Science of the Total Environment 917 (2024) 170454

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Ecologically and medically important black flies of the genus *Simulium*: Identification of biogeographical groups according to similar larval niches

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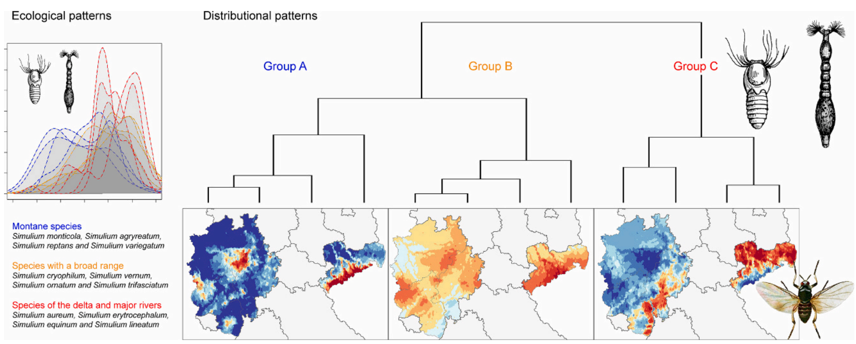
HIGHLIGHTS

- Three ecological groups were identified based on distributional patterns.
- Old assessments were confirmed with the latest occurrence data.
- For each group, we derived different population trends in times of global change.
- Global change elevates importance of vector-borne diseases.
- Our results serve as base for effective Simuliidae monitoring.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Damia Barcelo

Keywords:
Climatic conditions
Ecological requirements
Hematophagous arthropods
Maxent
Simuliidae
Species distribution modelling

ABSTRACT

The black fly genus *Simulium* includes medically and ecologically important species, characterized by a wide variation of ecological niches largely determining their distributional patterns. In a rapidly changing environment, species-specific niche characteristics determine whether a species benefits or not. With aquatic egg, larval and pupal stages followed by a terrestrial adult phase, their spatial arrangements depend upon the interplay of aquatic conditions and climatic-landscape parameters in the terrestrial realm. The aim of this study was to enhance the understanding of the distributional patterns among *Simulium* species and their ecological drivers. In an ecological niche modelling approach, we focused on 12 common black fly species with different ecological requirements. Our modelling was based on available distribution data along with five stream variables describing the climatic, land-cover, and topographic conditions of river catchments. The modelled freshwater habitat suitability was spatially interpolated to derive an estimate of the adult black flies' probability of occurrence. Based on similarities in the spatial patterns of modelled habitat suitability we were able to identify three biogeographical groups, which allows us to confirm old assessments with current occurrence data: (A) montane species, (B) broad range species and (C) lowland species. The five veterinary and human medical relevant species *Simulium equinum*, *S. erythrocephalum*, *S. lineatum*, *S. ornatum* and *S. reptans* are mainly classified in the lowland species group. In the course of climatic changes, it is expected that biocoenosis will slightly shift towards upstream regions, so that the lowland group will presumably emerge as the winner. This is mainly explained by

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https://doi.org/10.1016/j.scitotenv.2024.170454
Received 16 November 2023; Received in revised form 15 January 2024; Accepted 24 January 2024
Available online 28 January 2024

wider ecological niches, including a higher temperature tolerance and tolerance to various pollutants. In conclusion, these findings have significant implications for human and animal health. As exposure to relevant *Simulium* species increases, it becomes imperative to remain vigilant, particularly in investigating the potential transmission of pathogens.

1. Introduction

Black flies (Diptera: Simuliidae) are cosmopolitan hematophagous insects, occurring on all continents, except Antarctica. More than 2000 nominal species are known worldwide (Adler et al., 2010; Adler, 2022; Adler and McCreadie, 2019a), of which about 10–20 % are considered pests of humans, domestic animals and livestock (Adler and McCreadie, 2019a). About 230 simuliid species have been found in Europe (Sitarz et al., 2022) and about 57 in Germany (Seitz, 2022). Like mosquitoes (Culicidae), almost all black fly species have a hematophagous lifestyle and some are relevant as vectors – yet they have not received the scientific attention that mosquitoes have. Nearly 98 % of black fly species are blood-feeding (Adler et al., 2010), mandatory for the development of the eggs. Simuliids are usually host-specific and feed on birds and mammalians (including humans; Adler et al., 2010) and thus belong to the ectoparasites. Some Simuliidae species and complexes are considered vector-competent for various black fly associated pathogens: viruses, bacteria, protists, and helminths. The most well-known pathogen transmitted by black flies is the filarial nematode *Onchocerca volvulus* (an exclusive human parasite), as the causative agent of onchocerciasis (river blindness). According to the World Health Organisation (WHO, 2022), it is estimated that at least 220 million people worldwide would need preventive chemotherapy against onchocerciasis, 14.6 million of infected people already had a skin disease and 1.15 million had a loss of vision. The spatial distribution of endemic river blindness is limited to tropical areas with focus in sub-Saharan Africa (Sitarz et al., 2022).

So far, only 1.5 % of the black fly species worldwide are known to be vector-competent (Adler et al., 2010). However, they are also considered medically relevant because they are pool feeders, creating subdermal hematoma with their mouthparts and feed on the blood. The bites are painful and may cause strong reactions in the host, as wounds often become infected. Components (e.g. anticoagulant proteins) of the saliva excreted to the host during the blood meal can induce various pathological reactions (Sitarz et al., 2022). They can cause local skin lesions, painful erythema and oedema, allergic reactions, respiratory and circulatory symptoms (Akhoundi et al., 2020; Ebmer et al., 2022). In addition to human medical importance, simuliids are also of veterinary medical relevance. Simultaneous hatching results yields high abundances of simuliids at certain times (López-Peña et al., 2021; Ruiz-Arrondo et al., 2017). Those mass occurrences with significant impacts on humans and domestic animals have been described for the species ***Simulium erythrocephalum***, ***Simulium ornatum***, ***Simulium reptans***, ***Simulium equinum*** and ***Simulium lineatum*** (Ignjatović-Ćupina et al., 2006; López-Peña et al., 2022b). These are all mammalophilic species, with ***S. erythrocephalum***, ***S. ornatum*** and ***S. lineatum*** primarily feeding on cattle, while ***S. equinum*** feeds on equines and cattle (López-Peña et al., 2022b). Anthropophilic behaviour is known from ***S. erythrocephalum***, ***S. reptans***, ***S. ornatum*** and ***S. equinum*** (López-Peña et al., 2022b).

Beside the human and veterinary relevance, simuliids constitute an important component in aquatic and terrestrial ecosystems. The pre-imaginal stages (larvae and pupae) of black flies develop in flowing waters. Locally, the larvae can often be found in high abundances. Together with Chironomidae, Simuliidae belong to the dominant component of the dipteran fauna in flowing waters, constituting an important component of biomass. They play an important role as filter feeders representing a link between suspended particles and predators (Lock et al., 2014). While the life cycle of all black flies is basically the same – with larval development in freshwater – the ecological needs within the family are diverse. Especially the pre-imaginal stages of black flies are characterized by different species specific habitat needs (Rühm and Kiel, 1991; Timm and Juhl, 1992), closely linked to the physical and chemical conditions of the water body (Rühm and Kiel, 1991; Timm and Juhl, 1992). Relevant factors that determine the pre-imaginal niches are substrate (Roberts, 1986), flow velocity (Rivers-Moore et al., 2007), water temperature (Rivers-Moore and Palmer 2018), food supply and pollutant load. Both larvae and pupae can serve as indicators for water quality (Adler and McCreadie, 1997; López-Peña et al., 2022a) with tolerances to water pollution varying among species.

The pre-imaginal life phase ends with the – often synchronised (Adler and McCreadie, 2019a) – hatching of the pupae (Timm and Juhl, 1992). The terrestrial imagines have habitat requirements related to the floodplain vegetation (e.g., habitat, mating and oviposition sites). Furthermore, the availability of hosts for blood-feeding females needs to be given even though little is known about their specific host preferences (Chakarov et al., 2020). The classification of black fly species into two main groups is primarily based on their morphological characteristics: mammalophilic species, which primarily target mammals, and ornithophilic species, which primarily target birds (Table 1).

Of particular concern are the larval freshwater habitats, which have been significantly affected by human activities (Maasri et al., 2022), implying that these changes are likely to affect the distributional patterns of black fly species. The destruction of habitats, increasing pollution and excessive nutrient inputs from intensified agriculture, as well as the ongoing introduction and spread of non-native species, are considered the main drivers of biodiversity restructuring (Bernhardt et al., 2017; Jourdan et al., 2018; Lock et al., 2014). Such changing environmental conditions put pressure on native species, which they can overcome either by adapting or dispersing to new habitats (Jourdan et al., 2019; Shah et al., 2020). Additionally, physiological traits such as tolerance to temperature fluctuations or ability to cope with varying water flow rates may also play a role in determining a species' resilience. Often, even closely related species differ in their ability to adapt to new

Table 1
Selected simuliid species with host preferences and numbers of generation per year. In bold – species of human and veterinary relevance. References: 1 (Hywel-Jones and Ladle, 1986), 2 (Lock and van Maanen, 2014), 3 (Chakarov et al., 2020), 4 (Seitz, 1992), 5 (López-Peña et al., 2022b), 6 (Reidelbach and Christi, 2002), 7 (Ignjatović-Ćupina et al., 2006), 8 (Zahar, 1951), 9 (Malmqvist et al., 2004).

Species	Host preferences	Generations per year	Reference
Simulium argyreatum	Mammalophilic	Up to 3	1,2
Simulium aureum	Ornithophilic	1–2	2,3
Simulium cryophilum	Ornithophilic (mammalophilic)	2–3	4
Simulium equinum	**Mammalophilic, anthropophilic**	**4–6**	5,6
Simulium erythrocephalum	**Mammalophilic, anthropophilic**	**Up to 5**	2,5,7
Simulium lineatum	**Mammalophilic, anthropophilic**	**?**	5
Simulium monticola	Mammalophilic	2–3	2,4,8
Simulium ornatum	**Mammalophilic, anthropophilic**	**2–3**	2,5,6,9
Simulium reptans	**Mammalophilic, anthropophilic**	**Up to 4**	2,5,6,9
Simulium trifasciatum	?	2	2
Simulium variegatum	Mammalophilic	?	8
Simulium vernum	Mammalophilic, anthropophilic	2–3	2,5,6

conditions and are replaced by congeneric species. For example, if a species requires pristine stenotherm upstream habitats that are becoming scarce due to human activities, it may be at risk of declining in numbers or even go extinct. On the other hand, if a species is able to tolerate a wide range of conditions or is able to shift its niche requirements, it may be better equipped to expand its range and persist in the face of changing conditions. Therefore, understanding the ecological requirements and niche characteristics of black flies is essential for predicting their distributional patterns and potential response to environmental changes. Sensitive upstream black flies may particularly be endangered by increasing habitat destruction and climate change.

In this study, we conducted ecological niche modelling to analyse the ecological preferences, requirements and spatial distribution patterns of the 12 most prevalent black fly species in Germany. Our primary goal was to advance our understanding of black fly ecology by examining their ecological preferences and providing a spatial interpolation. Within the group of 12 considered species, *S. equinum*, *S. erythrocephalum*, *S. lineatum*, *S. ornatum* and *S. vernum* stand out as the five species classified as nuisance species with notable observed impacts on humans and domestic animals. The models were based on occurrences of pre-imaginal stages and project the potential distribution of terrestrial adult black flies. We hypothesize that we can 1.) identify different environmental preferences by which we can classify black fly species. This will allow us to 2.) identify species/groups that persist in anthropogenically shaped regions and species that will become increasingly threatened. 3.) The classification of species based on current occurrence data, allows us to validate existing literature assessments regarding stream zonation preference and tolerance to pollutants.

2. Material and methods

2.1. Occurrence data

We used the occurrence data provided by the Global Biodiversity Information Facility GBIF (GBIF, 2022) (data as of 24 January 2022) and downloaded all records of the black fly genus *Simulium* (Latreille, 1802) from Germany. We then excluded records for which a considerable uncertainty (>100 m) in the accuracy of the coordinates was reported (Fig. S1). We found that for the German federal states of North Rhine-Westphalia, Rhineland-Palatinate, Hesse and Saxony (Fig. S2) extensive and reliable data is available across the entire federal states. These data originate from monitoring programmes of the respective federal state authorities that were recorded as part of the Water Framework Directive (WFD), which means that these data are available in a spatially comprehensive and reliable quality. Species identification in these monitoring programmes is currently still carried out at the morphological level, and species that are difficult to differentiate may have remained unobserved (e.g., Leese et al., 2021; Keck et al., 2022).

GBIF occurrence data mostly refer to the aquatic larval and pupal stages. So we adjusted - if necessary - the position of the occurrence data to the geometry of the available layer of stream parameters (Domisch et al., 2015, see below). For the most part, the position of the occurrence records matches the geometry of the stream variable layers. Points that were in close proximity but just outside the stream layer were manually assigned to the nearest grid cell. This mismatch is due to the fact that the layers of stream parameters are in raster format and may therefore locally differ slightly from the detailed geometry of the watercourses. Points located further away from any grid cells were excluded from the dataset. These points refer either to terrestrial observations of adults, to observations in small waterbodies not included in the layer dataset, or to inaccurately located observations.

Duplicates (i.e., same species, same coordinates) were removed. Only one occurrence record per species and per grid cell was considered at maximum (spatial resolution of 30 arc sec, i.e. ~1 km). Further thinning was not applied, which seemed appropriate at the spatial scale considered. We also refrained from using tools such as the CoordinateCleaner R Package (Zizka et al., 2019), since the data are provided by the state offices and are therefore expected to be of high quality.

2.2. Species selection

Niche modelling was carried out for the 12 most common *Simulium* species in the database. These are *S. argyreatum* ($N = 161$), *S. aureum* ($N = 43$), *S. cryophilum* ($N = 103$), *S. equinum* ($N = 134$), *S. erythrocephalum* ($N = 59$), *S. lineatum* ($N = 38$), *S. monticola* ($N = 42$), *S. ornatum* ($N = 503$), *S. reptans* ($N = 126$), *S. trifasciatum* ($N = 40$), *S. variegatum* ($N = 98$) and *S. vernum* ($N = 179$). Numbers of records refer to the prepared data as described above.

2.3. Environmental data

The spatial distribution patterns of amphibionts, i.e. species whose life cycle includes both aquatic and terrestrial phases, depend on both aquatic and terrestrial conditions (Petrozhitskaya and Rodkina, 2018). We modelled habitat suitability for the larval and pupal stages of *Simulium* species in freshwaters using freshwater environmental data provided by Domisch et al. (2015). We downloaded the data at a spatial resolution of 30 arc sec and cropped them to the following extent 5.8° to 15.1° West and 47.2° to 55.1° North that covers Germany. Because high-quality occurrence data were only available for four states, we clipped the raster data to the geometry of the four federal states.

Among the available environmental variables (Domisch et al., 2015), we chose two topography-based variables (Lehner et al., 2008), two climatically variables derived from the worldclim data (Hijmans et al., 2005) and one land cover variables (Tuanmu and Jetz, 2014). Specifically we considered the minimum elevation across sub-catchment, i.e. altitude of the record points (elev1) and the average slope across sub-catchment (slope4). As climatic variables, we considered the maximum temperature of warmest month (bio05) and the minimum temperature of coldest month (bio06) across the sub-catchment (weighted average percentage). In addition, we considered the percentage of cultivated vegetation (lc07) across the sub-catchment (weighted average percentage). These five variables are supposed to be ecologically meaningful for the distributional patterns of the larvae and pupae and are only little intercorrelated (Pearson correlation coefficient < 0.75, Table S2). Land cover can be a crucial parameter for the distribution patterns, as it may affect the occurrence of host species (e.g. human settlements, presence of animal farms) (Jordaan and van Ark, 1990). Furthermore, agricultural fertilisation and the use of pesticides in the catchment area negatively affects the water quality of watercourses (Allan, 2004; López-Peña et al., 2022b).

2.4. Niche modelling

In view of the data available, we decided to use the maximum entropy approach for niche modelling (Elith et al., 2011; Phillips et al., 2017), implemented in the Maxent software (Phillips et al., n.d.). This approach is widely used and performs well in comparative studies (e.g. Elith et al., 2006). As a presence background approach, it copes well with partly collected data.

For each of the 12 black fly species we run 20 replicates (cross-validation) with the following modifications of the default settings: We increased the maximum number of iterations to ensure convergence, we only used linear, quadratic and product features to obtain smooth, ecologically sound response curves (Cunze and Tackenberg, 2015). We trained the models on the area of the four federal states and then projected the results (average over 20 replicates) to the entire country (5.8° to 15.1° West and 47.2° to 55.1° North). In this projection, it is important to avoid extrapolations. Therefore, we tested for potential extrapolations in a multivariate environmental similarity surface (MESS) analysis (Elith et al., 2010) implemented in Maxent (Fig. S5).

The receiver operating characteristic (ROC) curve relates the rate of true positives to the rate of false positives. The area under the ROC curve (AUC) value is a commonly used measure of quality for evaluating modelling results. The AUC value depends strongly on the prevalence and thus also on the number of occurrence records used for modelling. Rare species generally show a higher AUC than species that can occur in a broad range. Therefore, the AUC value is not a valid measure for comparing model performance between species, nor as an absolute measure of whether a model is performing well or poorly. The AUC is a measure that evaluates the discriminatory power of a model.

To identify species with similar spatial distribution patterns, we calculated cosine similarity of the modelled habitat suitabilities for the pre-imagines of the 12 black fly species. We present the results of the cluster analysis (Wards) on the associated dissimilarity as a dendrogram.

2.5. Interpolation of the freshwater habitat suitabilities as a proxy of potential terrestrial distributions

The habitat suitability projected for the watercourses was spatially interpolated (Inverse distance weighting - IDW) to the entire study area, thus providing an estimate of the probability of occurrence of terrestrial adult black flies. The IDW approach seems appropriate here as it can be assumed that the occurrence probability decreases with the distance to the nearest suitable breeding habitat. Adult black flies are good flyers and can move over distances of several hundred kilometres (Ebmer et al., 2022).

2.6. Further analysis

To visualise the realised niches of the species according to the groups found in the cluster analysis, we plotted the density functions of the observed occurrences along the five gradients of environmental factors used as explaining variables in niche modelling.

We further put the found spatial patterns in context with species traits from literature and databases (mainly from the freshwater information platform freshwaterecology.info, Schmidt-Kloiber and Hering, 2015).

All maps were generated using Esri ArcGIS; analysis was carried out with R, ArcGIS and Maxent.

3. Results

Based on 1526 occurrence records, we modelled the freshwater habitat suitabilities and estimated the terrestrial occurrence probabilities of 12 common black flies in Germany (Fig. 1). The patterns found in habitat suitability reflect well the observed distribution patterns. The AUC values ranged from 0.62 for *S. trifasciatum* to 0.91 for *S. monticola* (Table S1). *S. monticola* probably covers a distinct range of conditions, while *S. trifasciatum* occurs along larger gradients. The modelled aquatic habitat suitability as well as the interpolated terrestrial potential distribution patterns vary between the considered species. Based on the cosine similarity of modelled freshwater habitat suitability we could identify three biogeographical groups with similar distributional patterns (Figs. 1 and S5; medically relevant species are written in bold):

Group A: Montane species

S. monticola, *S. argyreatum*, ***S. reptans*** and *S. variegatum*

Group B: Species with a broad range

S. cryophilum, *S. vernum*, ***S. ornatum*** and *S. trifasciatum*

Group C: Species of the delta and major rivers/lowland species

S. aureum, ***S. erythrocephalum***, ***S. equinum*** and ***S. lineatum***

These group patterns are also roughly found in the focal occurrence of the 12 species along the five gradients considered in niche modelling (Fig. 2): Group A tends to occur under lower temperatures (in summer – bio05 and winter bio06), group C under comparably higher temperatures, and group B takes an intermediate position (Fig. 2a, b). The most distinct group differences are found in the elevation gradient (Fig. 2c), with group C (in red) occurring in lowland freshwaters (0–200 m.a.s.l.), while the species of group A (in blue) show a wide amplitude and also occur in montane areas. Group B takes an intermediate position. With respect to the slope gradient (i.e., the relief energy of the terrain; Fig. 2d), the species show only minor variations. Steeper elevations in the catchment correspond to higher slope (measured in degrees, [°] * 100), with *S. erythrocephalum* standing out. The variation in agricultural land cover across the subcatchment (LC7, Fig. 2d) highlights again differences among the groups. Group A species are confined to regions with lower agricultural land use proportions, while group C species tend to be present in areas with higher agricultural coverage, except for *S. lineatum*. Group B species fall in between these two and tolerate some degree of agricultural land use.

On average over the 12 considered species, the predictor variable maximum temperature of warmest month (bio05) contributes the most to the models (Fig. S6a), followed by percentage of agricultural land in the sub-catchment (LC7). Overall, however, the relative contribution of variables varies among species (Fig. S6b). The distribution of *S. erythrocephalum*, for example, is strongly affected (>80 % contribution) by geomorphological variables (elevation and slope), while *S. trifasciatum* and *S. monticola* are largely driven by climatic factors (bio05, bio06).

4. Discussion

Based on our modelling approach, we successfully delineated three distinct clusters with unique distribution patterns, reflecting the species' specific ecological requirements and varying resilience to human-shaped landscapes. Temperature and land cover emerged as important predictors for the spatial patterns of the studied black fly species. *Simulium* species from the upstream group A are expected to be threatened as a result of ongoing anthropogenic change, while lowland species may benefit (Ruiz-Arrondo et al., 2020). This is due to the higher tolerance of lowland species to higher temperatures and higher organic and pollutant loads in larger streams (Ficsór and Csabai, 2021). According to our results *S. erythrocephalum*, *S. equinum* and *S. lineatum*, which are prone to mass occurrence, were classified as lowland species. Their predominant occurrence in main rivers, particularly in delta regions notably demonstrates an ability to tolerate higher temperatures and pollution. These species are likely to cope well with an expected further increase in temperatures and ongoing anthropogenic changes. Furthermore, the duration of larval development strongly depends on the water temperatures, with shorter intervals at higher temperatures (Bernotiene and Bartkeviciene, 2013). Higher temperatures over a long periods of times thus enable ectothermic insects to produce more generations per year (e.g. Bale et al., 2002; Skendžić et al., 2021). On the other hand, temperature sensitive montane species of group A may tend to be threatened by a rise in temperature. This is – apart from general biodiversity loss – particularly relevant in terms of the importance of simuliids in freshwater food webs. Decreases in simuliid population densities may alter predator prey relationships, for example, negatively affect predatory plecopterans (Wipfli and Merritt, 1994).

Land cover is another important driver of black fly distribution patterns in Germany. Land cover determines the habitat for adults through the availability of food resources (nectar or honeydew; Burgin and Hunter, 1997) and the presence of hosts for the blood meal of females (contact probability). In addition, the land cover situation in the catchment also affects water parameters (e.g. pollutant and nutrient introduction through agriculture, water level variations through sealed surfaces). In our study region, the upper stream regions were mostly

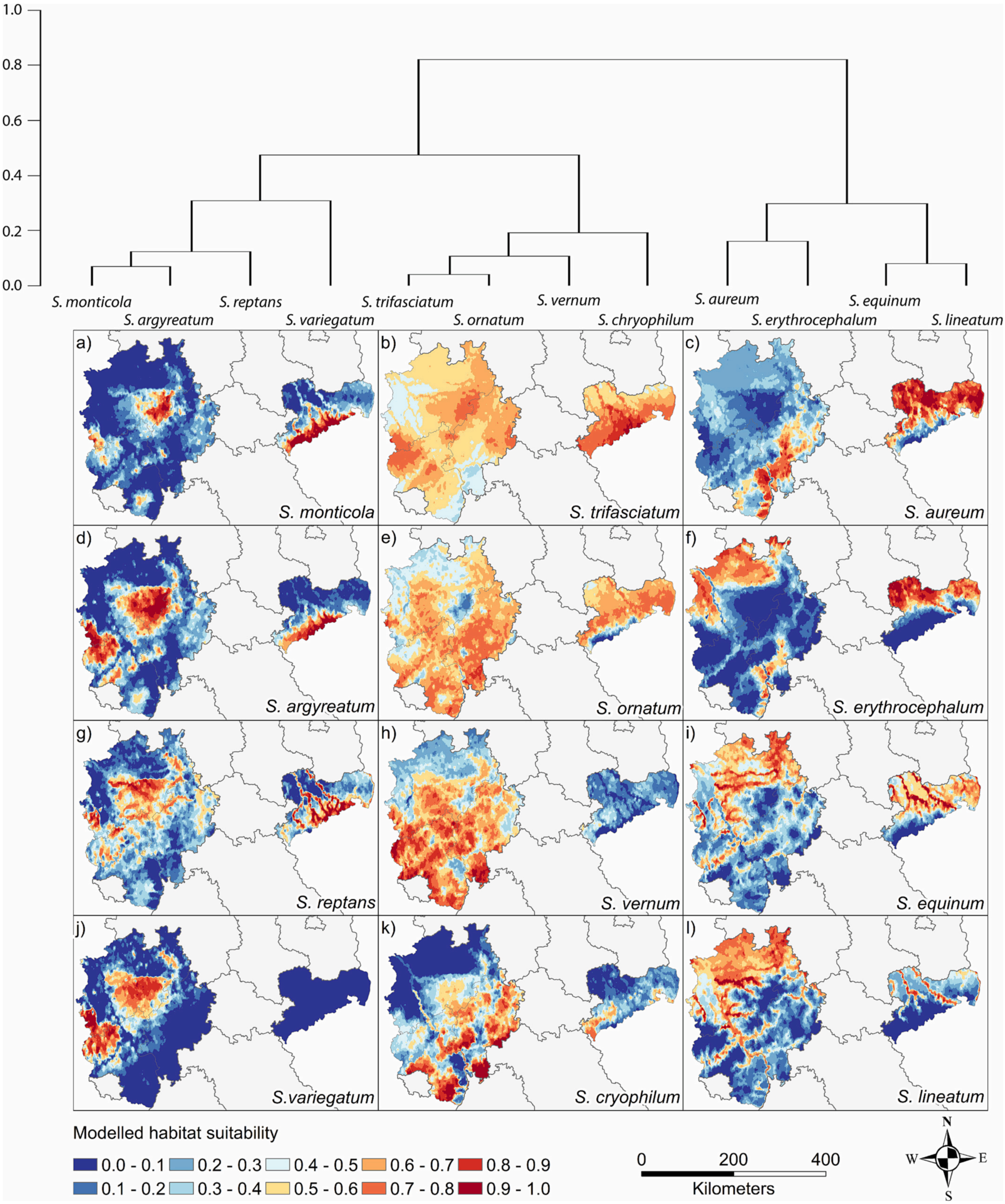

Fig. 1. Three identified biogeographical groups of the most common German black fly species (based on cosine similarity and wards algorithm of the modelled freshwater habitat similarities) and their modelled distribution. We identified three groups of similarly distributed *Simulium* species: Group A: Montane species *S. monticola*, *S. argyreatum*, *S. reptans* and *S. variegatum*; group B: Broad range species: *S. cryophilum*, *S. vernum*, *S. ornatum* and *S. trifasciatum* and group C: Species of the delta and major rivers/lowland species: *S. aureum*, *S. erythrocephalum*, *S. equinum* and *S. lineatum*. AUC values can be found in Table S1. Projection: Transverse Mercator, ETRS 1989 UTM.

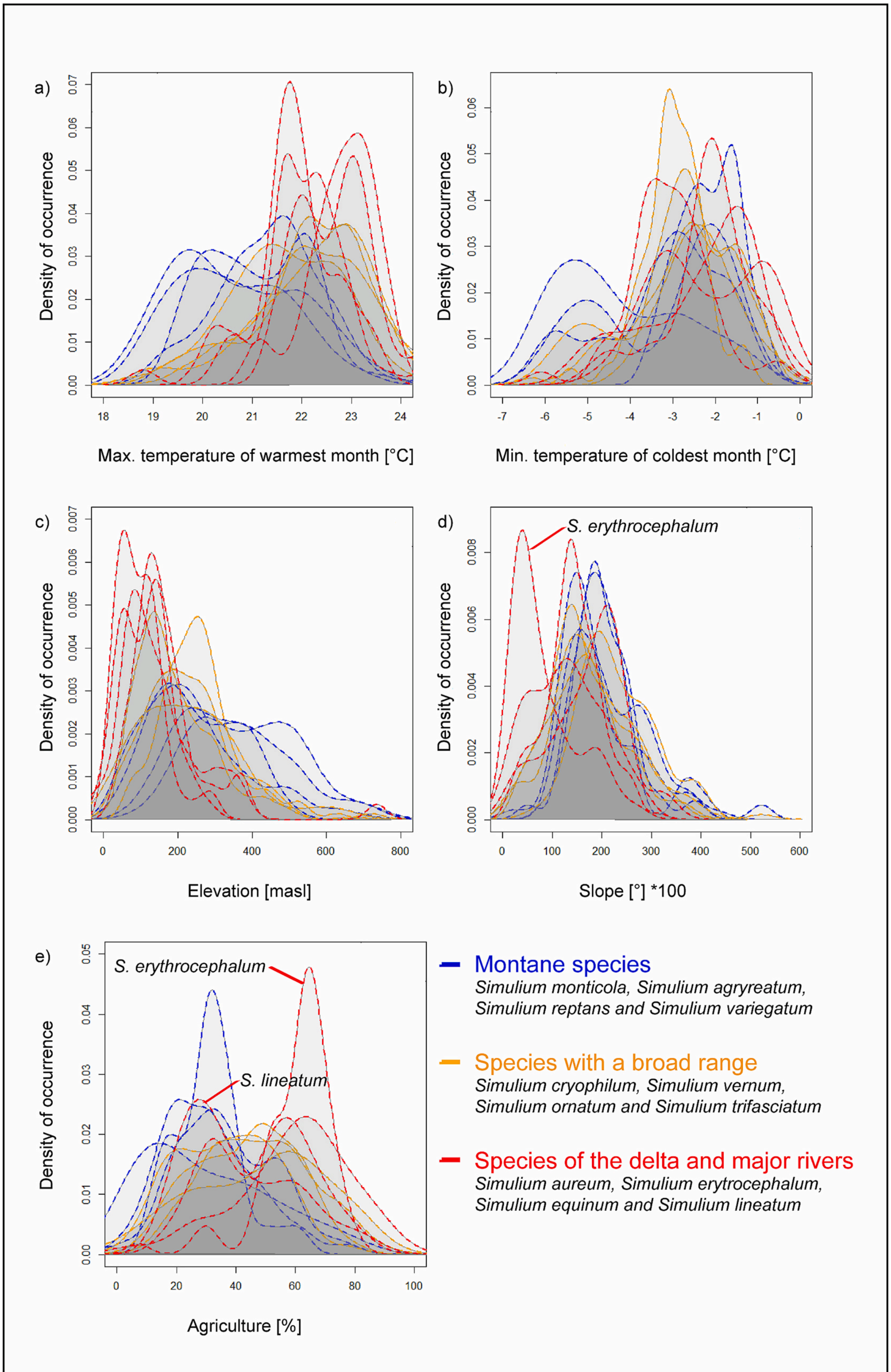

Fig. 2. Density functions of occurrence records of the 12 black fly species along the five environmental gradients considered as predictor variables in the niche modelling. Species are grouped according the cosine similarity if modelled freshwater habitat suitability (Fig. 1). In blue: Group A - montane species *S. monticola*, *S. argyreatum*, *S. reptans* and *S. variegatum*; in orange: Group B - species with a broad range: *S. cryophilum*, *S. vernum*, *S. ornatum* and *S. trifasciatum* and in red: Group C: species of the delta and major rivers/lowland species: *S. aureum*, *S. erythrocephalum*, *S. equinum* and *S. lineatum*. (Fig. S8 shows the plots for each species individually).

forested areas, while the proportion of agricultural land and urban area increased with increasing stream length. Species of the montane group A occur in areas with rather low percentages of agriculture, group C species also occur in highly agricultural areas. The breeding sites of the mammalophilic lowland species *S. equinum* and *S. erythrocephalum* have been found in Spain to be associated with the presence of pig farms and the presence of cattle, respectively, at the landscape level (López-Peña et al., 2022b). In addition, agriculture plays an important role through the release of nutrients and pollutants (Liess et al., 2021; Thompson et al., 2020). Similarly important input pathways are wastewater treatment plants as point sources (Enns et al., 2023). Various contaminants discharged via agriculture or wastewater treatment plants (WWTPs) typically accumulate along the water gradient. However, no large-scale pollution data is available so far. Considering that pollution and organic load clearly have a crucial impact on the distribution patterns of freshwater species (Enns et al., 2023; Muñoz et al., 2016; Peng et al., 2020) such data should – as soon as available – be urgently considered for future modelling approaches (Burdon et al., 2019; Sylvester et al., 2023).

The classification of the species based on the current occurrence data well reflects older stream zonation preference assessments of the species (Tables 2 and 3). Group A and group B mainly represent the upstream and midstream species, while in group C species with occurrence focus in the epipotamal, barbel region can be found, with the exception of *S. aureum*, which would fit better into group B according to this classification (Table 2). The five medically relevant species were considered to be potammalian species (*S. erythrocephalum*, *S. equinum* and *S. lineatum*) and species with a broad range regarding stream zonation preferences (*S. reptans* and *S. ornatum*). In general, simuliid larvae with low SI values (SI $\leq$ 2.4, Table 3) occur in low-polluted waters. *S. ornatum* is considered the most tolerant *Simulium* species to pollution with a SI value of 2.4 and focal distribution in alpha mesosaprobic waters (Table 3). The downstream group with the three medically relevant species *S. erythrocephalum*, *S. equinum* and *S. lineatum* also shows comparatively high SI values. These results thus confirm older assessments in line with the latest occurrence data.

In recent decades, there have been increasing reports of nuisance and outbreaks of black flies in Europe. (Ruiz-Arrondo et al., 2020; Wegner, 2006). Wegner (2006) reports from Poland that problems related to mass occurrences of simuliids (nuisance to the public, loss of livestock grazing, and increased mortality of nestlings) have increased strongly in recent years and increasingly cover new regions.

Three of the five particularly medically relevant species, which can be a nuisance to humans and even dangerous to livestock due to their mass occurrence, are classified in-group C – the lowland species. Hence, we could conclude that especially the medically relevant species *S. erythrocephalum*, *S. equinum* and *S. lineatum* could follow a positive trend in the future, as they are able to cope with higher temperatures and anthropogenic pressures to a certain extent. Accordingly, it is likely that the importance of these simuliid species as a nuisance agent will expand in the future. In recent years, particular attention has been paid to *S. erythrocephalum* (Ruiz-Arrondo et al., 2020), due to an aggressive anthropophilic behaviour (Sukhomlin et al., 2022) and mass occurrences at some times (Ignjatović-Ćupina et al., 2006; López-Peña et al., 2022a). Regarding its occurrence along the elevation gradient, *S. erythrocephalum* stands out in comparison to the other species considered here. The species was only observed in large streams throughout the study area. The gonotrophic cycle of *S. erythrocephalum* is shorter than that of other European simuliid species (Ruiz-Arrondo et al., 2017) implying potentially higher abundances and stronger temperature effects. *Simulium erythrocephalum* is particularly associated with Black fewer outbreaks (López-Peña and Cheke, 2023). Black fever occurs in humans after bites and is characterized by headache, nausea, fever, and swollen lymph nodes in the neck (Adler and McCreadie, 2019b). Severe allergic reactions and secondary infections of the bites intensified by scratching have also increasingly reported. Together with *S. lineatum*, *S. erythrocephalum* has been found in laboratory studies (Baužienė et al., 2004; Ham and Bianco, 1983) to be vector competent for *Onchocerca volvulus*, the causative agent of the currently exclusively tropical and subtropical occurring river blindness (López-Peña and Cheke, 2023).

While the filarial nematode *O. volvulus* exclusively affects humans and is not endemic in Europe, other nematode species of the genus *Onchocerca*, such as *O. lupi*, *O. gutturosa*, *O. lienalis*, *O. cervicalis*, *O. dewittei japonica* and *O. jakutensis*, are also known from temperate regions across Europe, the USA and Japan (Wesołowska et al., 2020). These zoonotic nematodes are usually transmitted between wild and domestic animals (including dogs; Sréter-Lancz et al., 2007) via black flies, horse flies and biting midges and they may occasionally infect humans (Morandi et al., 2011; Wesołowska et al., 2020). Among the *Simulium* species considered in this study, *S. erythrocephalum*, *S. ornatum* and *S. equinum* are vector competent for *O. lienalis*, the most common filarial nematode parasite in Europe (Adler and McCreadie, 2019b). In addition, *S. erythrocephalum* has been described as vector competent for the parasites *O. gutturosa*. Both parasite species can cause bovine onchocerciasis (López-Peña et al., 2022a). The prevalence in cattle is thought to be quite high. However, diagnosis is difficult, so exact numbers are not known (Adler and McCreadie, 2019b). The microfilariae of *O. gutturosa* occur in the hosts skin, particularly of the neck and back, whereas the microfilariae of *O. lienalis* infest the umbilical region (i.e., the area around the navel) of the host (Adler and McCreadie, 2019b).

Table 2
Species stream zonation preferences. According to Schröder (1988), with I. montane species (inhabiting headwaters and forested stream sections), II. sylvatic species (inhabiting woodland streams mainly), III. campestric species (with main concentration in field and meadow brooks and streams), IV epiphytic species (restricted to stream sections rich in macrophytes suitable larval and pupal attachment) and VI. potamal species (in rivers and lake outlets), (na – not available) and according to Moog (2017) with euc = eucrenal, spring region; hyc = hypocrenal, spring-brook; erh = epirhithral, upper-trout region; mrh = metarhithral, lower-trout region; hrh = hyporhithral, grayling region; epo = epipotamal, barbel region; mpo = metapotamal, bream region; hpo = hypopotamal, brackish water region; lit = littoral, lake and stream shorelines, lentic sites, ponds etc.. Species of human and veterinary relevance are written in bold.

Group	Species	Zone	euc	hyc	erh	mrh	hrh	epo	mpo	hpo	lit
A	*Simulium monticola*	I	–	1	4	4	1	–	–	–	–
A	*Simulium argyreatum*	na	–	+	3	3	3	1	–	–	–
A	***Simulium reptans***	III	–	+	1	2	3	3	1	–	–
A	*Simulium variegatum*	I	–	–	2	4	4	–	–	–	–
B	*Simulium cryophilum*	I	–	2	5	3	–	–	–	–	–
B	*Simulium vernum*	II	–	1	4	4	1	–	–	–	–
B	***Simulium ornatum***	III	–	1	2	2	2	2	1	+	–
B	*Simulium trifasciatum*	na	–	1	4	4	1	–	–	–	–
C	*Simulium aureum*	IV	–	+	6	4	+	–	–	–	–
C	***Simulium erythrocephalum***	VI	–	–	–	–	2	6	2	–	–
C	***Simulium equinum***	VI	–	–	–	+	3	6	1	–	–
C	***Simulium lineatum***	VI	–	–	–	–	2	6	2	–	–

Table 3
Tolerances of simuliid species to pollution. Saprobity according to Tachet et al. (2010) describes the distribution of taxa along a gradient of organic matter availability/contamination from x – xenosaprobic (i.e. the lowest water saturation rate with decomposing organic substances in any water body), o – oligosaprobic, β and α mesosaprobic to p – polysaprobic (i.e. the richest water bodies in decomposable organic matter) systems. SI refers to the saprobic index with G as indicator weight. Rhithron Type index RTI and ecology type (Biss et al., 2002) indicate the specificity of a taxon for a particular biocenotic region of the rhithral (the higher the value the more specific the species is). Species of human and veterinary relevance are written in bold.

Group	Species	x	o	β	α	p	G	SI	RTI	EcoP
A	*Simulium monticola*	–	5	4	1	–	2	1.6	5	1
A	*Simulium argyreatum*	–	3	6	1	–	3	1.8	5	1
A	***Simulium reptans***	–	2	7	1	–	3	1.9	4	3
A	*Simulium variegatum*	1	5	3	1	–	1	1.4	5	1
B	*Simulium cryophilum*	1	3	5	1	–	1	1.6	4	1
B	*Simulium vernum*	1	3	5	1	–	1	1.6	5	1
B	***Simulium ornatum***	–	1	4	5	–	2	2.4	4	1
B	*Simulium trifasciatum*	+	5	5	+	–	3	1.5	5	1
C	*Simulium aureum*	1	5	4	–	–	2	1.3	5	1
C	***Simulium erythrocephalum***	–	1	6	3	–	3	2.2	2	4
C	***Simulium equinum***	–	+	8	2	–	4	2.2	2	4
C	***Simulium lineatum***	–	+	8	2	–	4	2.2	2	4

The main veterinary medical problem, however, is not the transmission of nematodes but rather livestock losses with animals being killed by excessive blood feeding and acute toxaemia (simuliotoxicosis) from black fly salivary compounds (Adler and McCreadie, 2019a). In Poland, in areas with a known high abundance of simuliids, livestock are kept indoors during the relevant periods or are only allowed to pasture at night. Authorities have also tried biological control methods based on *Bacillus thuringiensis* var. *israelensis* (Bti) against larvae stages in running waters, but with inadequate success (Wegner, 2006). Bti has also been widely used in mosquito control programmes in Europe and is often considered an environmentally safe, effective and targeted biocide but is also controversially discussed with regard to accumulation in food webs (Brühl et al., 2020).

Our novel approach of using a cluster analysis in combination with habitat suitability patterns has proven to be effective in classifying species according to their ecological niches. Paper addressing the potential distribution of freshwater invertebrates using correlative niche modelling or species distribution modelling approaches are rare. To our knowledge, this is the first ecological niche modelling approach on simuliid species in Europe. This omission/underrepresentation of freshwater species is due to the challenging availability of reliable input data. Environmental data on freshwater conditions are difficult to obtain. The data set of Domisch et al. (2015) is the first global area-wide finscale data set of freshwater related variables available. The data is derived from geomorphological data (digital elevation model) and terrestrial climatic and land cover variables, each related to the successive subcatchment. This covers many relevant factors that determine the distribution patterns of aquatic species. Nevertheless, other important factors, such as organic and chemical loads, are missing because they are not yet quantified regularly on large-scale. Moreover, Domisch et al. (2015) only parameterized water bodies above a certain size. Very small water bodies are not included in the data set. Therefore, we had to omit some observed occurrences from the analysis because no environmental variables were available at these sites. Overall, this leads to an underrepresentation of the source regions and thus to a bias in the occurrence data. Source regions provide unique habitats for a high number of species in all or some life stages (Richardson, 2019) and therefore contribute significantly to biodiversity.

5. Conclusion

Simuliidae includes medically and ecologically important species, characterized by a wide variation of ecological niches, which largely determine their distributional patterns. In a rapidly changing environment, characteristics of the species-specific niches determine whether a species benefits (i.e. increases in distribution range and/or abundance) or experiences negative population trends. We still know little about actual tolerances and sensitivities of the studied black flies to global change stressors (e.g. critical maximum temperatures, lethal limits to pesticides and other pollutants). Our species sensitivity scoring was made using the saprobic index, but this essentially estimates sensitivity to organic pollution. Empirical data on actual vulnerability to global change stressors (e.g. temperature, pesticides) are lacking. Our modelling provides important estimates and should now be supported by appropriate empirical testing to see if group C species are indeed more resilient to global change conditions. In addition, suitable laboratory tests must be applied to clarify the extent to which simuliid species are able to transmit certain pathogens under the conditions currently prevailing in Europe (vector competence). Against this background, surveillance and control measurements of Simuliidae and pathogen populations are becoming increasingly important. Our results can serve as a base for effective monitoring programmes of Simuliidae.

CRediT authorship contribution statement

Sarah Cunze: Conceptualization, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Jonas Jourdan:** Conceptualization, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Sven Klimpel:** Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing.

Funding sources

The present study was financially supported by the Uniscientia Foundation (project number P 180-2021).

Declaration of competing interest

The authors declare that they have no competing interests.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.170454.

References

Adler, P.H., 2022. World Blackflies (Diptera: Simuliidae): a comprehensive revision of the taxonomic and geographical inventory. https://biomia.sites.clemson.edu/pdfs/blackflyinventory.pdf. https://biotaxa.org/Zootaxa/article/view/zootaxa.4455.1.2.

Adler, P.H., McCreadie, J.W., 1997. Insect life: the hidden ecology of black flies. Sibling species and ecological scale. Am. Entomol. 43 (3), 153–162. https://doi.org/10.1093/ae/43.3.153.
Adler, P.H., McCreadie, J.W., 2019a. Black flies (Simuliidae). In: Medical and Veterinary Entomology. Elsevier, pp. 237–259.
Adler, P.H., McCreadie, J.W., 2019b. Chapter 14 - black flies (Simuliidae). In: Mullen, G. R., Durden, L.A. (Eds.), Medical and Veterinary Entomology (Third Edition). Academic Press, pp. 237–259.
Adler, P.H., Cheke, R.A., Post, R.J., 2010. Evolution, epidemiology, and population genetics of black flies (Diptera: Simuliidae): infection, genetics and evolution. J. Mol. Epidemiol. Evol. Genet. Infect. Dis. 10 (7), 846–865. https://doi.org/10.1016/j.meegid.2010.07.003.
Akhoundi, M., Sereno, D., Marteau, A., Bruel, C., Izri, A., 2020. Who bites me? A tentative discriminative key to diagnose hematophagous ectoparasites biting using clinical manifestations. Diagnostics (Basel, Switzerland) 10 (5). https://doi.org/10.3390/diagnostics10050308.
Allan, J.D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annu. Rev. Ecol. Evol. Syst. 35 (1), 257–284. https://doi.org/10.1146/annurev.ecolsys.35.120202.110122.
Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., et al., 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Glob. Chang. Biol. 8 (1), 1–16. https://doi.org/10.1046/j.1365-2486.2002.00451.x.
Baužienė, V., Būda, V., Bernotienė, R., 2004. Mating activity of the mammalophilic blackflies *Simulium* (*Wilhelmia*) *lineatum* (Meigen, 1804) (Diptera: Simuliidae) under laboratory conditions. Acta Zool. Lituanica 14 (4), 34–40. https://doi.org/10.1080/13921657.2004.10512597.
Bernhardt, E.S., Rosi, E.J., Gessner, M.O., 2017. Synthetic chemicals as agents of global change. Front. Ecol. Environ. 15 (2), 84–90. https://doi.org/10.1002/fee.1450.
Bernotiene, R., Bartkeviciene, G., 2013. The relationship between water temperature and the development cycle beginning and duration in three black fly species. J. Insect Sci. 13, 1. https://doi.org/10.1673/031.013.0101.
Biss, R., Kübler, P., Pinter, I., Braukmann, U., 2002. Leitbildbezogenes biozönotisches Bewertungsverfahren für Fließgewässer (aquatischer Bereich) in der Bundesrepublik Deutschland. Ein erster Beitrag zur integrierten ökologischen Fließgewässerbewertung 62 (02). Umweltbundesamt Texte.
Brühl, C.A., Després, L., Frör, O., Patil, C.D., Poulin, B., Tetreau, G., et al., 2020. Environmental and socioeconomic effects of mosquito control in Europe using the biocide *Bacillus thuringiensis* subsp. *israelensis* (Bti). Sci. Total Environ. 724, 137800 https://doi.org/10.1016/j.scitotenv.2020.137800.
Burdon, F.J., Munz, N.A., Reyes, M., Focks, A., Joss, A., Räsänen, K., et al., 2019. Agriculture versus wastewater pollution as drivers of macroinvertebrate community structure in streams. Sci. Total Environ. 659, 1256–1265. https://doi.org/10.1016/j.scitotenv.2018.12.372.
Burgin, S.G., Hunter, F.F., 1997. Sugar-meal sources used by female black flies (Diptera: Simuliidae): a four-habitat study. Can. J. Zool. 75 (7), 1066–1072. https://doi.org/10.1139/z97-128.
Chakarov, N., Kampen, H., Wiegmann, A., Werner, D., Bensch, S., 2020. Blood parasites in vectors reveal a united blackfly community in the upper canopy. Parasit. Vectors 13 (1), 309. https://doi.org/10.1186/s13071-020-04177-0.
Cunze, S., Tackenberg, O., 2015. Decomposition of the maximum entropy niche function – a step beyond modelling species distribution. Environ. Model. Software 72, 250–260. https://doi.org/10.1016/j.envsoft.2015.05.004.
Domisch, S., Amatulli, G., Jetz, W., 2015. Near-global freshwater-specific environmental variables for biodiversity analyses in 1 km resolution. Scientific Data 2, 150073. https://doi.org/10.1038/sdata.2015.73.
Ebmer, D., Balfanz, F., Voracek, T., Hering-Hagenbeck, S., Pichler-Scheder, C., Walochnik, J., et al., 2022. The Palearctic blackfly *Simulium equinum* (Diptera: Simuliidae) as a biting pest of captive nyala antelopes (*Tragelaphus angasii*). Zoo Biol. https://doi.org/10.1002/zoo.21719.
Elith, J., Graham, H., C., P., Anderson, R., Dudík, M., Ferrier, S., Guisan, A., et al., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29 (2), 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x.
Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. Methods Ecol. Evol. 1 (4), 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x.
Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17 (1), 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x.
Enns, D., Cunze, S., Baker, N.J., Oehlmann, J., Jourdan, J., 2023. Flushing away the future: the effects of wastewater treatment plants on aquatic invertebrates. Water Res. 243, 120388 https://doi.org/10.1016/j.watres.2023.120388.
Ficsór, M., Csabai, Z., 2021. Longitudinal zonation of larval *Hydropsyche* (Trichoptera: Hydropsychidae): abiotic environmental factors and biotic interactions behind the downstream sequence of Central European species. Hydrobiologia 848 (15), 3371–3388. https://doi.org/10.1007/s10750-021-04602-0.
GBIF, 2022. Occurrence Download. https://doi.org/10.15468/dl.skssm7. Simulium.
Ham, P.J., Bianco, A.E., 1983. Development of *Onchocerca volvulus* from cryopreserved microfilariae in three temperate species of laboratory-reared blackflies. Tropenmed. Parasitol. 34 (2), 137–139 (PMID: 6879707).
Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25 (15), 1965–1978. https://doi.org/10.1002/joc.1276.
Hywel-Jones, N.L., Ladle, M., 1986. Ovipositional behaviour of *Simulium argyreatum* and *S. variegatum* and its relationship to infection by the fungus *Erynia conica* (Entomophthoraceae). Freshwater Biol. 16 (3), 397–403. https://doi.org/10.1111/j.1365-2427.1986.tb00980.x.
Ignjatović-Ćupina, A., Zgomba, M., Vujanović, L., Konjević, A., Marinković, D., Petrić, D., 2006. An outbreak of *Simulium erythrocephalum* (De Geer, 1776) in the region of Novi Sad (Serbia) in 2006. Acta Entomol. Serbica 11, 97–114.
Jordaan, L.C., van Ark, H., 1990. A survey of annoyance of livestock by *Simulium chutteri* Lewis along the Orange River, South Africa (Diptera: Simuliidae). Onderstepoort J. Vet. Res. 57 (3), 189–195 (PMID: 2234866).
Jourdan, J., O'Hara, R.B., Bottarin, R., Huttunen, K.-L., Kuemmerlen, M., Monteith, D., et al., 2018. Effects of changing climate on European stream invertebrate communities: a long-term data analysis. Sci. Total Environ. 621, 588–599. https://doi.org/10.1016/j.scitotenv.2017.11.242.
Jourdan, J., Baranov, V., Wagner, R., Plath, M., Haase, P., 2019. Elevated temperatures translate into reduced dispersal abilities in a natural population of an aquatic insect. J. Anim. Ecol. 88 (10), 1498–1509. https://doi.org/10.1111/1365-2656.13054.
Keck, F., Blackman, R.C., Bossart, R., Brantschen, J., Couton, M., Hürlemann, S., Kirschner, D., Locher, N., Zhang, H., Altermatt, F., 2022. Meta-analysis shows both congruence and complementarity of DNA and eDNA metabarcoding to traditional methods for biological community assessment. Mol. Ecol. 31, 1820–1835. https://doi.org/10.1111/mec.16364.
Leese, F., Sander, M., Buchner, D., Elbrecht, V., Haase, P., Zizka, V.M.A., 2021. Improved freshwater macroinvertebrate detection from environmental DNA through minimized nontarget amplification. Environ. DNA 3, 261–276. https://doi.org/10.1002/edn3.177.
Lehner, B., Verdin, K., Jarvis, A., 2008. New global hydrography derived from spaceborne elevation data. Eos Trans. Am. Geophys. Union 89 (10), 93. https://doi.org/10.1029/2008EO100001.
Liess, M., Liebmann, L., Vormeier, P., Weisner, O., Altenburger, R., Borchardt, D., et al., 2021. Pesticides are the dominant stressors for vulnerable insects in lowland streams. Water Res. 201, 117262 https://doi.org/10.1016/j.watres.2021.117262.
Lock, K., van Maanen, B., 2014. De kriebelmuggen van Nederland en Vlaanderen (Diptera: Simuliidae). Nederlandse Faunistische Mededelingen 43, 67–91. https://repository.naturalis.nl/pub/625715.
Lock, K., Adriaens, T., Goethals, P., 2014. Effect of water quality on blackflies (Diptera: Simuliidae) in Flanders (Belgium). Limnologica 44, 58–65. https://doi.org/10.1016/j.limno.2013.08.001.
López-Peña, D., Cheke, R.A., 2023. Blackflies (Diptera: Simuliidae) of the United Kingdom with comments on species of public health and veterinary importance, their parasites and predators. Simuliid Bull. 60, 18–52. https://gala.gre.ac.uk/id/eprint/43744/7/43744_CHEKE_Blackflies_Diptera_Simuliidae_of_the_United_Kingdom_with_comments_on_species_of_public_health.pdf.
López-Peña, D., Cheke, R.A., García-Roger, E.M., Jiménez-Peydró, R., 2021. Ecological characteristics of pre-imaginal stages of blackflies (Diptera: Simuliidae) in Southern England. Aquat. Insects 1–18. https://doi.org/10.1080/01650424.2021.1974486.
López-Peña, D., Asís-Pardo, J.D., Portillo-Rubio, M., Jiménez-Peydró, R., 2022a. Diversity and distribution of blackflies (Diptera: Simuliidae) of the Tormes river basin (western Spain). J. Eur. Mosquito Control Assoc. 40 (1), 37–47. https://doi.org/10.52004/JEMCA2022.0002.
López-Peña, D., García-Roger, E.M., Lis-Cantín, Á., Jiménez-Peydró, R., 2022b. Environmental drivers of breeding sites in blackfly species of medical and veterinary importance in eastern Spain. Med. Vet. Entomol. 36 (1), 97–112. https://doi.org/10.1111/mve.12557.
Maasri, A., Jähnig, S.C., Adamescu, M.C., Adrian, R., Baigun, C., Baird, D.J., et al., 2022. A global agenda for advancing freshwater biodiversity research. Ecol. Lett. 25 (2), 255–263. https://doi.org/10.1111/ele.13931.
Malmqvist, B., Strasevicius, D., Hellgren, O., Adler, P.H., Bensch, S., 2004. Vertebrate host specificity of wild-caught blackflies revealed by mitochondrial DNA in blood. Proc. R. Soc. B Biol. Sci. 271 (Suppl 4(Suppl 4)), S152–S155. https://doi.org/10.1098/rsbl.2003.0120.
Moog, O., 2017. In: Hertmann, A. (Ed.), Fauna Aquatica Austriaca 1995–2017. A Comprehensive Species Inventory of Austrian Aquatic Organisms with Ecological Notes, 3rd edition. Federal Ministry for Agriculture and Forestry, Vienna (ISBN: 978-3-85174-074-5).
Morandi, F., Krueger, A., Panarese, S., Sarli, G., Verin, R., Nicoloso, S., et al., 2011. First description of nodular onchocercosis (*Onchocerca jakutensis*) in free-ranging Italian red deer (*Cervus elaphus*). J. Wildl. Dis. 47 (4), 963–967. https://doi.org/10.7589/0090-3558-47.4.963.
Muñoz, I., López-Doval, J.C., Castro-Català, N. de, Kuzmanovic, M., Ginebreda, A., Sabater, S., 2016. Effects of emerging contaminants on biodiversity, community structure, and adaptation of river biota. In: Petrovic, M., Sabater, S., Elosegi, A., Barceló, D. (Eds.), Emerging Contaminants in River Ecosystems. Springer International Publishing, pp. 79–119.
Peng, F.-J., Pan, C.-G., Zhang, N.-S., ter Braak, C.J.F., Salvito, D., Selck, H., et al., 2020. Benthic invertebrate and microbial biodiversity in sub-tropical urban rivers: correlations with environmental variables and emerging chemicals. Sci. Total Environ. 709, 136281 https://doi.org/10.1016/j.scitotenv.2019.136281.
Petrozhitskaya, L.V., Rodkina, V.I., 2018. Landscape–zonal distribution of blackflies (Diptera: Simuliidae) in the Ob-Irtysh River Basin (overview). Inland Water Biol. 11 (3), 255–263. https://doi.org/10.1134/S1995082918020177.
Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: an open-source release of Maxent. Ecography 40 (7), 887–893. https://doi.org/10.1111/ecog.03049.
Phillips, S.J., Dudík, M., Schapire, R.E.. [Internet]. Maxent: Software for modeling species niches and distributions. https://biodiversityinformatics.amnh.org/open_source/maxent/.

Reidelbach, J., Christi, H., 2002. A quantitative investigation into the temporal and spatial variations in the emergence of adult blackflies (Diptera: Simuliidae) from the Breitenbach, a small upland stream in Germany. Limnologica 32, 206–235.
Richardson, J., 2019. Biological diversity in headwater streams. Water 11 (2), 366. https://doi.org/10.3390/w11020366.
Rivers-Moore, N.A., Moor, F.C. de, Morris, C., O'Keeffe, J., 2007. Effect of flow variability modification and hydraulics on invertebrate communities in the great fish river (Eastern Cape Province, South Africa), with particular reference to critical hydraulic thresholds limiting larval densities of *Simulium chutteri* Lewis (Diptera, Simuliidae). River Res. Appl. 23 (2), 201–222. https://doi.org/10.1002/rra.976.
Rivers-Moore, N.A., Palmer, R.W., 2018. The influence of turbidity and water temperature on black fly species in the middle and lower Orange River, South Africa. Can. J. Zool. 96 (6), 614–621. https://doi.org/10.1139/cjz-2017-0285.
Roberts, D.M., 1986. Some factors affecting substrate preferences by black-fly pupae (Diptera: Simuliidae). Int. J. Trop. Insect Sci. 7 (01), 107–109. https://doi.org/10.1017/S1742758400003209.
Rühm, W., Kiel, E., 1991. Zur Habitatbindung der Kriebelmücken (Simuliidae, Diptera) im präimaginalen Stadium. Anzeiger für Schädlingskunde Pflanzenschutz Umweltschutz 64 (5), 81–88. https://doi.org/10.1007/BF02021213.
Ruiz-Arrondo, I., Garza-Hernández, J.A., Reyes-Villanueva, F., Lucientes-Curdi, J., Rodríguez-Pérez, M.A., 2017. Human-landing rate, gonotrophic cycle length, survivorship, and public health importance of *Simulium erythrocephalum* in Zaragoza, northeastern Spain. Parasit. Vectors 10 (1), 175. https://doi.org/10.1186/s13071-017-2115-7.
Ruiz-Arrondo, I., Oteo, J.A., Lucientes, J., Muniesa, A., Blas, I. de, 2020. Surveillance of a pest through a public health information system: the case of the blackfly (*Simulium erythrocephalum*) in Zaragoza (Spain) during 2009–2015. Int. J. Environ. Res. Public Health 17 (10). https://doi.org/10.3390/ijerph17103734.
Schmidt-Kloiber, A., Hering, D., 2015. www.freshwaterecology.info – an online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. Ecol. Indic. 53, 271–282. https://doi.org/10.1016/j.ecolind.2015.02.007.
Schröder, P., 1988. Die Kriebelmücken (Diptera: Simuliidae) in den Fließgewässern des westlichen Bodenseebegietes. Mitteilungen des Landesverbandes Naturkunde und Naturschutz 3, 717–749. https://www.zobodat.at/pdf/Mitt-Bad-Landesver-Natkde-Natschutz-Freiburg_NF_14_0717-0749.pdf.
Seitz, G., 1992. Verbreitung und Ökologie der Kriebelmücken (Diptera: Simuliidae) in Niederbayern: Occurrence and ecology of black flies (Diptera: Simuliidae) in Niederbayern/Bavaria. Lauterbornia 11, 1–230. https://www.zobodat.at/pdf/Lauterbornia_1992_11_0001-0230.pdf.
Seitz, G., 2022. On the current status of German-Austrian black flies research (Diptera: Simuliidae): new records and updated checklists. Lauterbornia 88, 153–162. https://www.researchgate.net/publication/360384770_On_the_current_status_of_German-Austrian_black_flies_research_Diptera_Simuliidae_New_records_and_updated_checklists.
Shah, A.A., Dillon, M.E., Hotaling, S., Woods, H.A., 2020. High elevation insect communities face shifting ecological and evolutionary landscapes. Curr. Opin. Insect Sci. 41, 1–6. https://doi.org/10.1016/j.cois.2020.04.002.
Sitarz, M., Buczek, A.M., Buczek, W., Buczek, A., Bartosik, K., 2022. Risk of attacks by blackflies (Diptera: Simuliidae) and occurrence of severe skin symptoms in bitten patients along the Eastern Border of the European Union. Int. J. Environ. Res. Public Health 19 (13). https://doi.org/10.3390/ijerph19137610.
Skendžić, S., Zovko, M., Živković, I.P., Lešić, V., Lemić, D., 2021. The impact of climate change on agricultural insect pests. Insects 12 (5). https://doi.org/10.3390/insects12050440.
Sréter-Lancz, Z., Széll, Z., Sréter, T., 2007. Molecular genetic comparison of *Onchocerca* sp. infecting dogs in Europe with other spirurid nematodes including *Onchocerca lienalis*. Vet. Parasitol. 148 (3), 365–370. https://www.sciencedirect.com/science/article/pii/S0304401707003159.
Sukhomlin, K.B., Zinchenko, M.O., Zinchenko, O.P., Tepliuk, V.S., Biletskyi, Y.V., Ivantsiv, V.V., et al., 2022. The biology of *Simulium erythrocephalum* and *S. chelevini* (Diptera, Simuliidae): morphological, ecological and molecular data. Biosyst. Diversity 30 (1), 3–11. https://doi.org/10.15421/012201.
Sylvester, F., Weichert, F.G., Lozano, V.L., Groh, K.J., Bálint, M., Baumann, L., et al., 2023. Better integration of chemical pollution research will further our understanding of biodiversity loss. Nat. Ecol. Evol. https://doi.org/10.1038/s41559-023-02117-6.
Tachet, H., Bournaud, M., Richoux, P., Usseglio-Polatera, P., 2010. Invertébrés d'eau douce - systématique, biologie, écologie. CNRS Editions, Paris, pp. 600–p.
Thompson, D.A., Lehmler, H.-J., Kolpin, D.W., Hladik, M.L., Vargo, J.D., Schilling, K.E., et al., 2020. A critical review on the potential impacts of neonicotinoid insecticide use: current knowledge of environmental fate, toxicity, and implications for human health. Environ Sci Process Impacts 22 (6), 1315–1346. https://doi.org/10.1039/c9em00586b.
Timm, T., Juhl, W., 1992. Verbreitungsmuster der Kriebelmücken (Diptera, Simuliidae) in Bächen entlang der unteren Ruhr, an der Nahtstelle zwischen Mittelgebirge und Flachland. Dortmunder Beiträge zur Landeskunde 26, 13–28. https://www.zobodat.at/pdf/Dortmunder-Beitr-Landeskde_26_0013-0028.pdf.
Tuanmu, M.-N., Jetz, W., 2014. A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. Glob. Ecol. Biogeogr. 23 (9), 1031–1045. https://doi.org/10.1111/geb.12182.
Wegner, E., 2006. Mass occurrence of blackflies (Diptera Simuliidae) and controlactions against them in Poland. Acta Entomol. Serbia 155–159. http://www.eds.org.rs/AES/Vol11Suppl/18.pdf.
Wesołowska, M., Zając-Pytrus, H., Masny, A., Pytrus, W., Knysz, B., Golab, E., et al., 2020. *Onchocerca jakutensis* ocular infection in Poland: a new vector-borne human health risk? Parasit. Vectors 13 (1), 61. https://doi.org/10.1186/s13071-020-3925-6.
WHO, 2022. Factsheet - Onchocerciasis. https://www.who.int/news-room/fact-sheets/detail/onchocerciasis.
Wipfli, M.S., Merritt, R.W., 1994. Disturbance to a stream food web by a bacterial larvicide specific to black flies: feeding responses of predatory macroinvertebrates. Freshw. Biol. 32 (1), 91–103. https://doi.org/10.1111/j.1365-2427.1994.tb00869.x.
Zahar, A.R., 1951. The ecology and distribution of black-flies (Simuliidae) in South-East Scotland. J. Anim. Ecol. 20 (1), 33. https://doi.org/10.2307/1643.
Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., et al., 2019. CoordinateCleaner standardized cleaning of occurrence records from biological collection databases. Methods Ecol. Evol. 10 (5), 744–751. https://doi.org/10.1111/2041-210X.13152.