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Recent range shifts of European dragonflies provide support for an inverse relationship between habitat predictability and dispersal

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ABSTRACT

Aim We compared the effects of recent shifts of northern range boundaries of odonates adapted to either lentic (standing water) or lotic (running water) habitats in Europe. Lentic species are thought to have a higher dispersal propensity than lotic species because of the lower spatial and temporal persistence of lentic habitats on average. Hence, we expected shifts in the range boundaries particularly of lentic species.

Location Europe.

Methods Our analyses are based on odonate distribution maps from two field guides that present the European ranges of dragonflies and damselflies in 1988 and 2006. We categorized species according to their preference for lentic or lotic habitats, and then assigned each species to a southern or a northern group according to the centre of its distribution. Shifts in northern range boundaries were calculated as the average distance between the 10 northernmost grid cells in 1988 and 2006. Range boundary shifts were also analysed with regard to prevalence, phenology, body size and wing size.

Results Lentic species of the southern group expanded their range boundaries on average 115 km northwards per decade, whereas lotic species of the southern group on average did not change their range boundaries. Northern lentic and lotic species showed no consistent trends in their changes in range boundaries. These results did not qualitatively change when we considered the effects of phylogeny, phenology, body size and wing size.

Main conclusions Our results support the hypothesis that species adapted to lentic habitats, which are assumed to be less persistent in time and space, disperse better than lotic species.

Keywords

Climate change, Europe, freshwater, habitat persistence, lentic, lotic, odonates, range dynamics.

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INTRODUCTION

Most invertebrates adapted to aboveground freshwater habitats can be classified as either lentic or lotic species (Ribera, 2008). According to Southwood's template concept (Southwood, 1977), the spatial and temporal characteristics of lentic and lotic habitats should induce strong constraints for the evolution of life-history traits of freshwater species. Species confined to lentic

habitats are supposed to have a stronger propensity for dispersal than lotic species, because lentic habitats are less stable in space and time (Hof *et al.*, 2006; Marten *et al.*, 2006; Ribera, 2008). Southwood (1962) and Roff (1990) even proposed an inverse relationship between habitat persistence and dispersal propensity – hereafter referred to as the habitat-stability dispersal hypothesis (HSDH). A number of studies on the differences between lentic and lotic species support some important

predictions of the HSDH (e.g. Ribera & Vogler, 2000; Ribera *et al.*, 2001, 2003; Hof *et al.*, 2012), for instance that lentic species have on average larger range sizes than lotic species (Ribera & Vogler, 2000; Monaghan *et al.*, 2005; Hof *et al.*, 2006; Ribera, 2008; Damm *et al.*, 2010). Further support has been found in studies on the genetic population structure of species (Marten *et al.*, 2006; Abellán *et al.*, 2009) and in analyses based on expert knowledge (Harabiš & Dolný, 2011).

According to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2007), the 100-year trend from 1906 to 2005 shows an average global increase in surface temperature of 0.74 ± 0.18 °C (IPCC, 2007). These changes are predicted to change the distribution of terrestrial and aquatic species (Heino, 2001; Heino *et al.*, 2009). The responses of species to climate warming can be basically summarized along three pathways: movement towards suitable climate conditions, evolutionary adaptations or extinction (Holt, 1990; Hof *et al.*, 2011).

In this study, we used recent climate warming as a 'natural' experiment to evaluate whether proposed differences in dispersal and range movement between lentic and lotic species support the key assumption of the HSDH. We investigated shifts of the range boundaries of lentic and lotic odonates (dragonflies and damselflies) in Europe using distribution maps of European odonates from two recent compilations (Askew, 1988, and Dijkstra & Lewington, 2006). Several studies on national scales report strong expansions of southern European dragonfly species into central Europe that are likely to be caused by climate warming (e.g. Hickling *et al.*, 2005; Termaat *et al.*, 2010). Odonates are well suited for such investigations as they are one of the best-known taxa of freshwater insects and invertebrates in general (e.g. Corbet, 2004; Kalkman *et al.*, 2008; Clausnitzer *et al.*, 2009) and many of their life-history traits are affected by temperature (Hassall & Thompson, 2008). According to the predictions of the HSDH we expected that lentic species shift their northern range boundaries more strongly polewards than lotic species. Moreover, we analysed whether body size, wing size and the length of the flight period are related to such changes in distribution.

MATERIALS AND METHODS

The distributional ranges of 112 species of odonates in Europe were extracted from outline maps published in Askew (1988) and Dijkstra & Lewington (2006) and transferred into WORLD-MAP (Williams, 2000) using a 50 km × 50 km Universal Transverse Mercator (UTM) grid cell size (total 2278 grid cells).

The two sources of range maps differ in their accuracy. The maps in Dijkstra & Lewington (2006), for instance, use different colours to indicate the status of the species, and we considered only the main and the uncommon or scattered occurrence areas as delineated by the colour code. We excluded parts of eastern Europe (see Fig. 1) because distributions of odonate species in this region are not well documented (e.g. Dijkstra & Lewington, 2006). We also excluded records from the inner Alps because there were differences in mapping accuracy between the two time periods (32 grid cells). The remaining area covered

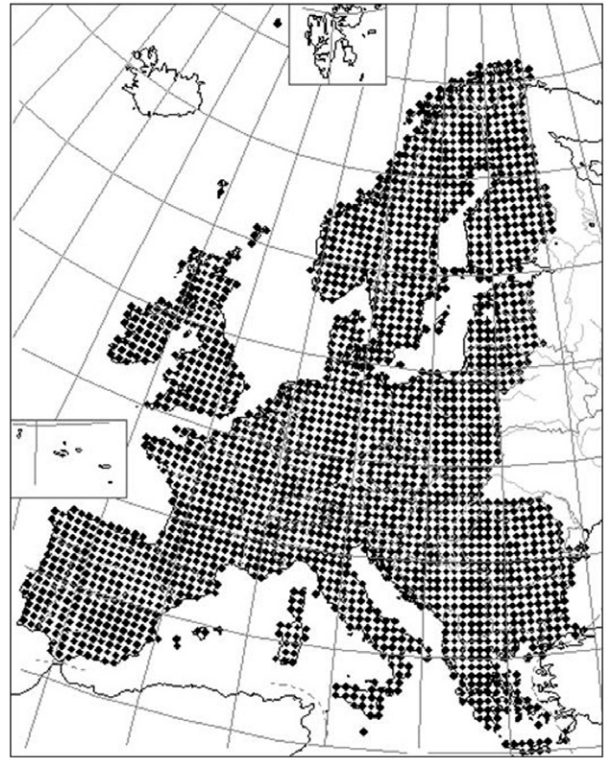


Figure 1 Map of the area considered in the study.

approximately 560,000 km², subdivided into 2246 grid cells of 2500 km² each.

On large geographic scales it is always difficult to obtain high-quality distribution data over the entire area, and therefore our analyses may suffer from inaccuracies. However, a bias in the distribution estimates should only matter if there were strong differences in mapping accuracy between lentic and lotic species. Detailed distribution maps based on grid occupancy are available for a number of countries, e.g. the UK, France, the Netherlands, Austria and Germany, but high-quality data for other parts of Europe, in particular eastern and southern Europe, are still lacking (Dijkstra & Lewington, 2006; but see Boudot *et al.*, 2009). Thus, the outline maps used here can only represent a rough approximation of the actual distributions of the European dragonflies (Dijkstra & Lewington, 2006). Detailed analyses of particular species will certainly require distributional data with a higher spatial resolution. Furthermore, outline distribution maps transferred onto a gridded map usually overestimate distributions, particularly measures of distributional range size using occupancy of grids. However, as shown for butterflies by Hawkins & Porter (2003), grid occupancy data are in general closely related to those derived from outline maps; therefore, such overestimations should not have strong impacts on our results.

We categorized species according to the habitat preference of their larvae into three groups: lentic, lotic and generalists (species without a distinct habitat preference) using updated data on habitat preference provided by Dijkstra & Lewington

(2006). We excluded generalists (15 species), wandering species (one species), species that occupied fewer than 10 grid cells in one of the two periods (three species) and species with strong ambiguities in the resolution of maps between 1988 and 2006 (two species). Of the remaining 91 species, 62 were categorized as lentic species and 29 as lotic species (see Appendix S1 in Supporting Information).

Shifts of northern range boundaries of each species were calculated using the method introduced by Thomas & Lennon (1999; see also Pöyry *et al.*, 2009). This method estimates range boundary shifts by comparing the location of the northernmost grid cells between two time periods. For each species, we calculated the average latitude of the 10 northernmost grid cells in 1988 and in 2006. Range boundary shifts were then calculated by subtracting the mean of 1988 from the mean of 2006. A positive value indicates a shift northwards, and a negative value indicates a shift southwards.

Species with a range midpoint north of 46° latitude were classified as northerly distributed, while species with a range midpoint south of 46° latitude were classified as southerly distributed. This subdivision roughly separates species mainly distributed in the Mediterranean region (the southern group) from species mainly distributed in central and northern Europe (the northern group). We applied this subdivision for two reasons: (1) northern species may already have colonized all the available area in the north, and northward shifts may simply be limited by the availability of space; and (2) the specific distributional borders of species from which range expansion starts may strongly affect northward shifts – species starting their range expansion in the south are exposed to very different geographic constraints and environmental conditions than species with a more northerly distributional border. In this regard, it is important to note that within the southern group, the range centres of lentic and lotic species did not differ significantly in 1988 ($P > 0.05$) which suggests a common starting line. However, within the northern group, the lentic species showed, on average, a more northerly located range centre ($P = 0.002$), probably caused by a faster recolonization of Europe after the last glaciations (see Hof *et al.*, 2006, 2008; Dehling *et al.*, 2010). To test whether lentic and lotic species differed in shifts of their northern range boundary, we used a two-way ANOVA with habitat (lentic/lotic) and region (northerly/southerly distributed species) as factors.

To evaluate which factors explain changes in range boundary shifts of species in more detail, we considered a number of species traits linked to dispersal propensity (e.g. Malmquist, 2000; Rundle *et al.*, 2007) and conducted a multivariate analysis. First, we compiled data on abdomen and hind-wing length from d'Aguilar *et al.* (1986). We calculated midpoints between given ranges and averaged them for males and females. Larger wings relative to body size may indicate stronger dispersal ability (Pöyry *et al.*, 2009). Second, we estimated the length of the flight period as the span between the months of the first and last records (Askew, 1988). Species with a longer flight period may have a higher ability to disperse. Third, we calculated the prevalence of a species as the proportion of occupied grid cells out of the total number of grid cells in 1988. Species with a larger

distribution in 1988 were more likely to undergo range shifts than narrowly distributed species (see Pöyry *et al.*, 2009). All these variables were related to species range boundary shifts. The type of habitat utilized and the distributional categorization (southerly/northerly) were coded as factors.

Comparative studies suffer from 'pseudo-replication' when species are treated as independent observations. Therefore, we compiled a phylogeny of the European odonates based on molecular and morphological phylogenies as well as taxonomic information (Appendix S2). However, the phylogeny of odonates in Europe is controversial or in part unknown. In particular, the relationships among species within genera are only available for a subset of genera. Furthermore, due to the combination of molecular phylogenies, morphological phylogenies and taxonomic information, a consideration of branch lengths was not applicable. In the following, we report only the results based on a compiled multifurcated tree in which all branch lengths were set to 1. Nevertheless, to analyse whether phylogenetic uncertainties affect our results, we randomly resolved all multifurcations (1000 times). The frequency distributions of the parameter estimates from subsequent analyses are shown in Appendix S3. We used generalized estimation equations (GEE; Paradis & Claude, 2002; Paradis, 2006) and Pagel's 'lambda' correlation structure (Pagel, 1994), as implemented in the ape package of R (Paradis, 2006; R Development Core Team, 2008), to analyse our data while simultaneously considering phylogeny. These approaches were used because they provide a greater flexibility of data analysis than analyses based on phylogenetic contrasts and also allow the incorporation of categorical variables and calculations of complex models (Paradis, 2006). For Pagel's correlation structure, we estimated lambda using generalized least-squares (GLS), but also explored the effects of fixed lambda values assuming that evolution is strongly constrained by phylogeny ($\lambda = 1$).

To evaluate the robustness of our results, i.e. the decision to use the 10 northernmost grids, we ran all analyses separately for the 5, 15 and 20 northernmost grid cells (see Appendix S4). All statistics were computed in R version 2.8 (R Development Core Team, 2008).

RESULTS

Northern range boundary shifts per decade varied considerably among species and between habitat groups (Appendix S1). On average, lentic species shifted their northern boundary more northwards than lotic species (two-way ANOVA, $F_{1,87} = 20.58$, $P < 0.001$; lentic species, 52.6 km, SD \pm 91.7; lotic species, -1.6 km, SD \pm 71.3). However a significant interaction term of habitat \times region ($F_{1,87} = 5.89$, $P = 0.017$) indicates that this is only true for the southerly distributed species (Fig. 2; northern group: lentic = 17.8 km, SD \pm 64.3, lotic = -0.8 km, SD \pm 37.1; southern group: lentic = 115.9 km, SD \pm 101.3, lotic = -1.8 km, SD \pm 78.4). In addition, on average, southern species shifted their northern range boundary more strongly than northern species ($F_{1,87} = 6.23$, $P = 0.015$; northern group: 15.4 km, SD \pm 61.4; southern group: 55.7 km, SD \pm 107.3).

Independent of whether or not we considered the phylogeny of the species, multivariate analyses of average shifts in northern range boundary revealed that species prevalence, wing size, body size and flight period were mostly unrelated to the shift in a species' northern range boundary (Table 1). In contrast, all analyses consistently showed that region, habitat affiliation and their interaction were significantly related to northern range boundary shifts.

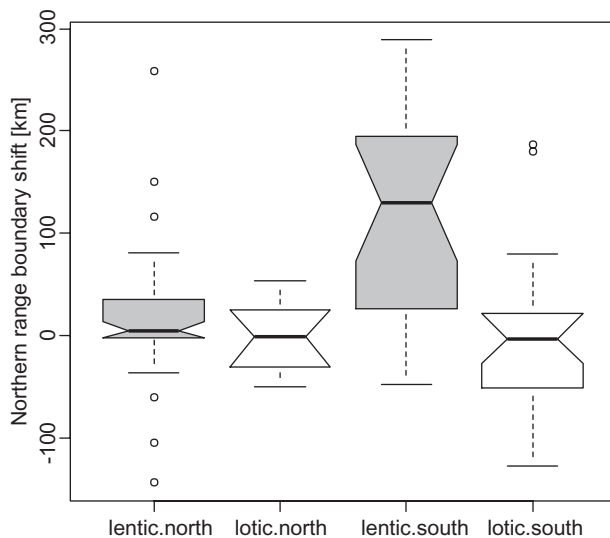


Figure 2 Boxplot of average northern range boundary shift per decade (km) of lentic (grey notches) and lotic (white notches) odonate species. Left: northern and central European odonate species (species with a range centre above 46° latitude). Right: southern odonate species (species with a range centre below 46° latitude). Horizontal bold lines represent medians, whiskers minimum and maximum excluding outliers. If notches do not overlap there is strong evidence that medians differ from each other.

Table 1 The effects of species prevalence in 1988, abdomen length, wing size, flight period (phenology), region and habitat (lentic/lotic) on northern range boundary shifts of odonates in Europe.

	GLM			GEE		Pagel's 'lambda' correlation structure			
	Estimate	SE	P	Estimate	P	Estimate	P	Estimate (1)	P
Prevalence	0.33	42.05	0.994	-14.39	0.508	-4.26	0.904	-15.15	0.717
Abdomen length	-1.28	1.67	0.446	-7.25	0.004	0.31	0.731	-7.25	0.061
Wing size	1.90	2.05	0.356	3.85	0.159	0.66	0.579	3.98	0.395
Flight period	-1.00	6.70	0.881	-12.28	0.007	-2.79	0.660	-11.19	0.113
Region	-101.47	22.93	< 0.001	-127.53	< 0.001	-94.61	< 0.001	-123.23	< 0.001
Habitat	-116.54	25.72	< 0.001	-72.83	< 0.001	-120.73	< 0.001	-71.52	0.016
Habitat × region	102.81	44.59	0.024	152.26	< 0.001	100.06	0.020	154.33	0.002

GLM, general linear model ($R^2 = 0.32$, $P < 0.001$, residual d.f. = 83).

GEE, phylogenetically controlled analysis with generalized estimation equations (phylogenetic d.f. = 20.36).

Pagel's 'lambda' correlation structure (left, lambda estimated by GLS; right, lambda = 1).

Bold indicates $P < 0.05$.

DISCUSSION

Overall, our results show that northern range boundary shifts vary between species with different geographic affiliations and between those adapted to different habitat types. Lentic dragonflies of the southern group shifted their range boundaries more than lotic species of the southern group. This result supports the HSDH and was robust when phylogeny was considered. The lower stability of lentic habitats indeed appears to induce evolutionary processes that cause a higher propensity for dispersal of lentic species (Hof *et al.*, 2006, 2012; Marten *et al.*, 2006; Ribera, 2008). For further proof of our main results, however, direct data on the dispersal ability of species are required, for instance from detailed mark-recapture studies. Unfortunately such direct dispersal estimates are available for only a small number of species, and vary greatly in terms of methodology and sample size. Hence meaningful comparisons of direct dispersal estimates between lentic and lotic species are currently not appropriate. Furthermore it is important to note that a higher dispersal ability does not necessarily implicate a higher success of colonization or vice versa. Habitat availability, biotic interactions and other factors will certainly interact with dispersal and establishment (see below). One should further note that the average expansion rates found in this study are estimates on the population level. Our reasoning rests on the assumption that dispersal rates and expansion rates are correlated. Assuming that range expansion is by simple diffusion, one would expect a linear relationship between the velocity of range expansion (km year^{-1}) and the square root of the diffusion coefficient (Andow *et al.*, 1990). However, this is a simplification, and the real relationship is influenced by other factors (e.g. long-range dispersal, habitat heterogeneity) and for odonates deserves further investigations.

Temperature is probably responsible for the recent range expansions of freshwater animals, in particular for odonates (Corbet, 2004). The importance of climatic factors for freshwater animals/odonates is documented by the decrease of freshwa-

ter species richness with latitude, which indicates that the distribution of freshwater organisms is influenced by temperature on large scales (Heino *et al.*, 2009), even though historical factors (e.g. Pleistocene glaciations) may cause deviations from this relationship (e.g. Hof *et al.*, 2008). Furthermore, the evolutionary origins of dragonflies in the tropics presumably led to temperature restrictions for their distributions (Heino, 2001; Hassall & Thompson, 2008). Finally, higher temperatures can increase the voltinism of species (Braune *et al.*, 2008) and may additionally cause changes in the diapause (Hassall & Thompson, 2008), which may facilitate range expansions. Previous studies concluded that the stronger dispersal propensity of lentic odonates may have enabled a faster post-glacial recolonization of suitable regions, resulting in larger ranges and more northerly distributions than those of lotic species (Ribera *et al.*, 2003; Hof *et al.*, 2006, 2008; Ribera, 2008). Hence, the same mechanism that presumably caused differences in recolonization after glaciations may operate on much smaller time-scales. However, in contrast to the suggestion of Hof *et al.* (2008), the ongoing northward expansion of European odonates and the invasion of African species into the Mediterranean (Dijkstra & Lewington, 2006; Boudot *et al.*, 2009) indicate that the range expansions of lentic species in Europe are still in progress.

Even though range boundary shifts of various taxa are well documented, little is known about how species traits influence the ability of species to respond to global warming (Pöyry *et al.*, 2009). We did not find strong support that range shifts are linked to morphological traits such as body size (Table 1). This finding contradicts the results of previous studies on damselflies (Rundle *et al.*, 2007), mayflies and stoneflies (Malmquist, 2000) and butterflies (Pöyry *et al.*, 2009). More sophisticated measures of wing size (e.g. wing area) or wing shape (Johansson *et al.*, 2009) may be necessary to increase the predictive power of wing characteristics in analyses of range changes. In addition, measures of the size of flight muscles may provide further insights (e.g. Marden, 2000).

The importance of adult phenology (flight period) for dispersal remains unclear. As the flight period of a given species varies, for instance, with altitude and latitude (Corbet, 2004), the averaged data used here may not represent the actual flight period at the northern range boundary. Most importantly, the beginning of flight periods shifts with latitude. Species with large distributional ranges may show a longer flight period across the total range even though flight periods on local or regional scales are actually much shorter. Furthermore, one may argue that a longer flight period may be used for enhanced reproduction rather than for dispersal. However, increased reproduction increases local population size, which in turn should favour migration and dispersal (Corbet, 2004).

Differences in range shifts between lentic and lotic species may also be explained by a number of other factors not considered in this study. Due to the (on average) lower dispersal propensity of lotic species, habitat fragmentation may affect lotic species more than lentic species. Furthermore, increasing temperature could also delay the induction of diapauses and thereby lead to an increased mortality because diapauses help to avoid

periods of low energy availability (Harrington *et al.*, 2001). Unfortunately, only a few studies have investigated the changes of phenology and their consequences with regard to climate change (e.g. Braune *et al.*, 2008).

An important criticism about studies focusing on climate-induced range expansions is that detected expansions are simply the outcome of a higher number of records in the following observation period. Hassall & Thompson (2010) suggested a combination of different approaches to account for such sampling heterogeneity. These approaches, however, require detailed data on the spatial distribution of sampling intensity. Such information may be available for single countries (e.g. the United Kingdom), but unfortunately not on continental scales. Nevertheless, although we cannot completely rule out such a bias, we believe that the distributions of odonates, at least those of central Europe, were already well known in 1988. The most significant northern range boundary shifts were found for species that invaded central Europe from the Mediterranean or extended their previous northern range boundaries in central Europe northwards (e.g. *Anax imperator*, *Anax parthenope*, *Aeshna mixta*, *Aeshna affinis*, *Crocothemis erythraea*; Appendix S1). Hence, the presumably lower sampling intensity in southern Europe should be of minor importance for the current range shifts. A further bias may occur with regard to only the 10 most marginal grid cells of a species' distribution. To elevate the robustness of our results, we repeated our analyses for the 5, 15 and 20 northernmost grid cells. Although an increase in the number of grid cells considered caused an exclusion of up to three species in the southern data set, all results of the subsequent analyses were approximately the same (Appendix S4). One could also expect that climate warming causes a poleward shift of southern range margins (Hampe & Petit, 2005). We also estimated the mean shifts of the southern range boundary for both lentic and lotic species of both geographic groups but did not find a significant shift of the southern range boundary. This might be due to the stretching of distributional ranges of many species across large parts of Africa and Asia as well so that the actual southern range boundaries lie outside Europe. Furthermore, distributional data along the southern range boundary are less well known because of the smaller number of records.

OUTLOOK

Our results provide support for an inverse relationship between habitat predictability and dispersal propensity. Because the considered traits of species linked to dispersal propensity could not sufficiently explain the observed differences, improved or additional factors must be considered. Landscape features, for example, are certainly important for dispersal. Mountain ridges or urban areas can act as barriers, whereas river courses are important migration pathways for both lentic and lotic species (Corbet, 2004). Furthermore, the availability and connectivity of suitable freshwater habitats outside the existing range should affect range movements. Such studies can only be done on much smaller spatial scales and also require much better data about the dispersal ability of single species. Finally, it has been shown

that thermal tolerance is important for understanding range size and thus dispersal (Brändle *et al.*, 2002). Odonates have evolved a number of different physiological and morphological adaptations for thermoregulation, e.g. different body coloration, the ability to change body colours or specialized behaviour (e.g. Damm *et al.*, 2010). We suggest that the analysis of thermoregulatory adaptations, their occurrence among species and their spatial distributions will offer valuable clues to improve our understanding of dispersal propensity and its impact on distribution and shifts of distribution due to global warming.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Data on the geographic affiliation of odonate species, habitat utilization, flight period, wing size, abdomen length, species distribution and northern range boundary shift per decade.

Appendix S2 Phylogenetic relationships among species used for the phylogenetically controlled analysis.

Appendix S3 Frequency distribution of parameter estimates obtained by the GEE and GLS models considering 1000 phylogenetic trees with randomly resolved multifurcations.

Appendix S4 The effects of species prevalence in 1988, abdomen length, wing size, flight period and habitat on northern range boundary shifts of European odonates.

BIOSKETCH

Yannic Grewe has interests in macroecology and conservation ecology. This study was part of his bachelor thesis at the Department of Ecology, Philipps-Universität Marburg.

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