponds to meet this requirement (151 ponds, Table S2 in supplementary material), but a large fraction of these ponds had low to zero carrying capacity due to low habitat density within the zone (Fig. 3).

In the *EnlargeAreas* scenario existing nature conservation areas were enlarged by 500 ha. The province of Gelderland has the ambition to enlarge existing nature conservation areas and create new areas in the Baakse Beek, in so called key areas, i.e. the grey segments in Fig. 2c (derived from the conservation plan 'Herijkte EHS', Province of Gelderland). The province has assigned specific nature conservation

Fig. 2 Landscape scenarios. **a** *NarrowZone*, **b** *BroadZone*, **c** *EnlargeAreas* and **d** *Optimal*. For each scenario 500 ha terrestrial habitat was added in the grey zones (see “Methods” section for details). Furthermore, ponds were added to achieve a minimum of two potential breeding sites per km² in the grey areas

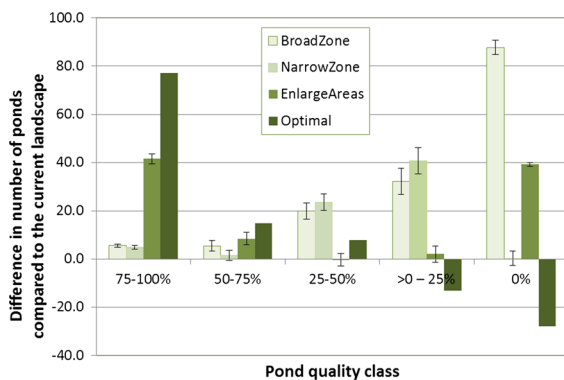
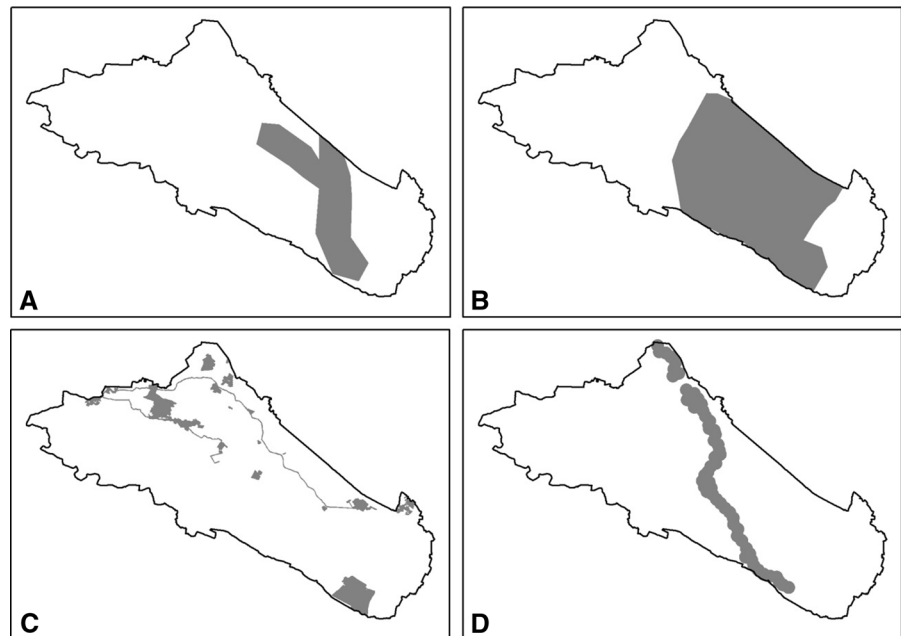


Fig. 3 Number of ponds more (positive values) or less (negative values) per landscape scenario, compared to the current landscape, categorized per pond quality class (pond quality is expressed as the percentage of maximum carrying capacity). See table S1 for absolute numbers per scenario and pond quality class. Error bars indicate the SD around the mean for the 10 replicate landscapes that were generated for scenarios *BroadZone*, *NarrowZone* and *EnlargeAreas*

targets to these key areas. First, we calculated the amount of projected habitat to be restored (according to the Provincial conservation plan) for the great crested newt within the key areas (i.e. 62.9 ha in total, see Table S1 in supplementary material for a list of habitat target types that were considered suitable for great crested newt). Subsequently, we added the

remaining hectares in a random fashion within the key area boundaries to a maximum of 500 ha. To do so, from all grid cells in the key areas that were adjacent to existing nature, one cell was selected at random. For the key area in which this cell is positioned, terrestrial newt habitat was added to all cells that were adjacent to the existing nature in that key area, with a maximum of 10 ha in total, or less when not enough space was available within the key area boundaries. Next, a new grid cell was selected at random and again a maximum of 10 ha was added until the target of 500 ha was reached. In line with the procedure described above, additional ponds were added to each 1-km² grid cell within key areas, to ensure each square kilometre of key area contained two potential reproduction sites at minimum. For each of the scenarios *BroadZone*, *NarrowZone* and *EnlargeAreas* ten random landscapes were created, to account for variation in habitat allocation.

In scenario *Optimal*, the zone for habitat allocation was selected in such a way that there was already a relatively high habitat density present within the zone and that it contained sections with a relatively high ground water table, compared to the surrounding landscape (Van Ek et al. 2012). Within the zone, the habitat density was increased by adding 500 ha of terrestrial habitat, combined with additional ponds.

Choosing the locations with high ground water tables, ponds were added at approximately 500 m intervals along the zone, and for these ponds the amount of terrestrial habitat (Table 1) was assessed within 250 m distance from the pond. If this summed up to less than 10 ha terrestrial habitat, which corresponds to a pond with maximum carrying capacity, additional GI was added to the cells surrounding the pond. On those locations where already sufficient terrestrial habitat was present only a pond was added. In total 59 ponds were added in this scenario, which was the lowest of all landscape scenarios (Table S2 in supplementary material). In scenario *Optimal*, the number of poor quality ponds reduced due to the addition of terrestrial habitat, and the number of ponds with high carrying capacity substantially increased (Fig. 3).

Climate scenarios

Three climate scenarios were used: the current climate and two contrasting scenarios, a mild climate change scenario (G) and a severe climate change scenario (W^+ , Van den Hurk et al. 2006). These national climate scenarios, developed by the Royal Dutch Meteorological Institute (KNMI) include translated global climate projections to detailed changes in temperature, precipitation, evapotranspiration, wind and sea level for the Netherlands. The G scenario assumes an increased warming of 1 °C in 2050 without changes in air circulation, increasing they early precipitation. The W^+ scenario assumes an increased warming of 2 °C in 2050 and changes in air circulation, leading to wetter winters and drier summers. The observations of current climate (1981–2010) and projections of future climate for G and W^+ were obtained from KNMI, for weather stations Twenthe-290 (temperature) and Twenthe-670 (precipitation and evapotranspiration), which are representative for the Baakse Beek. The 30 years of observations with daily values were used to project future weather patterns, under one of the three climate scenarios (see Bakker and Bessembinder 2012). As a result, for each year in the period 2011–2085, 30 alternative projections were available under each of the climate scenarios. From the respective climate scenario series, random samples were drawn per year out of the 30 alternative projections for that given year. To get consistent within-year values, sampling was done on a yearly basis. These random time series of weather events were used in the

metapopulation simulations. As we modelled 500 independent metapopulation simulations per landscape-climate scenario, 500 random time series of weather pattern were generated for each climate scenario.

Based on literature we deduced three seasonal weather effects that are expected to influence the reproduction success of the great crested newt:

Mild winters

In temperate climates, mild temperatures during the winter can result in hibernating animals continuing to deplete energy reserves while being unable to feed, resulting in higher mortality (Griffiths et al. 2010) and poorer reproductive capacity in the following spring (Jørgensen 1986; Reading 2007). Mild winters were captured in the metapopulation model as a reduction in recruitment success in the following season, using a multiplication factor MW on recruitment, which reduced recruitment with increasing average winter temperature:

$$MW = 1 - \frac{\max(\bar{T} - 6.0)^\beta}{(\alpha - 6)^\beta + \max(\bar{T} - 6.0)^\beta}$$

with \bar{T} representing the average temperature in the time period from the 1st of November till the 28th of February, and $\bar{T} - 6$ being the average temperature above 6 °C. α is the temperature at which the reproduction is assumed to be halved ($MW = 0.5$, at $\alpha = 9$ °C). β sets the steepness of the function and was set to 2. Under climate scenario G the number of mild winters was comparable to the current climate, with a slight increase towards the end of the century (Fig. 4). Under the W^+ scenario the number of wild minters increases, negatively affecting population recruitment especially towards end of the century (a reduction of 30 % on average; Fig. 4 left panel).

Early spring

As a result of warmer spring temperatures the breeding phenology of many species, including amphibians (Carroll et al. 2009), has started earlier (Van Vliet 2008). It is to be expected that these earlier spawning dates will result in an early date of metamorphosis, which has been shown to have a positive effect on first winter survival of juveniles (Schmidt et al. 2012). Therefore we assumed that an early spring had a

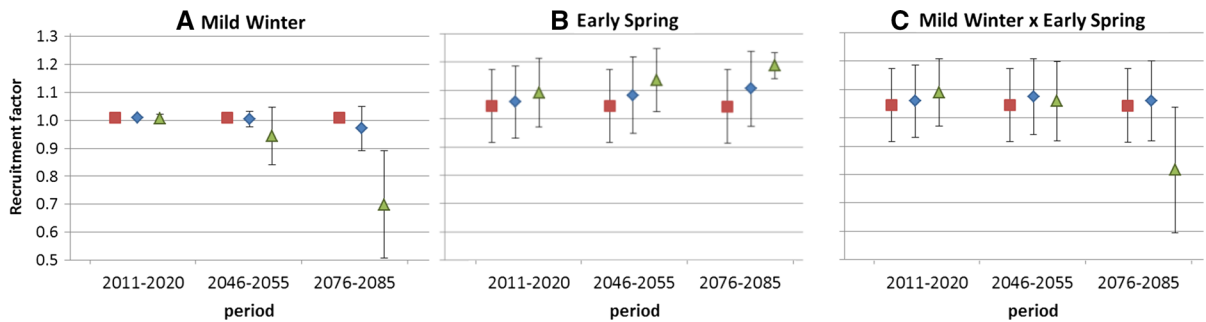


Fig. 4 The mean effect of weather events (\pm SD) on the recruitment of great crested newt in different time periods under different climate scenarios. **a** Mild winter; **b** Early spring; **c** The effects of Mild winter and Early spring combined. Symbols

represent the climate scenarios: squares Current climate; diamonds scenario G; triangles scenario W⁺. Values >1 indicate recruitment is better than average, values <1 indicate recruitment is worse than average

positive impact on recruitment. A year was considered to have an early spring (ES) when a 1-week moving average temperature rises above 7.9 °C, measured from the 14th of February till the 15th of April. This relationship was based on data from 2005 to 2012 on the first appearance of edible frogs (*Pelophylax kl. Esculentus*) from the phenological observatory network of the Netherlands (www.natuurkalender.nl), which we compared to data of the KNMI on 1-week moving average temperatures. The multiplication factor *ES* on recruitment was assumed to depend on the predicted emergence day *E*, following

$$ES = \frac{4}{5} + \frac{2}{5} \left(1 - \frac{E^\delta}{D^\delta + E^\delta} \right)$$

where *E* was calculated from the daily weather series that was generated for each run of the metapopulation model, *D* is the reference emergence day (set to day number 75 = March 16th), δ sets the steepness of the function (set to 5), and the fractions 4/5 and 2/5 are used to scale the function between 0.8 and 1.2, which was considered a reasonable range for the effect of ES. The frequency of ES events increased under the G and W⁺ climate scenarios, with a positive effect on recruitment (Fig. 4 middle panel). The effects of mild winters and ESs were combined in the metapopulation model (see Fig. 4 right panel for the combined effect in different time periods for different climate scenarios).

Pond desiccation

Since great crested newt eggs are laid in ponds and larvae use water resources to develop into

metamorphs, complete pond desiccation during egg and larvae development will result in few, if any, crested newt larvae surviving to metamorphosis, i.e. zero recruitment (Arntzen and Teunis 1993; Griffiths and Williams 2000, 2001; Ryan et al. 2014). Pond desiccation may also be beneficial to amphibians as it can periodically eliminate predators (Adams 2000; Ryan et al. 2014). However, irrespective of predation pressure, desiccation before the juveniles are ready to leave the pond is detrimental for recruitment. It is this effect of early desiccation on recruitment, which can be enhanced by climate change as shown by Ryan et al. (2014), that is relevant to consider here. The probability of pond desiccation was assumed to depend on a combination of the accumulated water deficit, and the ground water level at the pond's location. The accumulated water deficit was calculated as the daily evapotranspiration, times 1.25 to obtain the potential evapotranspiration of surface water (Hooghart and Lablans 1988), minus precipitation, both in mm, over the period March 1st–October 31st. Ponds in regions with high ground water levels (≤ 100 mm below ground level) were assumed not to be sensitive to pond desiccation and recruitment was not affected, irrespective of the water deficit in a particular year. For ponds in regions with medium ground water levels (between >100 and <150 mm below ground level) recruitment was assumed to be halved in years when the deficit was more than 220 mm. For ponds in the driest regions (ground water levels ≥ 150 mm below ground level) recruitment was assumed to be halved in years where the water deficit was between 145 and 220 mm, while recruitment was assumed to be zero in years with a water deficit of

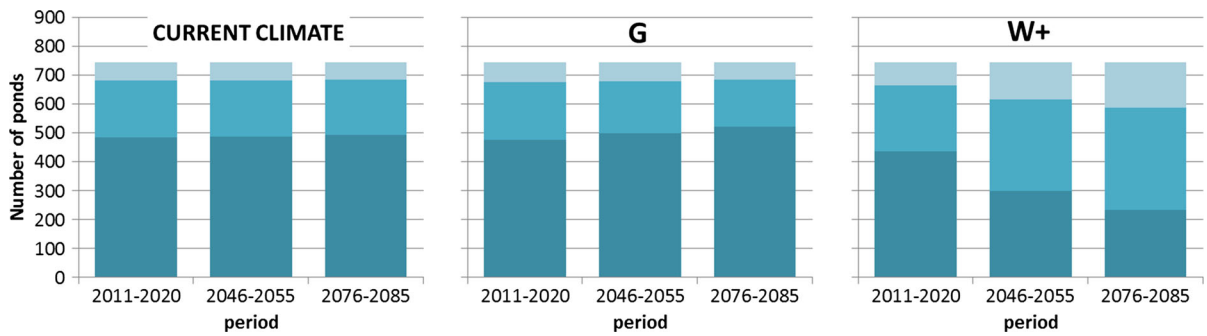


Fig. 5 The mean number of ponds in the current landscape that is subject to desiccation in different time periods under different climate scenarios. In *dark shading (bottom)* ponds that are not affected. In *medium shading (middle)*, ponds where recruitment

is halved as a result of partial pond desiccation. In *light shading (top)*, ponds where recruitment is zero as a result of complete pond desiccation

more than 220 mm. Under these assumptions, in the current landscape under current climate conditions, on average 35 % of the patches was affected by desiccation annually, and in 8 % of all patches recruitment failed completely (Fig. 5, left panel). Under the G climate scenario, less patches were subject to desiccation: towards the end of the century approximately 30 % of the patches was affected by desiccation, and the number of patches where recruitment failed completely was stable around 8 % (Fig. 5 middle panel). Under the W⁺ scenario the number of patches subject to desiccation increased to 68 % on average, with complete failure of recruitment in 21 % of all patches (Fig. 5, right panel).

Metapopulation model for great crested newt

We used the spatially-explicit demographic stochastic model METAPOP (Schippers et al. 2009b) to model the population dynamics of the great crested newt in annual time steps. Since great crested newts are known to be polygynous animals (Griffiths et al. 2010), we considered only female individuals, in three age classes: juveniles (1-year old), sub-adults (2-year old) and adults (3 years or older). During a year, three events were simulated: (i) survival/aging; (ii) dispersal; (iii) recruitment (see Table 2 for parameter values). Survival/aging was modelled as a probabilistic density-independent process. Recruitment was modelled as a density-dependent stochastic process, where each adult female produced a number of one-year-old recruits according to a Poisson distribution. Recruitment success was influenced by weather events (as described in “Landscape scenarios” section). The

dispersal process was divided into two parts: (a) probability to disperse, i.e. the likelihood that an individual newt will disperse, which for adults was assumed to be density dependent (Table 2); (b) probability to immigrate into another patch, determined by the distance from the original patch and the permeability of the intermediate landscape, as estimated using a grid-based movement model, described next.

Patch connectivity, defined as the probability of an individual newt that leaves one patch to arrive at each other patch, was estimated using a grid-based movement model (Schippers et al. 1996). The model simulated a correlated random walk on a grid (each cell with eight neighbours), with the probability of moving to a neighbour cell depending on this cell’s preference value multiplied by a normalized weight, which depends on the direction of the previous move. Preference values were based upon a cell’s amount of dispersal habitat (see Table 1), which was converted into a preference value assuming a logistic relationship with dispersal habitat area A :

$$Preference = \frac{1}{1 + e^{-0.1 \times A + 3.8}}$$

A mean ‘filter’ was applied, averaging the preference values over each focal cell and its eight neighbouring cells, to avoid anomalies in simulating movement behaviour caused by the high spatial discreteness in preference values. For each landscape map, separate movement simulations were performed using the preference map, to estimate patch-to-patch dispersal probabilities. Normalized weights were obtained from a circular von Mises distribution with

Table 2 Parameter values of the metapopulation model for great crested newt

Parameter	Value	Source
Patch carrying capacity (number of adult females per patch)	75*	(Arntzen and Teunis 1993; Griffiths et al. 2010; Halley et al. 1996; Karlsson et al. 2007; Rannap et al. 2008)
Survival probability: juveniles → sub-adults	0.37 ± 0.2	(Griffiths and Williams 2000, 2001)
Survival probability: (sub)adult → adult	0.68 ± 0.19	(Griffiths and Williams 2000, 2001)
Recruitment: # juvenile females per adult female at low population density	2.8**	(Griffiths and Williams 2000)
Recruitment: # juvenile females per adult female at high population density	1.4**	–
Maximum dispersal distance (km)	1	(Arntzen and Teunis 1993; Arntzen and Wallis 1991; Griffiths et al. 2010; Langton et al. 2001)
Sub-adult and juvenile dispersal probability (density independent)	0.10	(Griffiths and Williams 2000; Halley et al. 1996; Karlsson et al. 2007; Langton et al. 2001; Natural England 2001)
Adult dispersal probability at low density	0.01	(Griffiths and Williams 2000; Halley et al. 1996; Karlsson et al. 2007; Langton et al. 2001; Natural England 2001)
Adult dispersal probability at high density	0.10	–

* A carrying capacity of 75 adult females corresponds to densities that have been reported for great crested newts in comparable landscapes (Rannap et al. 2008; Table 1). Since newt density varies considerably in the field (about 100–300 adults depending on both pond and terrestrial habitat quality; Arntzen and Teunis 1993; Griffiths et al. 2010; Halley et al. 1996; Karlsson et al. 2007; Rannap et al. 2008), a sensitivity analysis with a minimum (50) and maximum (125) number of adult females per patch was conducted. These values can be considered realistic in the context of the Baakse Beek. See Table S3 (Supplementary material) for results of the sensitivity analysis. All other results are based on a carrying capacity of 75 adult females

** The value for recruitment is multiplied by a factor that is determined by the seasonal weather events *Mild winter*, *Early spring* and *Pond desiccation*, see “[Climate scenarios](#)” section

concentration coefficient k set to 0.75 as the total probability density within each of $360^\circ/8$ directions (representing forward, backward, left- and rightward moves, plus the four directions in between). From each cell belonging to a patch [i.e. all cells within 250 m of a pond that had a carrying capacity >0 (see “[Study area](#)” section)], 5000 movement paths were simulated. When an individual encountered a cell belonging to another patch before the maximum number of steps was reached, it immigrated into the patch and movement stopped. The maximum number of steps in the movement simulations (560 steps) was estimated using a simulation of random walk movement on a uniform grid with 25 m cells, as the number of steps required to get a 90-percentile maximum excursion distance of 1 km (thus only 10 % of the dispersers is predicted to cover larger maximum excursion distances). In principle a correlated random walk allows individuals to make longer excursions than a random walk, but as migrant interception is modelled as a deterministic process upon pond encounter, the

90-percentile maximum excursion distance did not exceed 1 km in the Baakse Beek landscape, but ranged between 775 and 875 m over all landscape scenarios. These probabilities were used in the metapopulation model, at step (b) of the dispersal process.

For each combination of a landscape map and climate scenario, 500 replicate simulations (runs) of the metapopulation dynamics were conducted. Each run was initiated with all sites occupied, with the number of individuals scaled by the relative patch quality r (carrying capacity/maximum carrying capacity) at a low density of $5r$ adults + $2.5r$ sub-adults + $2.5r$ juveniles. We first simulated population dynamics for a 75-year burn-in period (test runs demonstrated that metapopulation size reached a quasi-equilibrium within 75 years), followed by a 100-year simulation period. In each run, weather patterns derived from the current climate were used during the first 100 years, while the latter 75 years had weather patterns derived from the respective climate

scenario used (current, G, W⁺). For each run a new set of weather patterns was generated (see “Landscape scenarios” section). Results are based on the statistics of these 100-year periods after the burn-in period. Runs in which the metapopulation went extinct before the end of the burn-in period were omitted. For each combination of landscape scenario and climate we recorded (i) the metapopulation extinction probability after the 100-year simulation period, based on those runs in which the metapopulation was extant at the time the 100-year period started, (ii) the total number of females in the metapopulation, and (iii) the occupancy probability per km².

Results

In the current landscape under current climatic conditions the metapopulation extinction probability was estimated to be 11.0 % in 100 years. Under climate change, metapopulation extinction probability slightly decreased under the G scenario (9.4 %) but increased to 16.7 % under the W⁺ scenario (Fig. 6). The size of the metapopulation was estimated to increase by 14 % under the G scenario, but decrease by 61 % under the W⁺ scenario by the end of the simulation period (100 years) (Fig. 7). In the current landscape the occupancy pattern showed strongholds in the landscape at the Baakse Beek boundaries, but within the region occupancy patterns were relatively low (Fig. 8a). This is also supported by the landscape

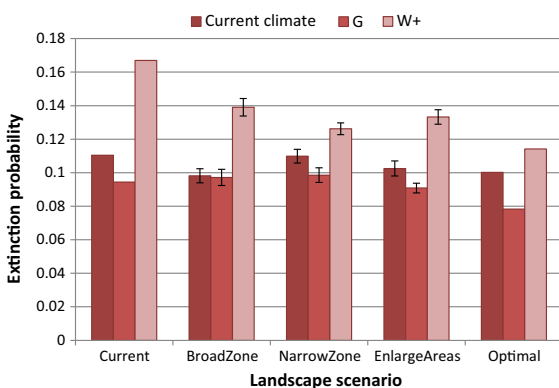


Fig. 6 Metapopulation extinction probability after 100 years estimated from 500 runs per landscape, for each climate scenario. Simulations were run for a single landscape for the current landscape and the optimal scenario, for other landscape scenarios the extinction probability is the mean over the 10 random landscapes ± the SE

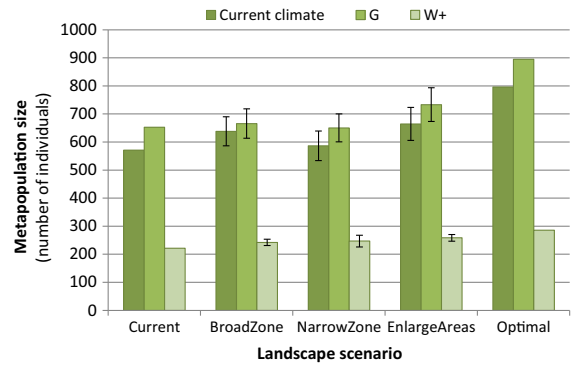


Fig. 7 The mean number of individuals in the metapopulation during the last 10 years of the 100-year simulation period, calculated over those simulations in which the metapopulation was extant after 100 years. Simulations were run for a single landscape for the current landscape and the *Optimal* scenario, for other landscape scenarios the metapopulation size is the mean over the 10 random landscapes ± the SE

permeability map (Fig. 9a): around the strongholds landscape permeability was high, but the central part of the study area, where habitat availability is low, dispersal activities by great crested newt were predicted to be low. Under a mild climate change scenario (G), the occupancy probabilities per km² during the last ten years of the simulation period changed marginally with at maximum −5 to 5 % points compared to the current climate scenario (Fig. 8b). The severe climate change scenario (W⁺) predominantly showed large scale decreases in occupancy frequency across the entire region, up to 15 % points (Fig. 8c). In particular under the W⁺ scenario the low density of habitat in the study region could therefore become a major bottleneck in population viability.

The differences between the current landscape and the landscape scenarios *BroadZone*, *NarrowZone* and *EnlargeAreas* were generally small (Figs. 6, 7), which held under the sensitivity analysis for carrying capacity (Tables S3 and S4 in supplementary material). This indicates that the additional 500 ha of terrestrial habitat and the additional ponds in these scenarios provided little benefit at the metapopulation level even though *NarrowZone* and *BroadZone* showed increases in permeability (Fig. 9b and Fig. S1) and some increase in occupancy frequency (Fig. S2) within these zones. Only under scenario *Optimal* the performance of the metapopulation as a whole improved considerably (Figs. 6, 7), especially under the W⁺ scenario, irrespective of the carrying capacity

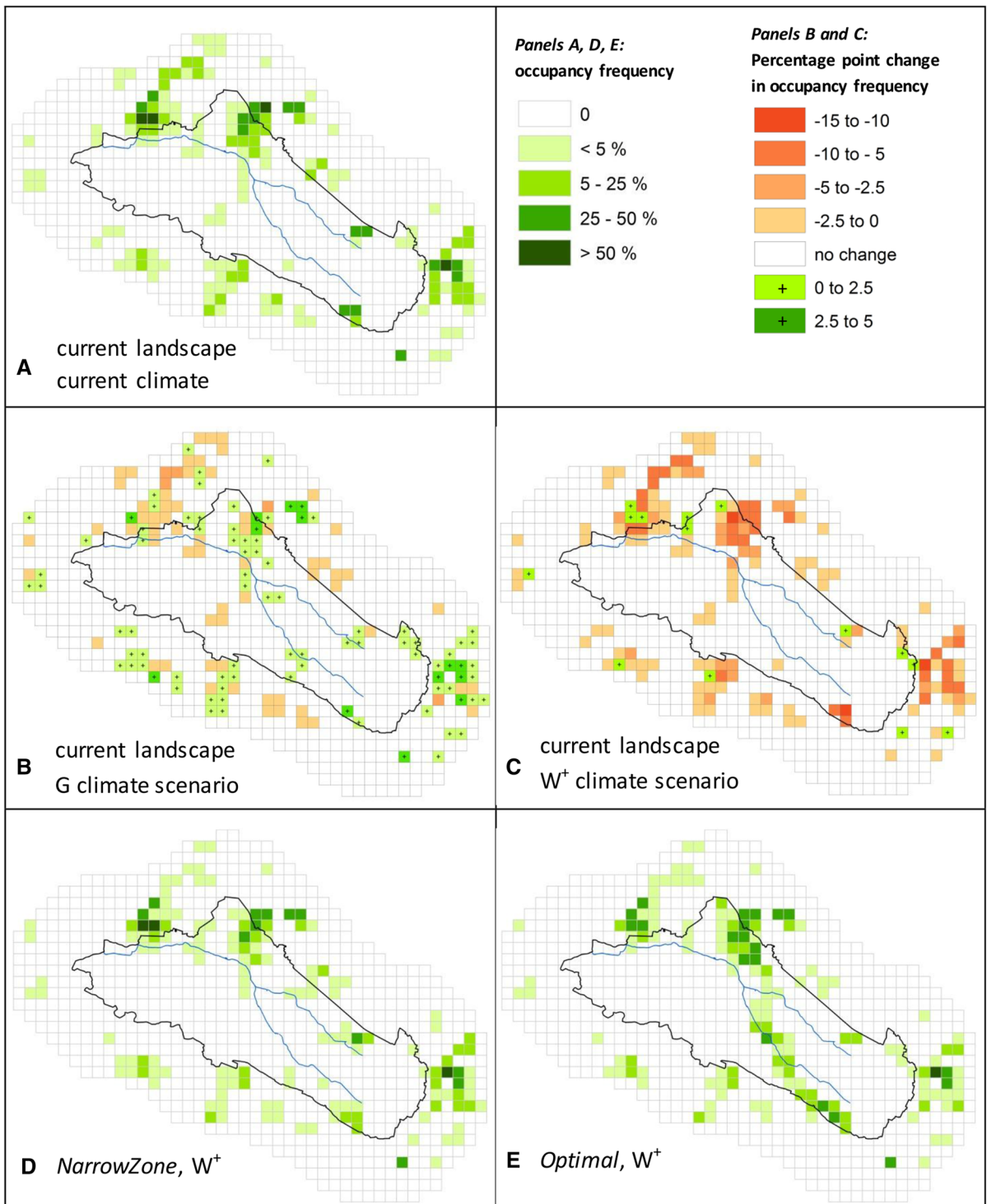
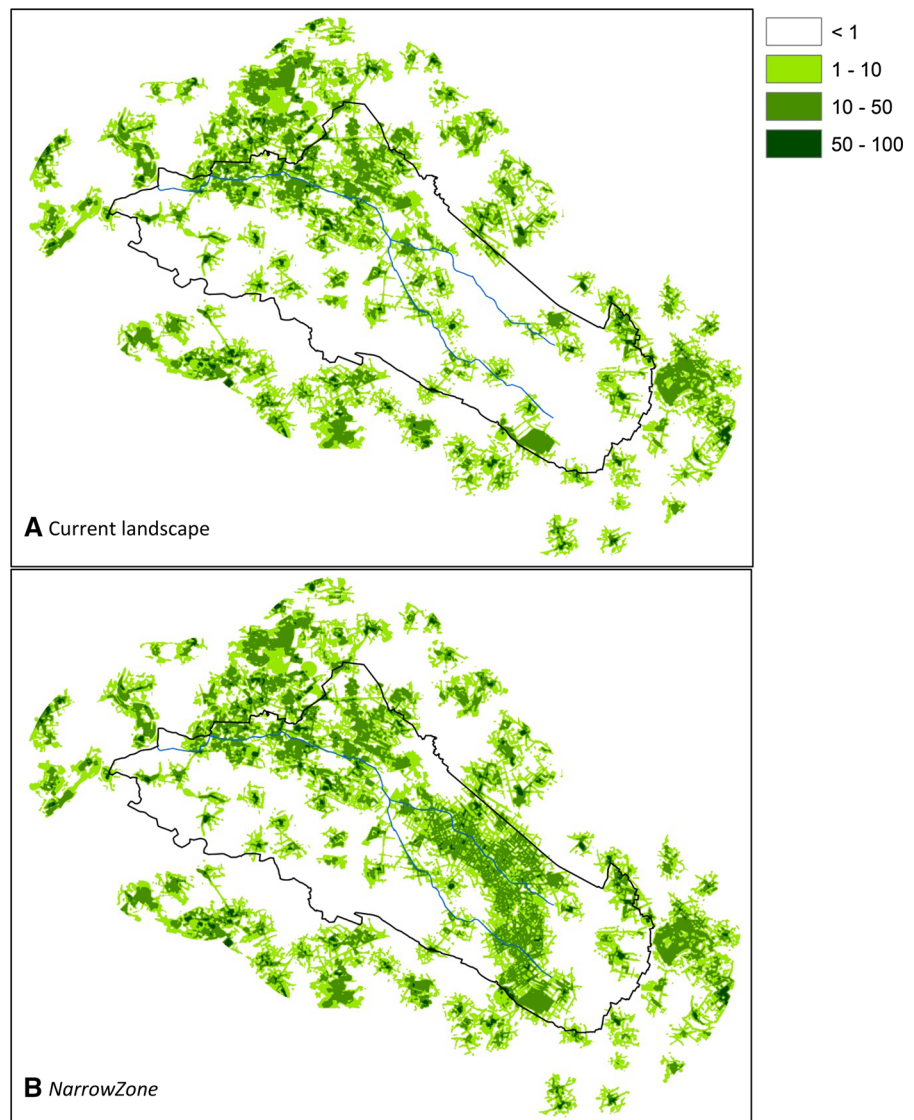


Fig. 8 The mean occupancy frequency of 1 km² grid cells (in percentage of years), for the last 10 years of the metapopulation simulation period. **a** The current landscape under the current climate; **b–c** the relative difference in occupancy frequency, compared to map **(a)**; **b** current landscape, climate scenario G; **c** current landscape, climate scenario W⁺, **d** *NarrowZone*, W⁺ climate scenario [the replicate landscape that is closest to the average out of 10 replicates is shown]; **e** *Optimal*, W⁺ climate scenario. The borders of the region as well as the Baakse Beek and Veengoot streams are indicated as a reference

(Tables S3 and S4). Occupancy patterns for *Optimal* (Fig. S2 panels J–L) clearly reflect the enhanced population performance in the central area.

Climate change had a comparable effect on metapopulation performance in all landscape scenarios: under the G scenario the metapopulation generally performed slightly better than under current climate, but differences were small. The W⁺ scenario was the most detrimental climate scenario, independent of the landscape scenario under study and irrespective of the carrying capacity (Tables S3 and S4). Adapting the landscape according to the *Optimal* scenario allowed the species to cope with the negative effects of a W⁺ climate regime, in terms of extinction risk. Nevertheless, the metapopulation size is expected to be almost twice as small (over 500 individuals on average versus

Fig. 9 Landscape permeability for great crested newt, as measured by the relative visiting frequency of sites by newts upon dispersal, based on the movement model simulations (newt dispersal was simulated from all ponds with carrying capacity >0). **a** Current landscape; **b** *NarrowZone* (one out of ten replicate landscapes). The frequency increases with the darkness of the shading. The borders of the region as well as the Baakse Beek and Veengoot streams are indicated as a reference. Maps for all scenarios are available as Supplementary material (Figure S1)



less than 300 individuals on average towards the end of the simulation period). In terms of occupancy, the areas with additional habitat showed higher occupancy patterns compared to the current landscape, also under the W^+ scenario (Fig. 8d, e and Fig. S2).

Discussion

Using a mechanistic modelling approach, we have assessed the potential effects of climate change on a species like great crested newt, and tested landscape adaptation options that differ in the spatial configuration of additional habitat, for a concrete study area. Our results indicate that climate change can have a considerable negative effect on population viability of great crested newts in fragmented landscapes, when events like pond desiccation and mild winters become more frequent and more pronounced, reducing reproduction success (W^+ climate scenario; Figs. 4, 5). Mild climate change, resulting in more frequent ESs, may entail a positive effect on species like great crested newt (G climate scenario; Figs. 4, 5).

To overcome such negative effects of climate change, we considered landscape adaptation options that involved the re-creation of ponds and terrestrial habitat, in four different spatial configurations including two scenarios where habitat was added in the form of additional GI. We assessed our results in the light of two properties that are typically assigned to successful climate adaptation measures: firstly, to support populations given more frequent and more severe environmental stochasticity due to extreme weather events; and secondly, to facilitate range shifts.

Regarding the first aspect, we showed that additional habitat can allow a metapopulation to better cope with more severe environmental stochasticity (mild winters, pond desiccation). The extent to which adaptation measures increased metapopulation resilience however, depended strongly on two factors that determined patch quality for great crested newt: the density of terrestrial habitat, and the location of new habitat in relation to abiotic conditions. In the *NarrowZone* and *BroadZone* scenarios, habitat was added in the form of GI, which resulted in relatively low terrestrial habitat density. Subsequently, the ponds that were added to these zones, had mostly low carrying capacity. Hence, although potential connectivity increased, metapopulation viability did not

improve despite these additional ponds. Habitat density and associated pond quality was higher in the *EnlargeAreas* scenario, and particularly in the *Optimal* scenario, where first ponds were located in the landscape which were subsequently surrounded by terrestrial habitat (Fig. 3).

In terms of abiotic conditions, the ground water level at the central part of the study region is relatively low to facilitate agriculture. As a result, additional ponds in the *BroadZone* and *NarrowZone* scenarios were sensitive to desiccation. In the *EnlargeAreas* and *Optimal* scenarios ponds were placed in locations with more suitable abiotic conditions. In scenario *Optimal* this was done deliberately by choosing the locations with the highest ground water levels in a zone from south to north. In scenario *EnlargeAreas*, the target areas for nature restoration are located in the more moist areas, as these are considered to have the highest nature value and low potential for agriculture. The combined effect of higher habitat density and higher abiotic conditions only come about in terms of species viability in the *Optimal* scenario as this scenario also enhanced connectivity, unlike *EnlargeAreas*.

With respect to the second requirement of adaptation measures i.e. the facilitation of range shifts, species need to be able to colonise suitable habitat patches at the expanding (here: northern) edge of their range. While the Baakse Beek region is small in comparison to range shifts, areas that predominantly consist of unsuitable land use types, such as the core area of the Baakse Beek, may cause spatial bottlenecks in range shifts. To alleviate such a bottleneck for dispersal-limited species in fragmented landscapes, adaptation measures that facilitate both dispersal and reproduction are a prerequisite (Opdam and Wascher 2004; Vos et al. 2010; Hodgson et al. 2012). From the landscape scenarios considered here, the *EnlargeAreas* scenario lacked such facilitation (Fig S1 in supplementary material), while the *BroadZone* and *NarrowZone* did provide dispersal habitat, but provided little to no reproduction habitat. In response to these findings, scenario *Optimal* was developed as a potential solution for the Baakse Beek area, which provided both dispersal habitat and reproduction habitat to the central part of the study area, and the occupancy patterns indicated a functional link between the southern and the northern strongholds in the region, also under more severe climate scenarios (Fig. 8e).

While GI had been found to support ecological networks (Grashof-Bokdam et al. 2009; Schippers et al. 2009a), our results provide some nuances to this general statement in the context of climate change. Additional habitat was only found to be effective if the density was sufficiently high to increase patch quality, which was not the case in the scenarios where habitat was added in the form of GI only (Fig. 3). Therefore we recommend that GI should be combined with ‘stepping stones’ of concentrated habitat. With careful design though (see *Optimal* scenario), additional habitat in multifunctional landscapes can indeed strengthen ecological networks, incorporating requirements for both the spatial conditions, habitat density and connectivity, and abiotic conditions (locations with high ground water levels). While it can be expected that different adaptation strategies are optimal for either the facilitation of range shifts, or the facilitation of species viability (e.g. Hodgson et al. 2011), our findings are in line with Hodgson et al. (2012), who found that when habitat has a channelled pattern (as in scenario *Optimal*, this study), it is possible to achieve both rapid advance and relatively high patch occupancy, for a large array of species.

Our study focussed on the great crested newt as an ambassador for a key habitat type of the Baakse Beek region: moist deciduous forests. Great crested newts are dispersal-limited, both in distance and sensitivity to land cover upon dispersal (Arntzen and Wallis 1991; Arntzen and Teunis 1993; Jehle and Arntzen 2000; Langton et al. 2001; Griffiths et al. 2010), and are sensitive to climate change (Reading 2007; Blaustein et al. 2010; Griffiths et al. 2010). As amphibians depend on both terrestrial and aquatic habitat, they are indicators for species that depend on wide array of habitat types. As such it can be assumed that our findings are illustrative for a wider group of dispersal-limited species of fragmented agricultural landscapes.

The spatial adaptation options that were assessed here, were developed in close collaboration with stakeholders who seek to climate proof this study region. Nevertheless, it needs to be assessed to what degree this ecological perspective aligns with other sectoral perspectives such as from the agricultural sector (see e.g. Bakker et al. 2015). Moreover, it is important to assess the relative effectiveness of these spatial adaptation options to other adaptation options. For example, our study revealed that pond desiccation

as a result of summer drought is a concern in the Baakse Beek area, the impact of which is expected to become a serious bottleneck in the W⁺ climate change scenario. Strategically locating new ponds and improving the terrestrial habitat around ponds with suitable abiotic conditions is therefore of crucial importance. An alternative measure to overcome these impacts, however, would be the elevation of the ground water table (Witte et al. 2015), which would reduce the vulnerability of ponds to desiccation. Such a measure might conflict with short term agricultural objectives for the region, but also agriculture will benefit from higher groundwater tables at the longer term, especially in the W⁺ scenario where summer drought decreases agricultural yields (Kros et al. 2015). In addition, given the small size of the study area, we recommend to assess the spatial adaptation options in a larger spatial context. Only then it is possible to identify where spatial bottlenecks for climate adaptation are expected to be most cost-effectively alleviated (Opdam and Wascher 2004; Vos et al. 2010; Lung et al. 2014).

There is an urgent need to move from general adaptation recommendations to context-specific, relevant options for spatial planning at local to regional scales (Van Teeffelen et al. 2014). However, the wide array of available adaptation options, together with uncertainties in climate change impacts are one factor leading to inaction in planning and management (Burch et al. 2014). Our approach allows to assess concrete spatial adaptation options in the face of climate change, as it mechanistically combines (i) spatial habitat use by the species, (ii) direct effects of climate change on species physiology and phenology (Bellard et al. 2012), and (iii) indirect effects of climate change as it alters habitat suitability (e.g. Keith et al. 2008; Cormont et al. 2013; Van Dijk et al. 2015). Concerning the latter, we incorporated the stochastic effect of pond desiccation as being the most relevant for the area and species under study, but the approach allows to assess the impact of spatial shifts in habitat suitability over time as well (see e.g. Anderson et al. 2009; Schippers et al. 2011). It is evident that uncertainties exist in the climate projections, model assumptions and parameter values (e.g. Beissinger and Westphal 1998; Drechsler et al. 2003; Naujokaitis-Lewis et al. 2009), which makes it very challenging to assess climate adaptation options for biodiversity conservation. Therefore, modelling frameworks such

as ours cannot be used to make exact inferences of species viability. Instead, the mechanistic representation of the effects of climate and habitat configuration on species viability and their joint assessment increased our understanding of the potential consequences of landscape-climate interactions on species viability and the relative effectiveness of adaptation options. These insights allowed a deduction of landscape design rules that incorporated both spatial and abiotic requirements that can be expected to result in more effective climate adaptation options.

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