Increased drying threatens alpine pond biodiversity more than temperature increase in a changing climate

M. Lamouille-Hébert, F. Arthaud, Aurélien Besnard, M. Logez, T. Datry

RESEARCH ARTICLE

Increased drying threatens alpine pond biodiversity more than temperature increase in a changing climate

M. Lamouille-Hébert[1,2,4] · F. Arthaud[3,4] · A. Besnard[5] · M. Logez[1] · T. Datry[1]

Abstract

Climate change is one of the main drivers of biodiversity decline. Rapidly changing climate in the form of warming, drying, and habitat isolation causes freshwater species to change their spatial extent, as most species have little capacity for in situ responses. However, the relative contribution of these three effects to freshwater species' changing spatial distributions is actively debated. To shed light on this debate, we explored temperature, hydroperiod, and habitat connectivity effects on alpine pond species occupancy probabilities in the northern French Alps. We studied alpine ponds as ideal test systems because they face climate change effects more rapidly, and in more concentrated areas, than any other freshwater ecosystem. We used multispecies occupancy models with three biological groups (amphibians, macrophytes, and Odonata) to examine contrasting responses to climate change. Contrary to expectations, temperature was not the main driver of species occupancy probabilities. Instead, hydroperiod and connectivity were stronger predictors of species occupancy probabilities. Furthermore, temperature increases had the same effect on occupancy probabilities of non-alpine specialist and alpine specialist species. Nonetheless, temperature disproportionately affected a greater number of specialist species compared with non-alpine specialists. We conclude that climate change mitigation will primarily benefit a greater number of alpine specialist species than non-alpine specialists. Finally, we suggest that enhancing our understanding of freshwater hydroperiods will improve our predictions of climate change effects on freshwater species distributions.

Keywords Conservation · Freshwater · Distribution · Models · Occupancy · Connectivity

✉ M. Lamouille-Hébert
marie.hebert@fne-aura.org

F. Arthaud
florent.arthaud@univ-smb.fr

A. Besnard
aurelien.besnard@cefe.cnrs.fr

M. Logez
maxime.logez@inrae.fr

T. Datry
thibault.datry@inrae.fr

1   INRAE, UR RiverLy, Centre Lyon-Grenoble Auvergne-Rhône-Alpes, 5 Rue de La Doua CS70077, 69626 Villeurbanne Cedex, France

2   FNE Haute-Savoie, 84 Route du Viéran, 74370 Pringy, France

3   Univ. Savoie Mont Blanc, INRAE, CARRTEL, 74200 Thonon-Les-Bains, France

4   Pole R&D ECLA, OFB, Direction de La Recherche et de L'Appui Scientifique, 01330 Montfort, Birieux, France

5   CEFE, Univ Montpellier, CNRS, EPHE-PSL University, IRD, Montpellier, France

Introduction

Climate change is one of the main drivers of biodiversity decline (Butchart et al. 2010; IPBES 2019). Rising global mean temperature is accompanied by greater temperature extremes, as indicated by the increasing frequency and strength of heat waves in many regions (Masson-Delmotte et al. 2018; Mukherji et al. 2023). Precipitation patterns are also changing (Milly et al. 2005; Walther et al. 2002), with increasing frequency and intensity of droughts (Barnett et al. 2005; Woodward et al. 2010) and floods (Donat et al. 2013; Masson-Delmotte et al. 2018).

Species possess intrinsic adaptive capacities to climate change characterized by three key components (Bellard et al. 2012; Swaegers et al. 2024): (1) adaptation, whereby species with very rapid generation times can adapt via evolutionary mechanisms (Hughes 2000; Swaegers et al. 2024); (2) plasticity, as certain species have the capacity to acclimate and modify their physiological traits, including growth, respiration, and tissue composition (Hughes 2000; Lindholm et al.

2015), and additionally, species may adapt their behavior, such as day–night activity rhythm and feeding locations (Dussault et al. 2004; Melin et al. 2014) and can also adapt their phenology, such as reproductive timing and dormancy cessation (Kannan et al. 2009; Roy & Sparks 2000; Walther et al. 2002); (3) dispersal, with certain species having the capacity to disperse quickly within their current habitat, when it has become unsuitable, to more suitable habitat (Dawson et al. 2011; Edelsparre et al. 2024; Swaegers et al. 2024).

One of the most prevalent responses to rapid climate change is for species to modify their geographic distributions, as most species do not exhibit in situ adaptation (Baur & Baur 2013). Indeed, species are moving to cooler climates (Freeman et al. 2018) as the global climate warms. The ranges of both flora and nonmigratory fauna are shifting toward higher elevations or/and latitudes, with altitude gains of 20–30 m/decade for flora (Kelly and Goulden 2008; Lenoir et al. 2008; Parolo and Rossi 2008) and 10–60 m/decade for fauna. Likewise, the ranges of many high-latitude fauna are moving northward at 30–70 km/decade (Baur and Baur 2013; Hickling et al. 2006; Roth et al. 2014).

Species are constrained by their thermal tolerances and the connectivity of suitable habitats (Culp et al. 2022; De Frenne et al. 2021; Fazlioglu et al. 2020). Species exhibiting a limited distribution range (e.g., thermal specialists such as cold or hot stenotherms) are more susceptible to the impacts of climate change than those with a wide distribution (e.g., thermal generalists such as eurytherms or ubiquist species) (Lindholm et al. 2015; Pallarés et al. 2020; Rosset and Oertli 2011). Freshwater species additionally are adapted to specific hydroperiods (the frequency, duration, and magnitude of water (Convertino et al. 2013)) to successfully complete their life cycle (Ryan et al. 2014). The escalation in the frequency of heatwaves and the decline in hydroperiods (Carlson et al. 2020; Diamond et al. 2023; Huang et al. 2022) can transform, for different durations, suitable habitat of some species into unsuitable habitat (Carlson et al. 2020; Galatowitsch and McIntosh 2016). Such changes have already led to mass mortality events with occasional species local extinction (e.g., amphibians and plants) and a shift in dominance to species that are tolerant to drier conditions (Carlson et al. 2020; He et al. 2016; Sandvik and Odland 2014). Another consequence of drying is loss of habitat connectivity, as suitable patches become increasingly isolated (Malish et al. 2023). Decreased connectivity among patch habitats reduces species migration success (when possible) as it lengthens travel distances, and recolonization of previously occupied patches becomes dependent on rewetting frequencies (Bogan et al. 2015).

Efforts to understand changing species geographic distributions under drying and warming are abundant and include empirical (Baur and Baur 2013; Kang et al. 2016; Lynch et al. 2016) and model-based methods (Buisson and Grenouillet 2009; Menéndez et al. 2014; Parmesan et al. 1999). However, for most of these efforts, the estimated shifts are based on global climate parameters, and they rarely integrate landscape structure (Opdam and Wascher 2004). Ignoring landscape and habitat structure is likely a critical omission, as distribution shifts predicted by climatic models are often incorrect (Warren et al. 2001). To overcome these problems, some researchers now integrate the dispersal abilities of species into predictive models (Keith et al. 2008; Vos et al. 2008). Still, the relative contribution of warming, drying, and habitat isolation on species distributions is actively debated and remains unclear.

Mountain ecosystems are warming more rapidly in response to climate change when compared with global averages, in particular for temperature (Gobiet et al. 2014; Thuiller et al. 2005) and heat waves (Huang et al. 2022). They thus provide a highly relevant study area because these climatic modifications are leading to rapid changes in habitat and species distribution (Dial et al. 2007; Gehrig-Fasel et al. 2007; Salerno et al. 2014). Owing to their altitude gradients, mountains also provide optimal environments for observing past and future global changes in biodiversity (Peterson et al. 1997) in what is referred to as the "altitude-for-latitude disparity" (Jump et al. 2009). Indeed, the various vegetation types spanning hundreds of kilometers in longitude or latitude in plains are condensed into just a few vertical kilometers within mountains (Peterson et al. 1997). Likewise, mountainous freshwater ecosystems offer valuable opportunities for studying the effects of climate change on the critical drivers of aquatic biodiversity: water temperature, hydroperiod, and connectivity (Beniston 2006; Lamouille-Hébert et al. 2024; Williamson et al. 2009).

Of the mountainous freshwater ecosystems, alpine ponds are especially susceptible to climatic changes (Beniston 2006). They are warming rapidly (+0.72 °C/decade (O'Reilly et al. 2015)) and drying more regularly (Carlson et al. 2020). At high altitudes, retreating glaciers increase the space for new ponds and glacier meltwater increases pond size (Bosson et al. 2023; Salerno et al. 2014). The rapid changes in the spatial distribution of alpine ponds (Salerno et al. 2014; Seimon et al. 2007) creates opportunities for the colonization of new species (Leibold et al. 2004; Macarthur and Wilson 1967; Redmond 2018). Simultaneously, at lower altitudes, south-facing ponds disappear or are reduced in size because of the increase of pejorative processes (Salerno et al. 2014). These combined changes to alpine pond extent may threaten freshwater stenotherms, endangered and endemic species (Khan and Baig 2017; Yang et al. 2017).

In this study, we explored the relationships between climate change effects (temperature, hydroperiod, and connectivity) and Odonata, Amphibia, and macrophytes occupancy probabilities in 73 ponds in the northern French Alps.

We specifically tested three predictions: (1) summer water warming leads to an increase in species occupancy probabilities for non-alpine specialist species and to a decrease for alpine specialist species, (2) increased drying leads to a decrease in species occupancy probabilities for all species, and (3) the more geographically isolated the alpine pond is, the lower the probability of occupancy by alpine pond species.

Materials and methods

Sampling design

The study area was in the Aiguille Rouges and Mont Blanc mountain ranges, in the Haute-Savoie Alpine National

Natural Reserve (Fig. 1). The alpine ponds studied were situated above the treeline. With the assistance of reserve guards, we identified accessible sectors where ponds were present. In each sector, we selected sampling sites in the field to represent alpine pond biodiversity, and spatial and altitude gradients (orange diamonds in Fig. 1).

A single trained observer (M.L.-H.), legally authorized to work in the studied National Natural Reserve and to handle the studied protected species, conducted the field survey between 15 July 2021 and 12 October 2023. The survey included 73 alpine ponds, natural or human-made, ranging from 1750 to 2335 m (median 2064 m) above sea level (Fig. 1). Among the ponds sampled, some were dry at each visit (so the maximum open-water area and maximum depth of the pond may be 0). The maximum open-water area varied between 0 and 3500 m^2 (median 28.5 m^2), and
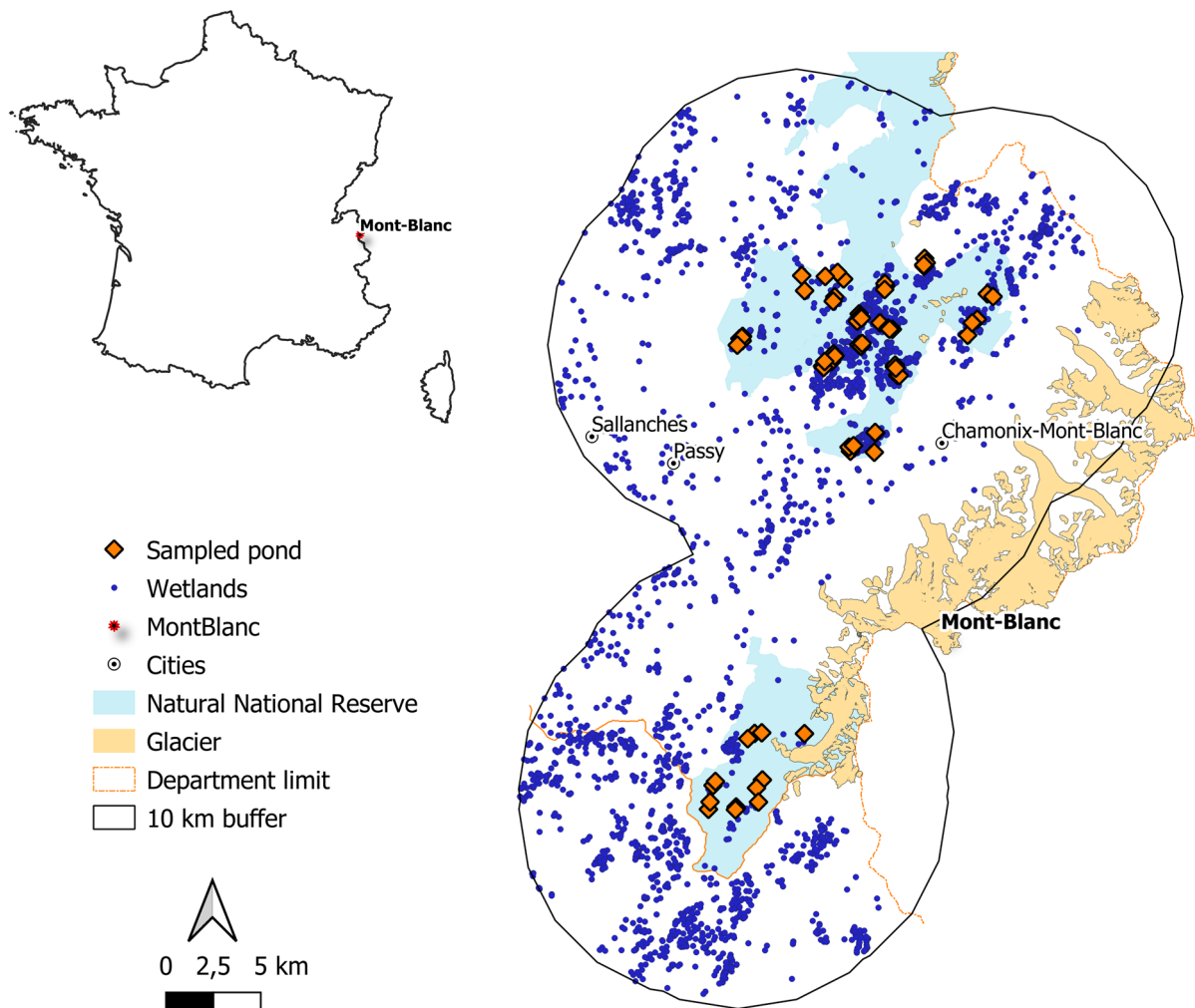
Fig. 1 The study was conducted in Haute-Savoie alpine National Natural Reserves, located in the northern French Alps near Mont Blanc. Seventy-three ponds were sampled in this area (orange diamonds). To explore the pond network, we built a 10-km buffer and made a dataset of all wetlands known in the French part (Haute-Savoie and Savoie departments) of this buffer (blue smaller dots). The department boundary is an administrative boundary (like a region or a country). This figure was made with Quantum GIS (version 3.16.3-Hannover)

their maximum depth ranged between 0 and 1.10 m (median 0.25 m). Four field visits were carried out to record the presence and absence of water in the ponds. Half of the ponds were visited two times in summer 2021 (between 15 July and 15 August with an interval of almost 2 weeks) and one time per summer in 2022 (between 18 August and 26 September) and in 2023 (between 2 July and 12 October 2023). The other ponds were visited one time in 2021 (between 6 September and 3 October), two times in 2022 (between 15 July and 15 August with an interval of almost 2 weeks), and one time in 2023 (between 2 July and 12 October). The 2023 survey was only designed to assess the presence or absence of water in the ponds.

Species sampling methods

To describe species and to improve the detectability of rare species, all sites were visited twice in the same year (2021 or 2022) for more than 30 min (sampling effort for all groups was proportional to sampled pond size: 46 min on average, minimum 30 min and maximum 2 h 35 min). Half of the sites were sampled in 2021, and half in 2022. We worked with three biological groups (amphibians, macrophytes, and Odonata) that (1) are good indicators of pond biodiversity (Oertli et al. 2005), (2) present a wide range of dispersal ability (Halliday 1999; Knaus and Wildermuth 2002), and (3) are known to show contrasting responses to climate change (Carlson et al. 2020; Grand and Boudot 2006; Heidemann & Seidenbusch 2002). All individuals were determined in situ. We counted the number of individuals of all detected species.

Odonata

To maximize the detection probability of adults of Odonata, the sampling was conducted between 15 July and 15 August. Sampling was conducted when the weather conditions were optimal for Odonata activity, i.e., no rain during 2 days before fieldwork, low to moderate wind speed (< 5 on the Beaufort scale), few clouds (cloud cover < 75%), and temperature above 17 °C. The maturation time from immature to mature (reproductive) adult Odonata is 2–3 weeks for the studied species (Grand and Boudot 2006; Wildermuth 2013). Usually, during the maturation phase, immature individuals move several hundred meters away (Khelifa 2017; Kirkton and Schultz 2001) from the pond where they emerged before returning to their natal pond as mature adults. Thus, to detect non-adults (emergent, larvae, and exuviae, i.e., the exoskeleton of emerging individuals) and adults, we set the second sampling 2 or 3 weeks after the first. The first visit was between 15 and 31 July, and the second between 1 and 15 August.

At each visit, we used different methods to detect non-adults (larvae, exuviae, and emergents) and adults of Odonata. In addition to visual species detection without collection, we used an Odonata net for flying adults (a brown 40-cm-diameter 90-cm-deep net), and when the pond was not dried-up, a specific water net (Surber net) for Odonata aquatic larvae. Exuviae were searched for within a minimum 2 m width buffer around the banks of the ponds, and were found close to the banks within 73 sites. All individuals were identified using a hand lens when necessary. We based the identification of the species on existing keys (larvae and exuviae (Doucet 2016), adults (Boudot et al. 2014; Dijkstra 2007)) and a key made exclusively for French alpine species (Lamouille-Hébert 2021). We counted only one individual when it emerged from its exuvia.

Amphibians

We used two methods to detect adults and non-adults of Amphibia: (1) visual detection without collection, and (2) Amphibia water net (Surber net) for adults and non-adults when water was present.

Macrophytes

Plants present in open-water were identified from different randomly located littoral quadrats (2 m × 2 m). In case of low visibility (i.e., when the bottom of the ponds in the quadrat could not be seen through the water), we used a grappling hook beyond each quadrat to explore the diversity at the bottom of the pond. This approach was necessary in one of the two visits to 12 ponds (8% of the 146 samples). We sampled flora on 1 to 20 quadrats per pond, depending on pond area: < 20 m², 1 or 2 quadrats; < 100 m², 2 to 9 quadrats; < 1500 m², 10 quadrats; < 3500 m², 15 quadrats; < 5000 m², 20 quadrats. Quadrats were distributed at equal distance all around the open water of the pond. Each visit had different quadrat distributions: the first quadrat at each visit was placed where open water was nearest to the observed site entry point, to maximize species detectability.

Species classification

To investigate the relationship between the main drivers of climate change and species that are alpine specialists or not, we categorized each species detected as either an alpine specialist or a non-alpine specialist. We used different datasets (Oertli, 2010; SINP AURA, 2023) that provide data on the distribution of species at different altitudes (1000–1500; 1500–2000) and allow us to categorize each species (SM. S1). If main localization data were situated above 1500 m, the species was considered to be an alpine specialist species;

Increased drying threatens alpine pond biodiversity more than temperature increase in a changing...

Page 5 of 19   25

if not, it was considered to be a non-alpine specialist species (Table 1).

Environmental covariates

Summer water temperature

We installed a temperature logger at the bottom of the pond at the first visit to each site to study the effect of water temperature on alpine pond biodiversity (HOBO, TidbiT-MXTemps400). Temperature was sampled every 30 min between 24 September 2021 and 31 July 2022. Water temperatures had risen above 0 °C for all ponds by 31 May 2022. Thus, we used data collected after water temperatures had risen above 0 °C (1 June 2022 and 31 July 2022) to calculate summer water temperature metrics. Because some loggers did not work during this period, we calculated four temperature metrics (°C) in only 58 alpine ponds:

- Cumulative growth-degree-days (GDD), i.e., the sum of daily temperature means
- Minimum temperature: the 5th quantile of minimum daily temperature
- Maximum temperature: the 95th quantile of maximum daily temperature
- Median temperature range: the median of daily difference between the maximum and the minimum temperature

Table 1 Occupancy and design sampling detection probabilities of Amphibia, macrophytes, and Odonata species at our study sites (31 species)

		Occupancy	p(detection) (95% CI)
Amphibia	*Bufo bufo*	0.02	0.85(0.40–0.99)
	Ichthyosaura alpestris	0.24	0.98 (0.91–1.00)
	Rana temporaria	0.15	0.93 (0.79–0.99)
Macrophytes	*Briophytes* sp.	0.26	0.99 (0.95–1.00)
	Caltha palustris	0.02	0.88 (0.49–0.99)
	Carex canescens curta	0.02	0.72 (0.28–0.97)
	Carex echinata	0.08	0.62 (0.34–0.86)
	Carex nigra	0.26	1.00 (0.98–1.00)
	Carex rostrata	0.06	0.97 (0.81–1.00)
	Eriophorum angustifolium	0.07	0.94 (0.75–0.99)
	Eriophorum latifolium	0.01	0.93 (0.47–1.00)
	Eriophorum vaginatum	0.02	0.92 (0.54–1.00)
	Menyanthes trifoliata	0.00	0.79 (0.23–0.99)
	*Callitriche palustris**	0.03	0.70 (0.30–0.95)
	*Carex foetida**	0.01	0.83 (0.36–0.99)
	*Carex pauciflora**	0.02	0.66 (0.24–0.95)
	*Carex paupercula magellanica**	0.03	0.75 (0.34–0.96)
	*Equisetum variegatum**	0.01	0.96 (0.61–1.00)
	*Eriophorum scheuchzeri**	0.05	0.99 (0.88–1.00)
	*Juncus arcticus**	0.01	0.87 (0.39–1.00)
	*Juncus filiformis**	0.06	0.75 (0.42–0.94)
	*Sparganium angustifolium**	0.02	0.92 (0.53–1.00)
	*Trichophorum cespitosum**	0.10	0.99 (0.91–1.00)
Odonata	*Aeshna cyanea*	0.02	0.78 (0.32–0.98)
	Coenagrion puella	0.01	0.73 (0.21–0.98)
	Libellula quadrimaculata	0.01	0.93 (0.48–1.00)
	Pyrrhosoma nymphula	0.02	0.93 (0.56–1.00)
	Coenagrion hastulatum	0.01	0.92 (0.46–1.00)
	*Aeshna juncea**	0.28	0.93 (0.83–0.98)
	*Leucorrhinia dubia**	0.07	0.94 (0.74–1.00)
	*Somatochlora alpestris**	0.12	0.90 (0.70–0.98)

To calculate these values based on the 73 sampling sites, we use the MSOM accounting for imperfect detection ((det.formula = factor(stade)*factor(session)); with "stade" as species stages: non-adult or adult) and any occurrence covariate. *Alpine specialist species. Species have probabilities of detection between 0.617 (CI 0.342–0.856) and 0.997 (CI 0.981–1.000)

Hydroperiod

All alpine ponds studied were shallow (depth 0–1.10 m). Pond water can be completely iced in winter or dried in summer. We could defined the winter period for 59 ponds as being between 1 November 2021 and 31 May 2022. We calculated two hydroperiod metrics respectively in 73 and 59 alpine ponds:

– Summer drying gradient: frequency of observed absence of water for each pond based on the four visits (from zero to four times): 59% of the sampled alpine ponds always had water (43), and 41% were observed without water at least once: 19% once (14), 11% twice (8), 5.5% three times (4), and 5.5% four times (4).

– Winter ice-stage duration: the number of days where maximum temperature was $\leq 0\,°C$

Connectivity

We calculated several connectivity metrics among alpine ponds in the study area. We used a known distribution of wetlands because the distribution of alpine ponds is currently largely unknown. We compiled two datasets: (1) the departmental inventory of wetlands made in 2021 by Haute-Savoie territorial department directory (DDT74) and the local conservatory (Asters-CEN74) and (2) the alpine ponds detailed by M.L.-H. during field campaigns (2017–2019, and for this study in 2021 and 2022). We calculated four groups of connectivity metrics within a 10-km buffer around sampled ponds (Fig. 1) using RStudio version 2023.5.0.335 (Posit team 2023) and R version 4.2.0 (R Core Team 2022):

– Topographical minimum distance between a pond and the nearest potential pond (m): in altitude, with reliefs and valleys, the Euclidean distance, which considers points on the same level, is not sufficient to understand the distance between alpine ponds. We a digital elevation model (DEM) information to integrate the elevation distance and calculate topographical distance between ponds. Topographical distance gives distances that are closer to what an individual would have to cross than Euclidean distance. The DEM raster was downloaded from the French national geographic institute (IGN). We utilized the RGE Alti® dataset at 5-m sampling (https://geoservices.ign.fr/documentation/donnees/alti/rgealti) that we resampled to Sentinel-2 spatial sampling, at 10 m. To calculate this metric, we used the TopoDistance package with the function topoDist (Wang 2020).

– Number and area of wetlands in different buffers around sampled ponds: we calculated these two metrics for each sampled pond in different buffers (100, 200, 300, 400, 500, 1000, 2000, 3000, 4000, 5000, 7500, and 10,000 m, using Euclidean distance to get areas of comparable surfaces around the sampled ponds). This metric was calculated up to a 10,000-m buffer because wind dispersers (adult Odonata or macrophytes) should be able to disperse over long distances (Knaus & Wildermuth 2002).

– Land cover in different buffers around the sampled pond: with the Python package beemap (Wu 2020); we used the Google Earth engine (Gorelick et al. 2017) with 38 images with less than 30% cloud extracted from Sentinel-2 spatial sampling (10 m) (Copernicus Sentinel data of Sentinel-2) to calculate the maximum of the median normalized difference vegetation index (i.e., NDVI, which is an indicator of the catchment productivity of terrestrial vegetation whose growth period is noticeable until September in the alpine belt) of 2022 (between 1 June and 1 September) in different buffers (100, 200, 300, 400, 500, and 1000 m Euclidean distance to get areas of comparable surfaces around the sampled ponds). This metric was calculated in a 1000-m buffer because terrestrial dispersers (non-adult Odonata and Amphibia) should be able to disperse over short distances across land cover (Halliday 1999).

– Number of tributaries in different buffers around sampled ponds and length of total tributaries: we calculated these two metrics for each sampled pond in different buffers (100, 200, 300, 400, 500, and 1000 m Euclidean distance to get areas of comparable surfaces around the sampled ponds) based on the river cartography made in 2019 by DDT74 (GéoCatalogue 2023). This metric was calculated in a 1000-m buffer as above.

Statistical methods

We tested whether correlations between summer water temperature, hydroperiod, connectivity, and alpine pond species occupancy probabilities were significant or not at the 5% threshold. We modeled the detection–nondetection data of the replicates per sampling site (i.e., 2 temporal replicates × 2 sampling stages (non-adults and adults)) using multispecies occupancy models (MSOMs) (Devarajan et al. 2020; Dorazio and Royle 2005; Zipkin et al. 2023). MSOMs rely on repeated sampling of a biological community at multiple spatial locations to estimate the number and composition of species in the community (Dorazio and Royle 2005; MacKenzie et al. 2002). This allows for imperfect detection of species to be taken into account (Devarajan et al. 2020). They can simultaneously model the effects of covariates at the species and community levels, using information from the most frequent species to improve the accuracy of estimates, particularly for the rarest species (Dorazio and Royle 2005; Mourguiart et al. 2021; Zipkin et al. 2023). We used the library spOccupancy (Doser et al. 2022) with RStudio version 2023.5.0.335 (Posit team 2023) and R version 4.2.0

(R Core Team 2022). We used the function sfMsPGOcc to account for spatial autocorrelation, and correlations between species. Imperfect detection was integrated in all our models, considering the interaction between temporal replicates and sampling stages. We fit 104 models (SM.S2) to analyze the simple and quadratic relationship between each scaled covariate and species occupancy probabilities. This relationship was considered significant when 95% credibility intervals (CIs) of the slope did not overlap with zero. When the quadratic coefficient between each scaled covariate and species occupancy probabilities was significant, we chose the quadratic model. Otherwise, the linear model or null model was selected, depending on the significance of the linear coefficient. The classification as alpine specialist or non-alpine specialist was a post-analysis interpretation and does not influence the analysis results. We fit a supplemental model without covariates and with sampling potential bias (stage × session) to determine the percent of sites where species are present (occurrence) and estimated our sampling design probability to detect these species when they are present (detection probabilities). The script can be found in SM.S3 with the data in the Data INRAE repository (https://doi.org/https://doi.org/10.57745/YFE6IJ) to follow the findability, accessibility, interoperability, and reusability (FAIR) guiding principles for managing scientific data (Wilkinson et al. 2016).

Results

Biological communities

We detected 31 species: 3 species of amphibian, 20 of macrophytes, and 8 of Odonata (Table 1). Specialist species represented 0% of Amphibia, 50% of Odonata (4 species), and 50% of macrophytes (10 species). Species had occurrences ranging between 0.00 and 0.28 (Table 1). They were detected with a detection probability depending on the species, ranging between 0.62 (CI 0.34–0.86) and 1.00 (CI 0.98–1.00) (Table 1).

We detected Odonata at 60% of the sampled alpine ponds (44 sites), representing 1108 individuals (841 non-adults and 149 adults of alpine specialist species; 14 non-adults and 104 adults of non-alpine specialist species). Per site, we detected between zero and five Odonata species from the eight present in our study. Amphibia were detected at 78% of the sampled ponds (57 sites), representing 1437 individuals (1099 non-adults and 338 adults). Per site, we counted zero to three Amphibia species from the three present. Macrophytes were recorded at 84% of the sampled alpine ponds (61 sites). Per site, we counted 0 to 11 macrophytes species from the 20 present.

Relationships between covariates and species occupancy probabilities

Sixty percent of species (71% of alpine specialists and 50% of non-alpine specialists) occupancy probabilities had a significant relationship with summer temperature. These species had a significant relationship with GDD, with summer minimum temperature, or with both metrics. Thirty percent of species had a significant quadratic relationship with GDD (whether or not they also had a relationship with summer minimum temperature) and 40% had a significant positive relationship with summer minimum temperature (whether or not they also had a relationship with GDD) (Fig. 2). Odonata species occupancy probabilities had no significant relationship with GDD. Amphibia (*Bufo bufo*) and macrophytes (50% of alpine specialist species and 30% of non-alpine specialists) species occupancy probabilities had a significant relationship with GDD (Fig. 2a).

This relationship had the same form with the same slope directions for Amphibia and macrophyte alpine specialist and non-alpine specialist species. The probability of all species occupancy was highest at intermediate values of GDD, from 636 to 671 °C (Fig. 2b). Amphibia (*Ichtyosaura alpestris*), macrophytes (30% of alpine specialist species and 30% of non-alpine specialists), and Odonata (75% of alpine specialist species and 50% of non-alpine specialists) species occupancy probabilities increased when the summer minimum temperature increased (Fig. 2a, b). Alpine species occupancy probabilities were marginally related to the increase of summer maximum temperature and summer median temperature (SM.S4). For *Bufo bufo*, a non-alpine specialist species, the occupancy probability increased with increasing maximum water temperature (when Temp max > 30 °C). On the contrary, the occupancy probability of *Aeshna juncea*, an alpine specialist species, decreased when the maximum water temperature exceeded 21 °C.

Ninety-three percent of species (92% of alpine specialists and 94% of non-alpine specialists) occupancy probabilities were correlated with one or two covariates describing hydroperiod (Fig. 3). These species had a significant relationship with summer drying gradient, with the length of winter ice stage, or with both metrics.. Only one amphibian species (*Bufo bufo*) and two macrophyte species (*Eriophorum angustifolium* and *Juncus articus*) were not correlated to the increase in summer drying gradient (whether or not they also had a relationship with the length of winter ice stage) (Fig. 3a). Odonata, Amphibia, and most macrophyte (except *Carex nigra* and *Bryophytes* sp.) probabilities of occupancy were almost zero when alpine ponds had been observed dried at each visit (Fig. 3b).
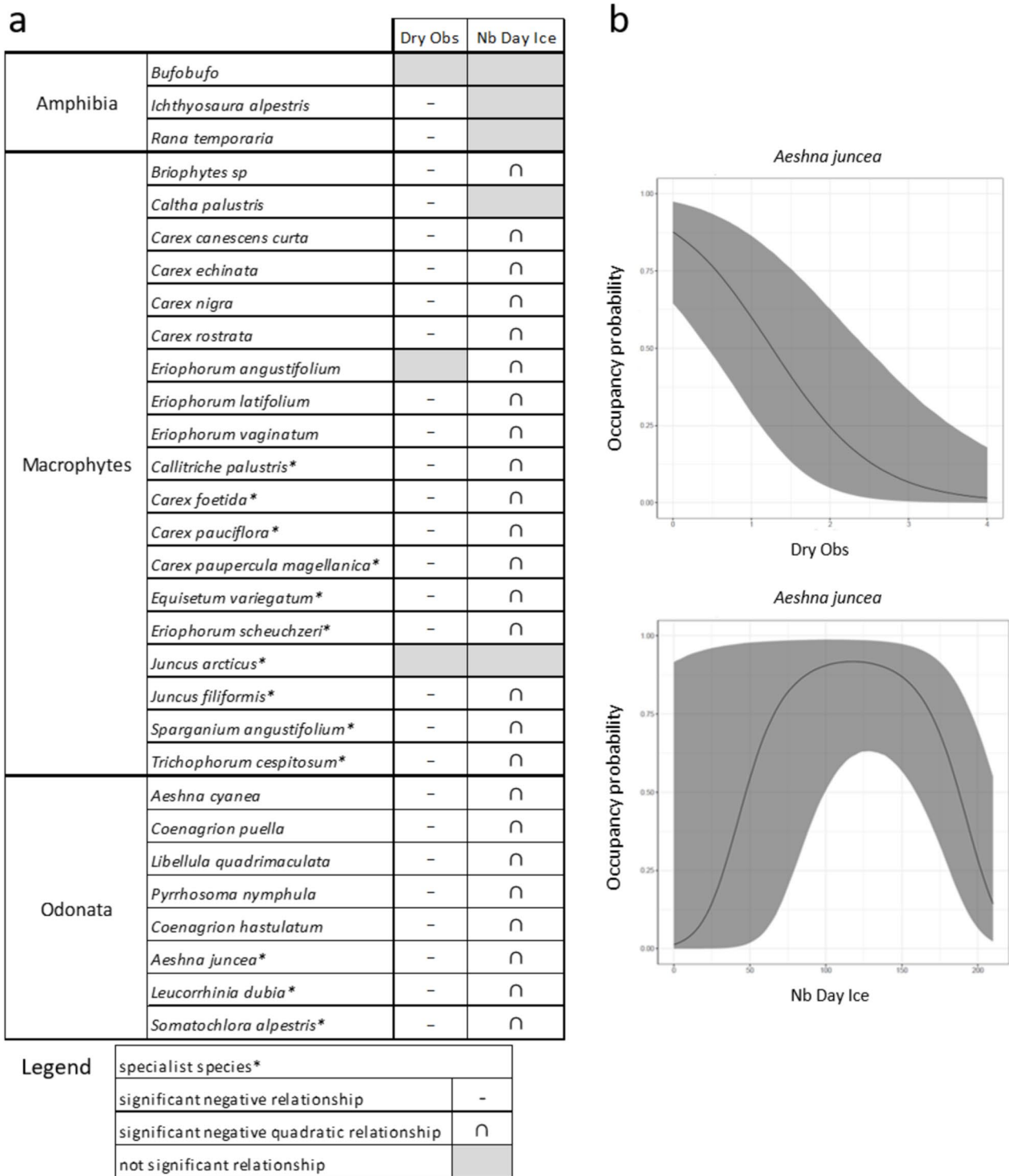
Amphibia species occupancy probabilities were not related to the length of the winter ice stage. Macrophytes (90% of non-alpine specialist and alpine-specialist species)
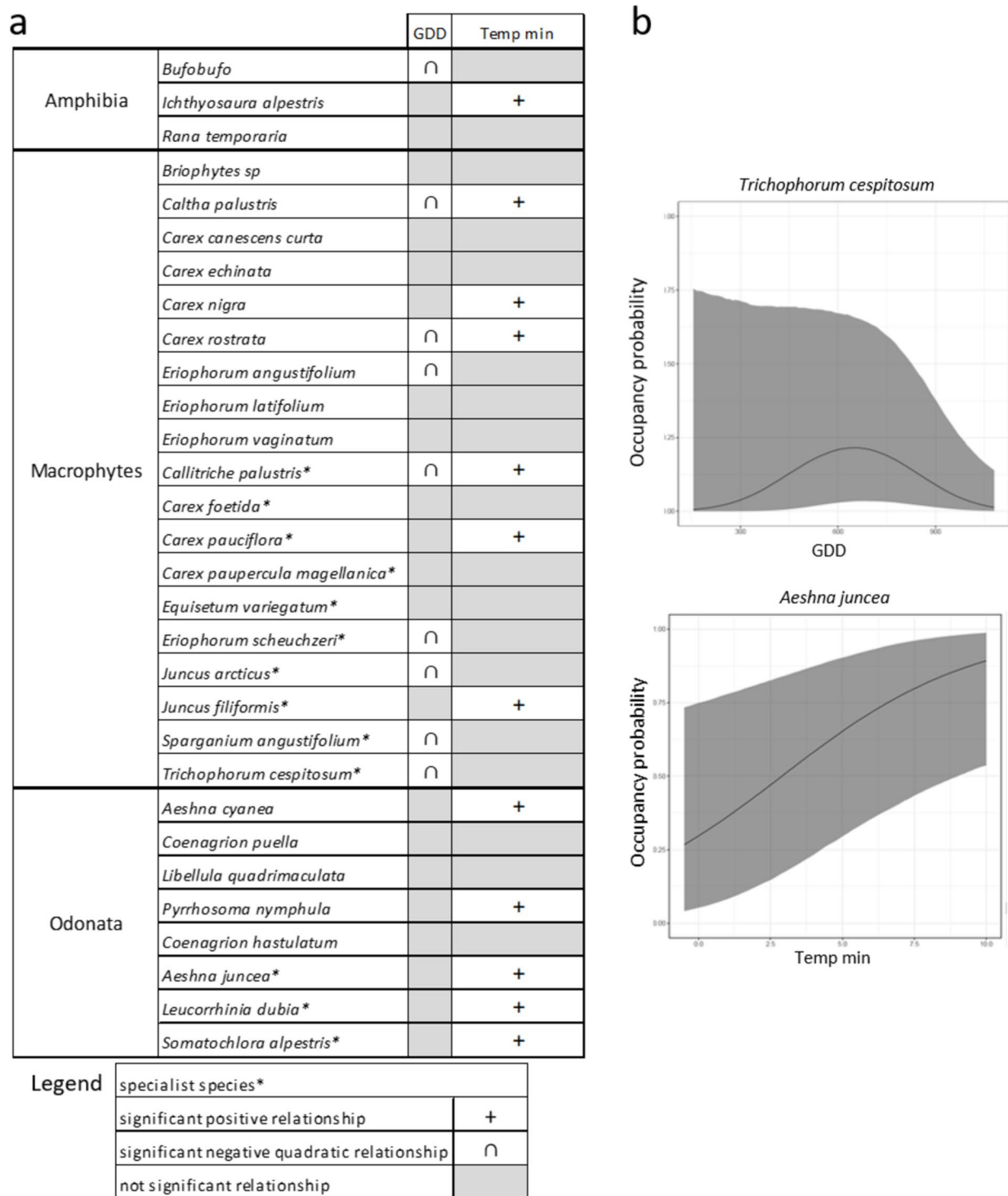
Fig. 2 Relationship between summer water warming and occupancy probabilities of alpine pond species (Amphibia, macrophytes, and Odonata). **a** Relationships were tested with different temperature metrics and with different MSOMs. For each species (listed by group: Amphibia, macrophytes, and Odonata), we report here the significant relationship between the metric (simple metric or with its quadratic effect) and their occupancy probability. *Alpine specialist species. **b** Relationships between the metrics and occupancy probability of two specialist species (*Trichophorum cespitosum* and *Aeshna juncea*): species occupancy probability by median (black curve) (in grey, CI 0.025–0.975). GDD is growth-degree-days (i.e., the summer accumulated warm); Temp min is the fifth quantile of the summer daily temperature

a

		Dry Obs	Nb Day Ice
Amphibia	Bufobufo		
	Ichthyosaura alpestris	–	
	Rana temporaria	–	
Macrophytes	Briophytes sp	–	∩
	Caltha palustris	–	
	Carex canescens curta	–	∩
	Carex echinata	–	∩
	Carex nigra	–	∩
	Carex rostrata	–	∩
	Eriophorum angustifolium		∩
	Eriophorum latifolium	–	∩
	Eriophorum vaginatum	–	∩
	Callitriche palustris*	–	∩
	Carex foetida*	–	∩
	Carex pauciflora*	–	∩
	Carex paupercula magellanica*	–	∩
	Equisetum variegatum*	–	∩
	Eriophorum scheuchzeri*	–	∩
	Juncus arcticus*		
	Juncus filiformis*	–	∩
	Sparganium angustifolium*	–	∩
	Trichophorum cespitosum*	–	∩
Odonata	Aeshna cyanea	–	∩
	Coenagrion puella	–	∩
	Libellula quadrimaculata	–	∩
	Pyrrhosoma nymphula	–	∩
	Coenagrion hastulatum	–	∩
	Aeshna juncea*	–	∩
	Leucorrhinia dubia*	–	∩
	Somatochlora alpestris*	–	∩

Legend		
specialist species*		
significant negative relationship	–	
significant negative quadratic relationship	∩	
not significant relationship		

b

Fig. 3 Relationship between absence of liquid water and alpine pond species (Amphibia, macrophytes, and Odonata) occupancy probabilities. **a** Relationships were tested with different drying metrics and with different MSOMs. For each species (listed by group: Amphibia, macrophytes, and Odonata), we report here the significant relationship between the metric (simple metric or with its quadratic effect) and their occupancy probability. *Alpine specialist species. **b** Relationship between the metrics and occupancy probability of a specialist species (*Aeshna juncea*): species occupancy probability by median (black curve) (in grey, CI 0.025–0.975). Dry Obs is the summer drying gradient; Nb Day Ice is the length of the winter ice stage

and all Odonata species occupancy probabilities had a significant quadratic relationship with this covariate (whether or not they also had a relationship with summer drying gradient) (Fig. 3a). This relationship had the same form with the same sign on the slope for both macrophyte and Odonata alpine specialist and non-alpine specialist species. The probability of all species occupancy was highest at intermediate values of winter ice stage duration between 83 and 121 days (Fig. 3b). The macrophyte threshold was 83–121 days when for Odonata it was 110–118 days.

Eighty-three percent of species (92% of alpine specialists and 76% of non-alpine specialists) occupancy probabilities had a significant quadratic relationship with topographical minimum distance between a pond and the nearest one (Fig. 4). These species were amphibians (*Ichtyosaura alpestris* and *Rana temporaria*), all macrophytes, 67% of Odonata alpine specialist species, and 40% of Odonata non-alpine specialists (Fig. 4a).

The relationship had the same form with the same slope directions for alpine specialist and non-alpine specialist species from the three groups. The probability of all species occupancy was highest at intermediate values of topographical minimum distance between a pond and the nearest pond between 117 and 208 m (Fig. 4b). The amphibian threshold was 132–181 m, while it was 117–208 m for macrophytes and 126–162 m for Odonata.

Among the four non-alpine specialist species whose occupancy probabilities were not correlated to topographical minimum distance between a pond and the nearest pond, *Aeshna cyanea* and *Libellula quadrimaculata* occupancy probabilities were not correlated with any connectivity covariates. *Bufo bufo* and *Pyrrhosoma nymphula* occupancy probabilities were negatively correlated with the number of wetlands and positively (after reaching a threshold) with the number of tributaries on the 100-m buffer (SM.S5). Furthermore, occupancy probabilities of *Aeshna juncea*, the only specialist not influenced by topographical minimum distance between a pond and the nearest pond, decreased with increasing number and area of wetlands in the 3000- and 4000-m buffers. Nevertheless, increasing area of wetlands on the 10,000-m buffer increased its occupancy probability.

Discussion

Our findings suggest that, contrary to what we expected, the significant effect of increased water summer temperature was limited to a few species only and with the same significant relationship for non-alpine specialist and alpine specialist species occupancy probabilities. We also found that the predicted decreasing hydroperiod and connectivity, especially considering topographic distance between ponds, resulted in reduced occupancy probabilities of species. This

relationship influenced a greater number of studied species than the increased summer water temperatures. Therefore, species distribution models that are primarily based on temperature may underestimate the effects of climate change on species occupancy probabilities.

Temperature was not the primary driver of biodiversity distribution

Temperature drives alpine species distribution. Its increase is influencing species densities (Alatalo et al. 2017) and increasing the risk of species local extinction. This last result has been demonstrated in mountain ecosystems for terrestrial (plants) (Jump et al. 2009), stream (Stoneflies, *Lednia*) (Green et al. 2022), and pond (Arctic fairy shrimp, *Branchinecta paludosa*) (Lindholm et al. 2015) species. Therefore, temperature increases are causing continued displacement of communities in mountain terrestrial ecosystems (Lenoir et al. 2008) as well as aquatic environments (Li et al. 2016; Sáinz-Bariáin et al. 2016). Consequently, temperature is the primary driver used to describe the effects of climate change on alpine species distribution (Adhikari et al. 2023; Engler et al. 2011; Tovar et al. 2022).

We observed that increasing summer heat accumulation in the water (GDD) limited the occupancy probabilities of up to 30% of the 30 alpine pond species studied. Summer minimum temperature increases had significant positive effects on the species occupancy of 40% of the alpine pond species studied. Temperature increase had significant effects only in a part of the studied species occupancy probabilities, contrary to our expectations, but in line with the main results of a global meta-analysis including both terrestrial and marine fauna (Parmesan and Yohe 2003).

Although there was a significant effect of temperature on species occupancy, the effects of accumulated summer temperature and minimum temperature variables differed. We found that increasing summer heat accumulation in the water (GDD) decreased amphibian and macrophytes species occupancy probabilities when a threshold was reached but had no effects on Odonata. Amphibia and macrophyte species occupancy probabilities increased when summer heat accumulation in the water was low and increased over the summer. This well-studied stage (Cross and Zuber 1972; Liu et al. 2022; McMaster and Wilhelm 1997) corresponds to the necessary thermal accumulation that triggers their development and growth. Yet, occupancy probabilities of species decreased after heat accumulation in the water reached a certain threshold. This is because their development stops, and if temperature accumulated continues to increase, it can reach their lethal point (Abbasi et al. 2023; Wahid et al. 2007). The unexpected absence of significant effects of summer heat accumulation in the water (GDD) on Odonata species occupancy probabilities could be due to
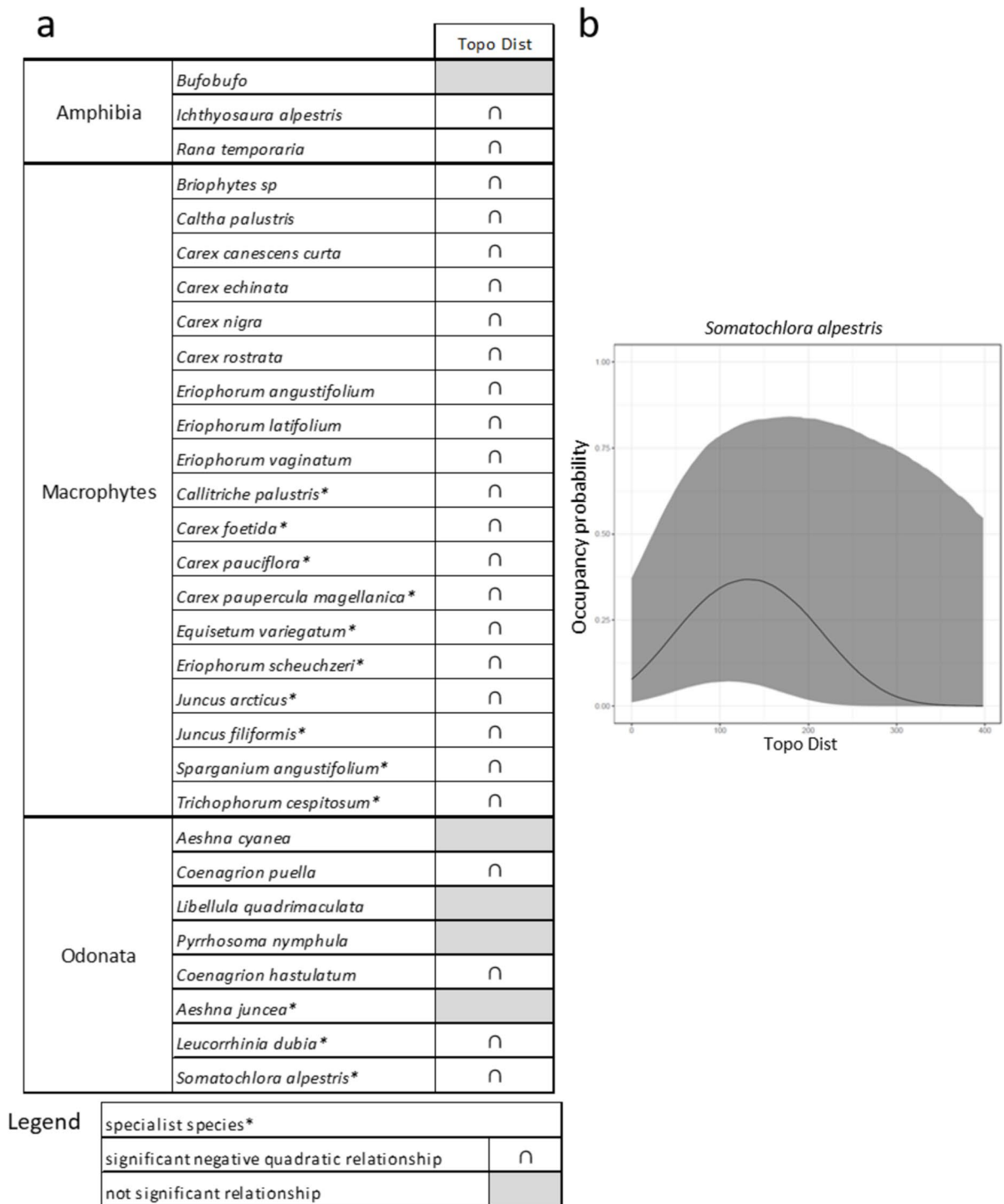
Fig. 4 Relationship between topographical minimum distance (Topo Dist: distance between a pond and the nearest pond) and alpine pond species (Amphibia, macrophytes, and Odonata) occupancy probabilities. **a** This relationship was tested with a MSOM. For each species (listed by group: Amphibia, macrophytes, and Odonata), we report here the significant relationship between this metric and their occupancy probability. *Alpine specialist species. **b** Relationship between this metric and occupancy probability of a specialist species (*Somatochlora alpestris*): species occupancy probability by median (black curve) (in grey, CI 0.025–0.975)

their thermoregulatory plasticity despite being ectothermic: color change, regulated hemolymph circulation in the thorax and abdomen, or employing "wing-whirring" behavior for thermoregulation (May 1976; Polcyn 1994; Sternberg 1997). Our results suggest that alpine specialist species of Odonata had the same capacity as other Odonata to colonize a broad

spectrum of thermal habitats along the temperature range in alpine ponds.

We also found that, for some species from the three different studied groups, their occupancy probabilities were increased by summer minimum temperature increase. This is because, in high mountains, low temperature stresses species, reducing their growth and survival (Cabrera 1996; Larcher et al. 2010). Alpine specialist species are adapted to high mountain extreme cold. For example, cold-adapted plants can express some particular forms/transcripts of proteins (e.g., rubisco) to increase their "carbon assimilation rate supporting the photochemical mechanism of photosynthetic acclimation to cold" (Jurczyk et al. 2016). Unexpectedly and contrary to our predictions, studied alpine specialists and non-alpine specialists species (40%) occupancy probabilities both increased with temperature increase. It may be that an increase in the minimum temperatures reduces the stress caused by low temperatures for all species, allowing them to colonize new alpine ponds. As we detected, temperature exerts a notable influence on species distribution, yet it is not the sole determinant of occupancy probabilities for all species in response to climate change.

Hydroperiod constrained more species occupancy probabilities than temperature

Hydroperiod reduction can be a major disturbance of aquatic communities and biodiversity (Greig et al. 2013; Leigh and Datry 2017; Stubbington et al. 2019). In lotic and lentic communities, absence of water results in a lower number of aquatic taxa at a given site than when water is present (Leigh and Datry 2017; Rosset et al. 2017; Wissinger et al. 2009). The few studies conducted in alpine lentic and lotic freshwaters identified a reduction of the density and diversity of macroinvertebrates, bryophytes, and high-soil-moisture vascular plant species with hydroperiod decrease (Doretto et al. 2020; He et al. 2016; Sandvik and Odland 2014). Hydroperiod decrease can lead to changes in species distribution (Tolonen et al. 2019) and local extinction of species, for example, amphibians, bryophytes, and aquatic vascular plants (Carlson et al. 2020; He et al. 2016; Sandvik and Odland 2014).

Here, we found that most (90%) studied species occupancy probabilities decreased when summer drying increased, corroborating previous studies on fishes and amphibians (Ogston et al. 2016; Walls et al. 2013). This was notably the case for species from the three biological groups we studied. From Odonata, amphibians, and macrophytes, some species are known to be summer drying resistant. For example, larvae of *Coenagrion hastulatum* can resist desiccation and *Somatochlora alpestris* is able to grow without open water, both by burrowing into the mud or damp peat (Heidemann and Seidenbusch 2002; Kury and Wildermuth

2013). In macrophytes, amphiphyte groups with the ability to produce both terrestrial and aquatic forms, or to grow leaves underwater and in air (phenotypic plasticity in heterophylly), may be adapted to avoid short-term drying (De Wilde et al. 2017; Wells and Pigliucci 2000; Zelnik et al. 2021): *Caltha palustris* (Dorotovičová, 2013), *Juncus* sp., and *Carex* sp. (Casanova 1997). However, like all studied species, drying-resistant species occupancy probabilities decreased as summer drying increased. This is probably because thresholds in drying resistance exist, as found in rivers and streams, for example (Stubbington and Datry 2013).

We found here that, as the length of the winter ice stage increased, the occupancy probabilities of most (83%) of the studied species decreased. This was the case for species from two of the biological groups studied (Odonata and macrophytes). The low occupancy probabilities of these species associated with a short length of winter ice stage could be explained by exposure to extreme air temperature, insufficient food resources in winter, low nutrients when the photoperiod is sufficient for species to break diapause, or the energetic cost to adapt to frequent water state changes (Bale and Hayward 2010). In fact, we showed for Odonata and macrophytes that species occupancy probabilities increased with the length of the winter ice stage up to a threshold, aligning with findings from ice enclosure stress-tolerant aquatic invertebrates and vascular plants (Green et al. 2022; McAllen 1997; Renman 1989). In fact, alpine freshwater species are adapted to a water-freezing state (Carbonell et al. 2024; Theissinger et al. 2013). These harsh conditions can help limit colonization by species from warmer habitats, including potential new competitors or predators (Carbonell et al. 2024). Nevertheless, when the threshold was reached, the occupancy probabilities of species decreased because long-term freezing still represents a possible lethal freezing risk for these species (Boudot et al. 2014; Hotaling et al. 2021; Rehm et al. 2021). Amphibians were the sole group examined whose species occupancy probabilities were unaffected by the potential long duration of these stresses, and this is probably because they are adapted to survive long-term freezing, as found in different studies (Costanzo and Lee 2013; Storey 1999; Yokum et al. 2023).

A shortened hydroperiod lowered the occupancy probabilities of more studied species (summer hydroperiod: 90%; ice-stage duration: 83%) than an increase in summer water temperature (summer temperature warm: 30%; minimum temperature: 40%). However, the main predictions of the effects of climate change on species distributions do not use hydroperiod, as these data are usually not available at a large scale, but are based on temperature and, to a lesser extent, precipitation scenarios (DeWeber and Wagner 2018). Then, main predictions may underestimate the effect of climate change on the distribution of numerous alpine species. It is important to incorporate alpine pond hydroperiod variation

with climate change, considering temperature and precipitation scenarios, into models to predict alpine pond species distribution. Because alpine ponds are understudied (Khan and Baig 2017), their hydroperiod is poorly known, but improving such knowledge is necessary to better understand the effects of climate change on species distributions. Using existing data could lay the foundations to develop a model of alpine pond hydroperiods adapted to different regions. Long-term monitoring of alpine pond hydroperiods could help to improve it.

Isolation constrains species occupancy probabilities

Theoretical models suggest that limiting connectivity will reduce colonization or recolonization and increase local extinctions in source–sink systems (Macarthur and Wilson 1967). Connectivity decrease should in turn affect metacommunity dynamics (sensu Leibold et al. 2004). Aquatic species are particularly susceptible to these isolation threats, altering their movement and survival (Serrano et al. 2020). In lotic and lentic ecosystems, dried hydrologic connections act as barriers to species displacement, for example, for fish (Baber et al. 2002; Jaeger et al. 2014; Perkin and Gido 2012) or macroinvertebrates (Bae and Park 2016; Gauthier et al. 2021; Sarremejane et al. 2021). In lentic patchy environments, drying impacts suitable habitat (patch) surface and connectivity between them, for example, for turtles (Kindlmann and Burel 2008; Serrano et al. 2020). To recolonize suitable patches, species need to be able to migrate to connected ones (patches not dried) (Macarthur and Wilson 1967). Decreases of connectivity affect persistence and turnover of species and ultimately lead to changes in their occupancy probabilities (Serrano et al. 2020).

As predicted and in coherence with previous investigations, we showed that decrease of connectivity decreased occupancy probabilities of most studied species. To analyze the effects of connectivity on species occupancy probabilities, we used different structural metrics linked with the patch spatial distribution in the landscape (patch number, patch sizes, and interpatch distances) (Tischendorf and Fahrig 2001; With and Crist 1995). We demonstrated that the number and sizes of patches around a studied patch had significant effects on the occupancy probabilities of fewer species than interpatch topographic distance (83%). We reinforced the previous finding that short topographic distances between patches are more important for maintaining most species populations than dense networks, to survive the rapid effects of climate change, such as isolation caused by drying (Hodgson et al. 2012). Interpatch topographic distances had the same effects on all species of all studied groups (Odonata, Amphibia, and macrophytes). One of our results was that the effects of interpatch topographic distance on the occupancy probabilities were also the same

for non-alpine specialist and alpine specialist species, as demonstrated in previous studies (Fahrig 2017). We showed for these three groups that species occupancy probabilities increased with interpatch topographic distance increase, before decreasing when a threshold was reached. These results illustrate the importance of maintaining the spatial heterogeneity of patches (interpatch distance), as demonstrated in previous studies (Gauze 1934; Huffaker 1958). This allows maintaining the persistence of prey and predator systems with separate prey refuges and dividing food resources in different habitats. It also can reduce the predator and parasitoid dispersal efficiency and decrease the covariance of competing species (Roland 1993). In addition, the distance between patches occupied by a matrix of terrestrial habitat is necessary for species (Duelli 1997), for example, for the maturation at different stages of studied species (Odonata and Amphibia). When the topographic interpatch distances increased, a threshold in occupancy probabilities was reached, probably when it exceeded the dispersal ability of species (Macarthur and Wilson 1967; Makoto and Wilson 2019).

The effect of interpatch topographic distance increase was neutral for the occupancy probabilities of few species. Of these, species with longer distance dispersal such as *Aeshna juncea*, *Aeshna cyanea*, and *Libellula quadrimaculata* are less sensitive to structural connectivity (Pearson and Dawson 2005). *Aeshna juncea* was the only alpine specialist species with a neutral effect of interpatch topographic distance on its occupancy probabilities. Nevertheless, we demonstrated that *Aeshna juncea* required high pond area within 10,000-m buffers to increase its occupancy probabilities. This could be due to its strong flight ability that allows it to travel across valleys to find new ponds. Such studies on connectivity for Odonata are rare, however, so additional studies investigating the genetic structure of this species would be useful in better contextualizing these results.

For *Bufo bufo* and *Pyrrhosoma nymphula*, the densities of ponds and tributaries close (100 m buffer) to the occupied pond were important to maintain their persistence. To increase their occupancy probabilities, it appears that these species may need to be isolated from the other ponds but be able to move to tributaries if conditions are unsuitable in their current living patch.

To improve knowledge about the effects of climate change on current and future distribution of species, interpatch topographical distances need to be included in distribution models. One of the future challenges is to enhance the distribution of ponds and their hydroperiod to limit biases. In fact, small decreases in hydroperiods lead to large decreases in connectivity between habitats in freshwater ecosystems (Baber et al. 2002; Malish et al. 2023; Stanley et al. 1997). Our results and future research will enable us to strengthen existing patch connectivity, identify where patch chains need

to be restored or completed, and thereby increase species resilience to ongoing climate change.

Climate change mitigation may benefit specialist species most

Consistent with prior research, we predicted that temperature increase would increase the occupancy probabilities of non-alpine specialist species, whereas alpine specialist species occupancy probabilities would decrease (Lindholm et al. 2015; Pallarés et al. 2020; Rosset and Oertli 2011). Contrary to what we expected, our results showed that the relationship between temperature and alpine specialist and non-alpine specialist species occupancy probabilities were similar in terms of slope. This was also the case for hydroperiod and connectivity. However, the forms of the relationships were specific to each factor. We found similar results in studies of the effect of climate change on the presence–absence distribution of amphibians and Insects. In fact, Shadle et al. (2023) compared experimental climate change effects on habitat specialist wood frogs (*Lithobates sylvaticus*) and more generalist spring peepers (*Pseudacris crucifer*) (Shadle et al. 2023). They demonstrated that warming accelerates the duration to metamorphosis, while drying leads to diminished body size at metamorphosis in both species. Other authors demonstrated that the insects' distribution trends over time were not significantly affected by species range size across Europe (Engelhardt et al. 2022). Finally, we found that the main difference between alpine specialists and non-alpine specialists was not in the form of their relationship with temperature, but rather in the proportion of species from each of these two groups particularly susceptible to the effects of temperature increase. This was also the case for hydroperiod and connectivity. Indeed, the impacts of temperature increase were observed to affect the occupancy probabilities of more alpine specialist species compared with non-alpine specialists (71% versus 50%). We found similar results in connectivity effects (93% versus 75%). Consequently, our results suggest that the mitigation of climate change effects may be beneficial to a greater number of alpine specialist species than non-alpine specialists.

Declarations

References

Abbasi M, Oshaghi MA, Mehdi Sedaghat M, Hazratian T, Rahimi Foroushani A, Jafari-Koshki T, Reza Yaghoobi-Ershadi M, Reza Abai M, Vatandoost H, Fekri Jaski S, Bozorg Omid F, Hanafi-Bojd AA (2023) Development of a degree-day model to predict the growth of *Anopheles stephensi* (Diptera: Culicidae): implication for vector control management. Environ Entomol 52(6):1126–1138. https://doi.org/10.1093/ee/nvad092

Adhikari B, Subedi SC, Bhandari S, Baral K, Lamichhane S, Maraseni T (2023) Climate-driven decline in the habitat of the endemic spiny babbler (*Turdoides nipalensis*). Ecosphere 14(6):e4584. https://doi.org/10.1002/ecs2.4584

Alatalo JM, Jägerbrand AK, Juhanson J, Michelsen A, Ľuptáčik P (2017) Impacts of twenty years of experimental warming on soil carbon, nitrogen, moisture and soil mites across alpine/subarctic tundra communities. Sci Rep 7(1):44489. https://doi.org/10.1038/srep44489

Baber MJ, Childers DL, Babbitt KJ, Anderson DH (2002) Controls on fish distribution and abundance in temporary wetlands. Can

J Fish Aquat Sci 59(9):1441–1450. https://doi.org/10.1139/f02-116

Bae, M.-J., & Park, Y.-S. (2016). Responses of the functional diversity of benthic macroinvertebrates to floods and droughts in small streams with different flow permanence. *Inland Waters*, 6(3), 461-475. 16th International Symposium on River and Lake Environments (ISRLE). https://doi.org/10.5268/IW-6.3.891

Bale JS, Hayward SAL (2010) Insect overwintering in a changing climate. J Exp Biol 213(6):980–994. https://doi.org/10.1242/jeb.037911

Barnett TP, Adam JC, Lettenmaier DP (2005) Potential impacts of a warming climate on water availability in snow-dominated regions. Nature 438(7066):303–309. https://doi.org/10.1038/nature04141

Baur B, Baur A (2013) Snails keep the pace: Shift in upper elevation limit on mountain slopes as a response to climate warming. Can J Zool. https://doi.org/10.1139/cjz-2013-0036

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecol Lett 15(4):365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Beniston M (2006) Mountain weather and climate: a general overview and a focus on climatic change in the Alps. Hydrobiologia. https://doi.org/10.1007/s10750-005-1802-0

Bogan MT, Boersma KS, Lytle DA (2015) Resistance and resilience of invertebrate communities to seasonal and supraseasonal drought in arid-land headwater streams. Freshw Biol 60(12):2547–2558. https://doi.org/10.1111/fwb.12522

Bosson JB, Huss M, Cauvy-Fraunie S, Clement JC, Costes G, Fischer M, Poulenard J, Arthaud F (2023) Future emergence of new ecosystems caused by glacial retreat. Nature. https://doi.org/10.1038/s41586-023-06302-2

Boudot, J.-P., Doucet, G., & Grand, D. (2014). *Cahier d'identification des libellules de France, Belgique, Luxembourg et Suisse* (Biotope). https://leclub-biotope.com/fr/librairie-naturaliste/558-cahier-d-identification-des-libellules-de-france-belgique-luxembourg-et-suisse-2eme-edition

Buisson L, Grenouillet G (2009) Contrasted impacts of climate change on stream fish assemblages along an environmental gradient. Divers Distrib 15(4):613–626. https://doi.org/10.1111/j.1472-4642.2009.00565.x

Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Watson R (2010) Global biodiversity: indicators of recent declines. Science 328(5982):1164–1168. https://doi.org/10.1126/science.1187512

Cabrera HM (1996) Low temperature and altitudinal limits in plant ecosystems: Species responses to cold in tropical and subtropical mountains. Rev Chil Hist Nat 69(3):309–320

Carbonell JA, Pallares S, Velasco J, Millan A, Picazo F, Abellan P (2024) Thermal biology of aquatic insects in alpine lakes: insights from diving beetles. Freshw Biol 69(1):34–46. https://doi.org/10.1111/fwb.14190

Carlson BZ, Hébert M, Van Reeth C, Bison M, Laigle I, Delestrade A (2020) Monitoring the seasonal hydrology of alpine wetlands in response to snow cover dynamics and summer climate: a novel approach with Sentinel-2. Remote Sens Environ. https://doi.org/10.3390/rs12121959

Casanova, M. (1997). *Plant life at the edge of wetlands: Ecological responses to wetting and drying patterns*. https://www.academia.edu/25970062/Plant_life_at_the_edge_of_wetlands_ecological_responses_to_wetting_and_drying_patterns

Convertino M, Nardi F, Kiker GA, Munoz-Carpena R, Troccolì A, Linkov I (2013) 518—Epitomes of Bottom-Up

Hydro-Geo-Climatological Analysis to Face Sea Level Rise in Complex Coastal Ecosystems. In: Pielke RA (ed) Climate Vulnerability. Academic Press, pp 267–282

Costanzo JP, Lee RE Jr (2013) Avoidance and tolerance of freezing in ectothermic vertebrates. J Exp Biol 216(11):1961–1967. https://doi.org/10.1242/jeb.070268

Cross HZ, Zuber MS (1972) Prediction of flowering dates in maize based on different methods of estimating thermal units 1. Agron J 64(3):351–355. https://doi.org/10.2134/agronj1972.00021962006400030029x

Culp JM, Goedkoop W, Christensen T, Christoffersen KS, Fefilova E, Liljaniemi P, Novichkova AA, Ólafsson JS, Sandøy S, Zimmerman CE, Lento J (2022) Arctic freshwater biodiversity: establishing baselines, trends, and drivers of ecological change. Freshw Biol 67(1):1–13. https://doi.org/10.1111/fwb.13831

Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM (2011) Beyond predictions: biodiversity conservation in a changing climate. Science 332(6025):53–58. https://doi.org/10.1126/science.1200303

De Frenne P, Lenoir J, Luoto M, Scheffers BR, Zellweger F, Aalto J, Ashcroft MB, Christiansen DM, Decocq G, De Pauw K, Govaert S, Greiser C, Gril E, Hampe A, Jucker T, Klinges DH, Koelemeijer IA, Lembrechts JJ, Marrec R, Hylander K (2021) Forest microclimates and climate change: Importance, drivers and future research agenda. Glob Change Biol 27(11):2279–2297. https://doi.org/10.1111/gcb.15569

De Wilde M, Puijalon S, Bornette G (2017) Sediment type rules the response of aquatic plant communities to dewatering in wetlands. J Veg Sci 28(1):172–183. https://doi.org/10.1111/jvs.12473

Devarajan K, Morelli TL, Tenan S (2020) Multi-species occupancy models: Review, roadmap, and recommendations. Ecography 43(11):1612–1624. https://doi.org/10.1111/ecog.04957

DeWeber JT, Wagner T (2018) Probabilistic measures of climate change vulnerability, adaptation action benefits, and related uncertainty from maximum temperature metric selection. Glob Change Biol 24(6):2735–2748. https://doi.org/10.1111/gcb.14101

Dial RJ, Berg EE, Timm K, McMahon A, Geck J (2007) Changes in the alpine forest-tundra ecotone commensurate with recent warming in southcentral Alaska: evidence from orthophotos and field plots. J Geophys Res-Biogeosci 112(G4):G04015. https://doi.org/10.1029/2007JG000453

Diamond JS, Moatar F, Recoura-Massaquant R, Chaumot A, Zarnetske J, Valette L, Pinay G (2023) Hypoxia is common in temperate headwaters and driven by hydrological extremes. Ecol Ind 147:109987. https://doi.org/10.1016/j.ecolind.2023.109987

Dijkstra, K.-D. (2007). *Guide des libellules: De France et d'Europe*. Delachaux et Niestlé.

Donat MG, Alexander LV, Yang H, Durre I, Vose R, Dunn RJH, Willett KM, Aguilar E, Brunet M, Caesar J, Hewitson B, Jack C, Tank AMGK, Kruger AC, Marengo J, Peterson TC, Renom M, Oria Rojas C, Rusticucci M, Kitching S (2013) Updated analyses of temperature and precipitation extreme indices since the beginning of the twentieth century: the HadEX2 dataset. J Geophys Res-Atmo 118(5):2098–2118. https://doi.org/10.1002/jgrd.50150

Dorazio RM, Royle JA (2005) Estimating size and composition of biological communities by modeling the occurrence of species. J Am Stat Assoc 100(470):389–398. https://doi.org/10.1198/016214505000000015

Doretto A, Bona F, Falasco E, Morandini D, Piano E, Fenoglio S (2020) Stay with the flow: how macroinvertebrate communities recover during the rewetting phase in Alpine streams affected by an exceptional drought. River Res Appl 36(1):91–101. https://doi.org/10.1002/rra.3563

Dorotovičová C (2013) Man-made canals as a hotspot of aquatic macrophyte biodiversity in Slovakia. Limnologica 43(4):277–287. https://doi.org/10.1016/j.limno.2012.12.002

Doser JW, Finley AO, Kéry M, Zipkin EF (2022) spOccupancy: An R package for single-species, multi-species, and integrated spatial occupancy models. Methods Ecol Evol 13(8):1670–1678. https://doi.org/10.1111/2041-210X.13897

Doucet, G. (2016). *Clé de détermination des exuvies des Odonates de France—3e édition* (3ème). http://www.insectes.org/shop/dtermination-exuvies-odonates-france-dition-p-352.html

Duelli P (1997) Biodiversity evaluation in agricultural landscapes: An approach at two different scales. Agr Ecosyst Environ 62(2):81–91. https://doi.org/10.1016/S0167-8809(96)01143-7

Dussault C, Ouellet J-P, Courtois R, Huot J, Breton L, Larochelle J (2004) Behavioural responses of moose to thermal conditions in the boreal forest 1. Écoscience 11(3):321–328. https://doi.org/10.1080/11956860.2004.11682839

Edelsparre AH, Fitzpatrick MJ, Saastamoinen M, Teplitsky C (2024) Evolutionary adaptation to climate change. Evol Lett 8(1):1–7. https://doi.org/10.1093/evlett/qrad070

Engelhardt EK, Biber MF, Dolek M, Fartmann T, Hochkirch A, Leidinger J, Löffler F, Pinkert S, Poniatowski D, Voith J, Winterholler M, Zeuss D, Bowler DE, Hof C (2022) Consistent signals of a warming climate in occupancy changes of three insect taxa over 40 years in central Europe. Glob Change Biol 28(13):3998–4012. https://doi.org/10.1111/gcb.16200

Engler R, Randin CF, Thuiller W, Dullinger S, Zimmermann NE, Araújo MB, Pearman PB, Le Lay G, Piedallu C, Albert CH, Choler P, Coldea G, De Lamo X, Dirnböck T, Gégout JC, Gómez-García D, Grytnes JA, Heegaard E, Høistad F, Guisan A (2011) 21st century climate change threatens mountain flora unequally across Europe. Glob Change Biol 17(7):2330–2341. https://doi.org/10.1111/j.1365-2486.2010.02393.x

Fahrig L (2017) Ecological responses to habitat fragmentation Per Se. Annu Rev Ecol Evol Syst 48(1):1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Fazlioglu F, Wan JSH, Chen L (2020) Latitudinal shifts in mangrove species worldwide: evidence from historical occurrence records. Hydrobiologia 847(19):4111–4123. https://doi.org/10.1007/s10750-020-04403-x

Freeman BG, Lee-Yaw JA, Sunday JM, Hargreaves AL (2018) Expanding, shifting and shrinking: the impact of global warming on species' elevational distributions. Glob Ecol Biogeogr. https://doi.org/10.1111/geb.12774

Gaiser EE, Philippi TE, Taylor BE (1998) Distribution of diatoms among intermittent ponds on the Atlantic Coastal Plain: development of a model to preduct drought periodicity from surface-sediment assemblages. J Paleolimnol 20(1):71–90. https://doi.org/10.1023/A:1007969500673

Galatowitsch ML, McIntosh AR (2016) Developmental constraints control generalist invertebrate distributions across a gradient of unpredictable disturbance. Freshw Sci 35(4):1300–1311. https://doi.org/10.1086/688959

Gauthier M, Goff GL, Launay B, Douady CJ, Datry T (2021) Dispersal limitation by structures is more important than intermittent drying effects for metacommunity dynamics in a highly fragmented river network. Freshw Sci 40(2):302–315. https://doi.org/10.1086/714376

Gauze, G. F. (1934). *The struggle for existence* (p. 1-188). The Williams & Wilkins company.

Gehrig-Fasel J, Guisan A, Zimmermann NE (2007) Tree line shifts in the Swiss Alps: climate change or land abandonment? J Veg Sci 18(4):571–582. https://doi.org/10.1111/j.1654-1103.2007.tb02571.x

GéoCatalogue. (2023). *Cartographie des cours d'eau de Haute-Savoie*. GéoCatalogue. https://www.geocatalogue.fr/geonetwork/srv/api/records/fr-120066022-jdd-92926027-cc0e-461f-a983-407fa513e9bf

Gobiet A, Kotlarski S, Beniston M, Heinrich G, Rajczak J, Stoffel M (2014) 21st century climate change in the European Alps—A review. Sci Total Environ 493:1138–1151. https://doi.org/10.1016/j.scitotenv.2013.07.050

Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R (2017) Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sens Environ 202:18–27. https://doi.org/10.1016/j.rse.2017.06.031

Grand, D., & Boudot, J.-P. (2006). *Les Libellules de France, Belgique et Luxembourg* (Biotope, Mèze). http://www.biotope-editions.com/index.php?article108/les-libellules-de-france-belgique-et-luxembourg

Green MD, Tronstad LM, Giersch JJ, Shah AA, Fallon CE, Blevins E, Kai TR, Muhlfeld CC, Finn DS, Hotaling S (2022) Stoneflies in the genus Lednia (Plecoptera: Nemouridae): sentinels of climate change impacts on mountain stream biodiversity. Biodivers Conserv 31(2):353–377. https://doi.org/10.1007/s10531-021-02344-y

Greig HS, Wissinger SA, McIntosh AR (2013) Top-down control of prey increases with drying disturbance in ponds: a consequence of non-consumptive interactions? J Anim Ecol 82(3):598–607. https://doi.org/10.1111/1365-2656.12042

Halliday JMRBATR (1999) Amphibian colonization of new ponds in an agricultural landscape. Herpetol J 9(2):55–63

He X, He KS, Hyvönen J (2016) Will bryophytes survive in a warming world? Perspect Plant Ecol Evol Syst 19:49–60. https://doi.org/10.1016/j.ppees.2016.02.005

Heidemann, H., & Seidenbusch, R. (2002). *Larves et exuvies des libellules de France et d'Allemagne:(sauf de Corse)*. Société française d'odonatologie.

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. Glob Change Biol 12(3):450–455. https://doi.org/10.1111/j.1365-2486.2006.01116.x

Hodgson JA, Thomas CD, Dytham C, Travis JMJ, Cornell SJ (2012) The speed of range shifts in fragmented landscapes. PLoS ONE 7(10):e47141. https://doi.org/10.1371/journal.pone.0047141

Hotaling S, Shah AA, Dillon ME, Giersch JJ, Tronstad LM, Finn DS, Woods HA, Kelley JL (2021) Cold tolerance of mountain stoneflies (Plecoptera: Nemouridae) from the high rocky mountains. West North Am Nat 81(1):54–62. https://doi.org/10.3398/064.081.0105

Huang H, Jie P, Yang Y, Mi S (2022) Spatial and temporal characteristics of high-temperature heat wave disasters in Chongqing. Atmosphere. https://doi.org/10.3390/atmos13091396

Huffaker C (1958) Experimental studies on predation: Dispersion factors and predator-prey oscillations. Hilgardia 27(14):343–383

Hughes L (2000) Biological consequences of global warming: Is the signal already apparent? Trends Ecol Evol. https://doi.org/10.1016/S0169-5347(99)01764-4

IPBES (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services. Zenodo. https://doi.org/10.5281/zenodo.3553579

Jaeger KL, Olden JD, Pelland NA (2014) Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. Proc Natl Acad Sci 111(38):13894–13899. https://doi.org/10.1073/pnas.1320890111

Jump AS, Mátyás C, Peñuelas J (2009) The altitude-for-latitude disparity in the range retractions of woody species. Trends Ecol Evol 24(12):694–701. https://doi.org/10.1016/j.tree.2009.06.007

Jurczyk B, Pociecha E, Grzesiak M, Kalita K, Rapacz M (2016) Enhanced expression of Rubisco activase splicing variants differentially affects Rubisco activity during low temperature

treatment in *Lolium perenne*. J Plant Physiol 198:49–55. https://doi.org/10.1016/j.jplph.2016.03.021

Kang W, Minor ES, Lee D, Park C-R (2016) Predicting impacts of climate change on habitat connectivity of *Kalopanax septemlobus* in South Korea. Acta Oecologica 71:31–38. https://doi.org/10.1016/j.actao.2016.01.005

Kannan R, James DA, Rawat G (2009) Effects of climate change on global biodiversity: a review of key literature. Trop Ecol 50:31–39

Keith DA, Akçakaya HR, Thuiller W, Midgley GF, Pearson RG, Phillips SJ, Regan HM, Araújo MB, Rebelo TG (2008) Predicting extinction risks under climate change: Coupling stochastic population models with dynamic bioclimatic habitat models. Biol Let 4(5):560–563. https://doi.org/10.1098/rsbl.2008.0049

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. Proc Natl Acad Sci. https://doi.org/10.1073/pnas.0802891105

Khan H, Baig S (2017) High altitude wetlands of the HKH region of northern Pakistan—status of current knowledge. Chall Res Oppor Wetlands 37(2):371–380. https://doi.org/10.1007/s13157-016-0868-y

Khelifa R (2017) Partial bivoltinism and emergence patterns in the North African endemic damselfly Calopteryx exul: Conservation implications. Afr J Ecol 55(2):145–151. https://doi.org/10.1111/aje.12332

Kindlmann P, Burel F (2008) Connectivity measures: a review. Landscape Ecol 23(8):879–890. https://doi.org/10.1007/s10980-008-9245-4

Kirkton SD, Schultz TD (2001) Age-specific behavior and habitat selection of adult male damselflies, Calopteryx maculata (Odonata: Calopterygidae). J Insect Behavior 14(4):545–556. https://doi.org/10.1023/A:1011180207852

Knaus P, Wildermuth H (2002) Site attachment and displacement of adults in two alpine metapopulations of *Somatochlora alpestris* (Odonata: Corduliidae). Int J Odonatol 5(2):111–128. https://doi.org/10.1080/13887890.2002.9748183

Kury, D., & Wildermuth, H. (2013). *Fiches de protection espèces—Libellules—Coenagrion hastulatum*. Groupe de travail pour la conservation des Libellules de Suisse, CSCF info fauna, Neuchâtel et Office fédéral de l'environnement, Berne.

Lamouille-Hébert M, Arthaud F, Datry T (2024) Climate change and the biodiversity of alpine ponds: challenges and perspectives. Ecol Evol 14(2):e10883. https://doi.org/10.1002/ece3.10883

Lamouille-Hébert, M. (2021). *CIMaE: Un projet de recherche inédit pour protéger les zones humides d'altitude*. FNE Haute-Savoie. https://www.fne-aura.org/actualites/haute-savoie/cimae-un-projet-de-recherche-inedit-pour-proteger-les-zones-humides-daltitude/

Larcher W, Kainmüller C, Wagner J (2010) Survival types of high mountain plants under extreme temperatures. Flora—Morphol Distribution Funct Ecol Plants 205(1):3–18. https://doi.org/10.1016/j.flora.2008.12.005

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecol Lett 7(7):601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Leigh C, Datry T (2017) Drying as a primary hydrological determinant of biodiversity in river systems: a broad-scale analysis. Ecography 40(4):487–499. https://doi.org/10.1111/ecog.02230

Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science. https://doi.org/10.1126/science.1156831

Li F, Shah DN, Pauls SU, Qu X, Cai Q, Shah RDT (2016) Elevational shifts of freshwater communities cannot catch up climate

warming in the Himalaya. Water 8(8):327. https://doi.org/10.3390/w8080327

Lillie RA (2003) Macroinvertebrate community structure as a predictor of water duration in Wisconsin wetlands 1. JAWRA J Am Water Resour Assoc 39(2):389–400. https://doi.org/10.1111/j.1752-1688.2003.tb04393.x

Lindholm M, Hessen DO, Færøvig PJ, Rognerud B, Andersen T, Stordal F (2015) Is distribution of cold stenotherms constrained by temperature? The case of the Arctic fairy shrimp (*Branchinecta paludosa* O.F. Müller 1788). J Therm Biol 53:46–52. https://doi.org/10.1016/j.jtherbio.2015.08.005

Liu LW, Lu CT, Wang YM, Lin KH, Ma X, Lin WS (2022) Rice (Oryza sativa L.) growth modeling based on growth degree day (GDD) and artificial intelligence algorithms. Agriculture. https://doi.org/10.3390/agriculture12010059

Lynch AJ, Myers BJE, Chu C, Eby LA, Falke JA, Kovach RP, Krabbenhoft TJ, Kwak TJ, Lyons J, Paukert CP, Whitney JE (2016) Climate change effects on North American inland fish populations and assemblages. Fisheries 41(7):346–361. https://doi.org/10.1080/03632415.2016.1186016

Macarthur, R. H., & Wilson, E. O. (1967). *The Theory of Island Biogeography* (REV-Revised). Princeton University Press. https://www.jstor.org/stable/j.ctt19cc1t2

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Andrew Royle J, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. Ecology. https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

Makoto K, Wilson SD (2019) When and where does dispersal limitation matter in primary succession? J Ecol 107(2):559–565. https://doi.org/10.1111/1365-2745.12988

Malish MC, Gao S, Kopp D, Hong Y, Allen DC, Neeson T (2023) Small increases in stream drying can dramatically reduce ecosystem connectivity. Ecosphere 14(3):e4450. https://doi.org/10.1002/ecs2.4450

Masson-Delmotte, V., Zhai, P., . Pörtner, O., . Roberts, D., Skea, J., Shukla, P. R., Pirani, A., Moufouma-Okia, W., Péan, C., Pidcock, R., Connors, S., Matthews, J. B. R., Chen, Y., Zhou, X., Gomis, M. I., Lonnoy, E., Maycock, T., Tignor, M., & Waterfield, T. (2018). *IPCC, 2018: Summary for Policymakers. In: Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty*. https://www.ipcc.ch/sr15/chapter/spm/

May ML (1976) Thermoregulation and adaptation to temperature in dragonflies (Odonata: Anisoptera). Ecol Monogr 46(1):1–32. https://doi.org/10.2307/1942392

McAllen R (1997) Using differential scanning calorimetry to study freezing in a euryhaline aquatic invertebrate. Cryo-Letters 18(6):369–374

McMaster GS, Wilhelm WW (1997) Growing degree-days: One equation, two interpretations. Agric for Meteorol 87(4):291–300. https://doi.org/10.1016/S0168-1923(97)00027-0

Melin M, Matala J, Mehtätalo L, Tiilikainen R, Tikkanen O-P, Maltamo M, Pusenius J, Packalen P (2014) Moose (Alces alces) reacts to high summer temperatures by utilizing thermal shelters in boreal forests – an analysis based on airborne laser scanning of the canopy structure at moose locations. Glob Change Biol 20(4):1115–1125. https://doi.org/10.1111/gcb.12405

Menéndez R, González-Megías A, Jay-Robert P, Marquéz-Ferrando R (2014) Climate change and elevational range shifts: Evidence from dung beetles in two European mountain ranges. Glob Ecol Biogeogr. https://doi.org/10.1111/geb.12142

Milly PCD, Dunne KA, Vecchia AV (2005) Global pattern of trends in streamflow and water availability in a changing climate. Nature. https://doi.org/10.1038/nature04312

Mourguiart B, Couturier T, Braud Y, Mansons J, Combrisson D, Besnard A (2021) Multi-species occupancy models: an effective and flexible framework for studies of insect communities. Ecol Entomol 46(2):163–174. https://doi.org/10.1111/een.12991

Mukherji, A., Thorne, P., Cheung, W. W. L., Connors, S. L., Garschagen, M., Geden, O., Hayward, B., Simpson, N. P., Totin, E., & Blok, K. (2023). *AR6 Synthesis Report: Climate Change 2023*. IPCC.

O'Reilly CM, Sharma S, Gray DK, Hampton SE, Read JS, Rowley RJ, Schneider P, Lenters JD, McIntyre PB, Kraemer BM, Weyhenmeyer GA, Straile D, Dong B, Adrian R, Allan MG, Anneville O, Arvola L, Austin J, Bailey JL, Zhang G (2015) Rapid and highly variable warming of lake surface waters around the globe. Geophys Res Lett. https://doi.org/10.1002/2015GL066235

Oertli B, Auderset Joye D, Castella E, Juge R, Lehmann A, Lachavanne J-B (2005) PLOCH: A standardized method for sampling and assessing the biodiversity in ponds. Aquat Conserv Mar Freshwat Ecosyst 15(6):665–679. https://doi.org/10.1002/aqc.744

Ogston G, Beatty SJ, Morgan DL, Pusey BJ, Lymbery AJ (2016) Living on burrowed time: aestivating fishes in south-western Australia face extinction due to climate change. Biol Cons 195:235–244. https://doi.org/10.1016/j.biocon.2016.01.008

Opdam P, Wascher D (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biol Cons 117(3):285–297. https://doi.org/10.1016/j.biocon.2003.12.008

Pallarés S, Millán A, Mirón JM, Velasco J, Sánchez-Fernández D, Botella-Cruz M, Abellán P (2020) Assessing the capacity of endemic alpine water beetles to face climate change. Insect Conserv Divers 13(3):271–282. https://doi.org/10.1111/icad.12394

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature. https://doi.org/10.1038/nature01286

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399(6736):579–583. https://doi.org/10.1038/21181

Parolo G, Rossi G (2008) Upward migration of vascular plants following a climate warming trend in the Alps. Basic Appl Ecol. https://doi.org/10.1016/j.baae.2007.01.005

Pearson RG, Dawson TP (2005) Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. Biol Cons 123(3):389–401. https://doi.org/10.1016/j.biocon.2004.12.006

Perkin JS, Gido KB (2012) Fragmentation alters stream fish community structure in dendritic ecological networks. Ecol Appl 22(8):2176–2187. https://doi.org/10.1890/12-0318.1

Peterson DL, Schreiner EG, Buckingham NM (1997) Gradients vegetation and climate: spatial and temporal dynamics in the Olympic Mountains USA. Glob Ecol Biogeogr Lett. https://doi.org/10.2307/2997523

Polcyn DM (1994) Thermoregulation during summer activity in Mojave Desert dragonflies (Odonata: Anisoptera). Funct Ecol 8(4):441–449. https://doi.org/10.2307/2390067

Posit team. (2023). *RStudio: Integrated Development Environment for R. Posit Software* [Logiciel]. Posit Software, PBC. http://www.posit.co/

R Core Team. (2022). *R: A language and environment for statistical computing.* [Logiciel]. R Foundation for Statistical Computing. https://www.R-project.org/

Redmond LE (2018) Alpine limnology of the rocky mountains of Canada and the USA in the context of environmental change. Environ Rev 26(3):231–238. https://doi.org/10.1139/er-2017-0046

Rehm EM, Yelenik S, D'Antonio C (2021) Freezing temperatures restrict woody plant recruitment and restoration efforts in abandoned montane pastures. GLOBAL ECOLOGY AND CONSERVATION 26:e01462. https://doi.org/10.1016/j.gecco.2021.e01462

Renman G (1989) Distribution of littoral macrophytes in a North Swedish riverside lagoon in relation to bottom freezing. Aquat Bot 33(3):243–256. https://doi.org/10.1016/0304-3770(89)90040-5

Roland J (1993) Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. Oecologia 93(1):25–30. https://doi.org/10.1007/BF00321186

Rosset V, Oertli B (2011) Freshwater biodiversity under climate warming pressure: Identifying the winners and losers in temperate standing waterbodies. Biol Conserv. https://doi.org/10.1016/j.biocon.2011.06.009

Rosset V, Ruhi A, Bogan MT, Datry T (2017) Do lentic and lotic communities respond similarly to drying? Ecosphere 8(7):e01809. https://doi.org/10.1002/ecs2.1809

Roth T, Plattner M, Amrhein V (2014) Plants, birds and butterflies: short-term responses of species communities to climate warming vary by taxon and with altitude. PLoS ONE 9(1):e82490. https://doi.org/10.1371/journal.pone.0082490

Roy DB, Sparks TH (2000) Phenology of British butterflies and climate change. Glob Change Biol 6(4):407–416. https://doi.org/10.1046/j.1365-2486.2000.00322.x

Ryan ME, Palen WJ, Adams MJ, Rochefort RM (2014) Amphibians in the climate vise: Loss and restoration of resilience of montane wetland ecosystems in the western US. Front Ecol Environ 12(4):232–240. https://doi.org/10.1890/130145

Sáinz-Bariáin M, Zamora-Muñoz C, Soler JJ, Bonada N, Sáinz-Cantero CE, Alba-Tercedor J (2016) Changes in Mediterranean high mountain Trichoptera communities after a 20-year period. Aquat Sci 78(4):669–682. https://doi.org/10.1007/s00027-015-0457-9

Salerno F, Gambelli S, Viviano G, Thakuri S, Guyennon N, D'Agata C, Diolaiuti G, Smiraglia C, Stefani F, Bocchiola D, Tartari G (2014) High alpine ponds shift upwards as average temperatures increase: a case study of the Ortles-Cevedale mountain group (Southern Alps, Italy) over the last 50years. Global Planet Change 120:81–91. https://doi.org/10.1016/j.gloplacha.2014.06.003

Sandvik SM, Odland A (2014) Changes in alpine snowbed-wetland vegetation over three decades in northern Norway. Nord J Bot 32(3):377–384. https://doi.org/10.1111/j.1756-1051.2013.00249.x

Sarremejane R, Stubbington R, England J, Sefton CEM, Eastman M, Parry S, Ruhi A (2021) Drought effects on invertebrate metapopulation dynamics and quasi-extinction risk in an intermittent river network. Glob Change Biol 27(17):4024–4039. https://doi.org/10.1111/gcb.15720

Seimon TA, Seimon A, Daszak P, Halloy SRP, Schloegel LM, Aguilar CA, Sowell P, Hyatt AD, Konecky B, Simmons JE (2007) Upward range extension of Andean anurans and chytridiomycosis to extreme elevations in response to tropical deglaciation. Glob Change Biol 13(1):288–299. https://doi.org/10.1111/j.1365-2486.2006.01278.x

Serrano F, Pita R, Mota-Ferreira M, Beja P, Segurado P (2020) Landscape connectivity affects individual survival in unstable patch networks: The case of a freshwater turtle inhabiting temporary ponds. Freshw Biol 65(3):540–551. https://doi.org/10.1111/fwb.13449

Shadle EJ, Hopkins WA, Belden LK, Hallmark MA, Mims MC (2023) Experimental warming and drying act independently on

developmental responses for two amphibian species. Freshw Biol 68(10):1647–1659. https://doi.org/10.1111/fwb.14156

Stanley EH, Fisher SG, Grimm NB (1997) Ecosystem expansion and contraction in streams. Bioscience 47(7):427–435. https://doi.org/10.2307/1313058

Sternberg K (1997) Adaptation of Aeshna caerulea (Ström) to the severe climate of its environment (Anisoptera: Aeshnidae). Odonatologica 26(4):439–449

Storey KB (1999) Living in the cold: freeze-induced gene responses in freeze-tolerant vertebrates. Clin Exp Pharmacol Physiol 26(1):57–63. https://doi.org/10.1046/j.1440-1681.1999.02990.x

Stubbington R, Datry T (2013) The macroinvertebrate seedbank promotes community persistence in temporary rivers across climate zones. Freshw Biol 58(6):1202–1220. https://doi.org/10.1111/fwb.12121

Stubbington R, Sarremejane R, Datry T (2019) Alpha and beta diversity of connected benthic-subsurface invertebrate communities respond to drying in dynamic river ecosystems. Ecography 42(12):2060–2073. https://doi.org/10.1111/ecog.04592

Swaegers J, De Cupere S, Gaens N, Lancaster LT, Carbonell JA, Sánchez Guillén RA, Stoks R (2024) Plasticity and associated epigenetic mechanisms play a role in thermal evolution during range expansion. Evol Lett 8(1):76–88. https://doi.org/10.1093/evlett/qrac007

Theissinger K, Balint M, Feldheim KA, Haase P, Johannesen J, Laube I, Pauls SU (2013) Glacial survival and post-glacial recolonization of an arctic-alpine freshwater insect (Arcynopteryx dichroa, Plecoptera, Perlodidae) in Europe. J Biogeogr 40(2):236–248. https://doi.org/10.1111/j.1365-2699.2012.02793.x

Thuiller W, Lavorel S, Araújo MB (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. Glob Ecol Biogeogr 14(4):347–357. https://doi.org/10.1111/j.1466-822X.2005.00162.x

Tischendorf L, Fahrig L (2001) On the use of connectivity measures in spatial ecology. A Reply Oikos 95(1):152–155. https://doi.org/10.1034/j.1600-0706.2001.950117.x

Tolonen KE, Picazo F, Vilmi A, Datry T, Stubbington R, Pařil P, Perez Rocha M, Heino J (2019) Parallels and contrasts between intermittently freezing and drying streams: from individual adaptations to biodiversity variation. Freshw Biol 64(10):1679–1691. https://doi.org/10.1111/fwb.13373

Tovar C, Carril AF, Gutiérrez AG, Ahrends A, Fita L, Zaninelli P, Flombaum P, Abarzúa AM, Alarcón D, Aschero V, Báez S, Barros A, Carilla J, Ferrero ME, Flantua SGA, Gonzáles P, Menéndez CG, Pérez-Escobar OA, Pauchard A, Hollingsworth PM (2022) Understanding climate change impacts on biome and plant distributions in the Andes: Challenges and opportunities. J Biogeogr 49(8):1420–1442. https://doi.org/10.1111/jbi.14389

Vos CC, Berry P, Opdam P, Baveco H, Nijhof B, O'Hanley J, Bell C, Kuipers H (2008) Adapting landscapes to climate change: Examples of climate-proof ecosystem networks and priority adaptation zones. J Appl Ecol 45(6):1722–1731. https://doi.org/10.1111/j.1365-2664.2008.01569.x

Wahid A, Gelani S, Ashraf M, Foolad MR (2007) Heat tolerance in plants: An overview. Environ Exp Bot 61(3):199–223. https://doi.org/10.1016/j.envexpbot.2007.05.011

Walls SC, Barichivich WJ, Brown ME, Scott DE, Hossack BR (2013) Influence of drought on salamander occupancy of isolated wetlands on the southeastern coastal plain of the United States. Wetlands 33(2):345–354. https://doi.org/10.1007/s13157-013-0391-3

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416(6879):389–395. https://doi.org/10.1038/416389a

Wang IJ (2020) Topographic path analysis for modelling dispersal and functional connectivity: Calculating topographic distances using the topoDistance r package. Methods Ecol Evol 11(2):265–272. https://doi.org/10.1111/2041-210X.13317

Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414(6859):65–69. https://doi.org/10.1038/35102054

Wells CL, Pigliucci M (2000) Adaptive phenotypic plasticity: the case of heterophylly in aquatic plants. Perspect Plant Ecol, Evol Syst 3(1):1–18. https://doi.org/10.1078/1433-8319-00001

Wildermuth, H. (2013). *Fiches de protection espèces—Libellules—Leucorrhinia dubia*. Groupe de travail pour la conservation des Libellules de Suisse, CSCF info fauna, Neuchâtel et Office fédéral de l'environnement, Berne.

Wilkinson MD, Dumontier M, Aalbersberg J, Appleton G, Axton M, Baak A, Blomberg N, Boiten JW, da Santos LB, Bourne PE, Bouwman J, Brookes AJ, Clark T, Crosas M, Dillo I, Dumon O, Edmunds S, Evelo CT, Finkers R, Mons B (2016) Comment: the FAIR guiding principles for scientific data management and stewardship. Sci Data 3:160018. https://doi.org/10.1038/sdata.2016.18

Williamson CE, Saros JE, Schindler DW (2009) Sentinels of change. Science 323(5916):887–888. https://doi.org/10.1126/science.1169443

Wissinger SA, Greig H, McIntosh A (2009) Absence of species replacements between permanent and temporary lentic communities in New Zealand. J N Am Benthol Soc 28(1):12–23. https://doi.org/10.1899/08-007.1

With KA, Crist TO (1995) Critical thresholds in species' responses to landscape structure. Ecology 76(8):2446–2459. https://doi.org/10.2307/2265819

Woodward G, Perkins DM, Brown LE (2010) Climate change and freshwater ecosystems: impacts across multiple levels of organization. Philos Trans R Soc b: Biol Sci 365(1549):2093–2106. https://doi.org/10.1098/rstb.2010.0055

Wu Q (2020) Geemap: a python package for interactive mapping with Google Earth engine. J Open Source Softw 5(51):2305. https://doi.org/10.21105/joss.02305

Yang G, Peng C, Chen H, Dong F, Wu N, Yang Y, Zhang Y, Zhu D, He Y, Shi S, Zeng X, Xi T, Meng Q, Zhu Q (2017) Qinghai–tibetan plateau peatland sustainable utilization under anthropogenic disturbances and climate change. Ecosyst Health Sustain 3(3):e01263. https://doi.org/10.1002/ehs2.1263

Yokum EE, Goldstein DL, Krane CM (2023) Novel observations of "freeze resistance" and dynamic blue and green dorsal coloration in frozen and thawing *Dryophytes chrysoscelis*. J Exp Zool Part a: Ecol Integr Physiol 339(10):1044–1051. https://doi.org/10.1002/jez.2753

Zelnik I, Kuhar U, Holcar M, Germ M, Gaberščik A (2021) Distribution of vascular plant communities in Slovenian watercourses. Water. https://doi.org/10.3390/w13081071

Zipkin EF, Doser JW, Davis CL, Leuenberger W, Ayebare S, Davis KL (2023) Integrated community models: a framework combining multispecies data sources to estimate the status, trends and dynamics of biodiversity. J Anim Ecol 92(12):2248–2262. https://doi.org/10.1111/1365-2656.14012

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.