Inland Norway
University of
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Faculty of Applied Ecology, Agricultural Sciences and Biotechnology

Jérémy Monsimet

Predicting future changes in the distribution of wandering spiders

Habitat requirement, cold tolerance, and dispersal are crucial traits for *Dolomedes* species.

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PhD thesis

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“It’s easy to think that as a result of the extinction of the dodo
we are now sadder and wiser, but there’s a lot of evidence
to suggest that we are merely sadder and better informed”
Last chance to see
by Douglas Adams and Mark Carwardine

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Sammendrag

Å forstå dynamikken i en arts utbredelsesområde er viktig for å kunne forvalte den best mulig. Teoretiske modeller forutsier ekspansjon av utbredelsen til arters habitater mot polene i takt med klimaendringene. Noen arter er i stand til å tilpasse seg sine nye klimatiske forhold, andre arter vil det bli mindre vanlige, og andre igjen er i stand til å følge etter den geografiske habitatutbredelsen. Disse tre mulighetene er ikke gjensidig utelukkende for en art. Denne oppgaven tar sikte på å evaluere de to europeiske fiskeedderkoppene sine evner til å følge fremtidig habitatsutbredelse. *Dolomedes plantarius* og *Dolomedes fimbriatus* er begge utbredt i Europa, men førstnevnte har færre populasjoner og er klassifisert som sårbar på IUCNs rødliste for trua arter. Begge artene er semi-akvatiske og er derfor avhengig av våtmarker, som er truet av klimaendringer og menneskelig aktivitet. Hovedmålet med oppgaven var å undersøke habitatkravene, tilbøyeligheten for spredning og kuldetoleransen til begge nevnte arter for å effektivt kunne forutsi deres fremtidige habitatutvalg samt deres evne til å forflytte seg for å nå disse innenfor Fennoscandia.

Vi gjennomgikk hvordan og i hvilket omfang artsdistribusjonsmodeller (SDMer) benyttes i studier på leddyr, og gjorde tilnærminger for å redusere forstyrrelsene i SDM-prediksjonene. Vi viste at bruk av hybride artsdistribusjonsmodeller (hybride SDMer) bør favoriseres over enkle korrelative SDMer ved å inkludere prosessbasert informasjon i korrelasjonsmodeller. Vi bestemte oss for å utvikle hybride SDMer for å forutsi innvirkningen klimaendringer vil kunne ha på *Dolomedes*. For å gjøre dette, samlet vi forekomstdata på begge arter og kjørte fysiologiske og eksperimentelle tester for å utforske henholdsvis deres habitatkrav, kuldetoleranse og tilbøyelighet til spredning.

Vi fant smalere habitatkrav for *D. plantarius* enn for *D. fimbriatus*; sympatriske leveområder var faktisk mer lik *D. plantarius*-leveområder enn *D. fimbriatus*-leveområder. Løvskog, (langsomtflytende) vann og lavereliggende områder er nødvendig for *D. plantarius*, mens *D. fimbriatus* tåler lavere pH (barskog), fravær av vann og kan okkupere i høyereliggende områder. Når det gjelder kuldetoleranse for fiskeedderkopper, fant vi at ungdommer av *D. fimbriatus* fra nordlige (kontinentale) populasjoner var mer tolerante enn ungdommer fra sørlige (tempererte) populasjoner. Videre var *D. plantarius* litt mindre kuldetolerant enn *D. fimbriatus* i Fennoscandia. *D. fimbriatus* hadde en høyere tilbøyelighet til spredning av langdistanse (balloning) og vannbåren (seilende), mens tilbøyeligheten for kortdistansespredning (rappellering) ikke var forskjellig mellom arter. For kortreist vannbåren spredning, derimot, fant vi høyere tilbøyelighet for roing og lavere tilbøyelighet til å løpe for *D. plantarius* enn for *D. fimbriatus*. Til slutt, med korrelative SDM-er, viste vi at utbredelsen av egnede habitat og klima vil utvide seg nordover i takt med klimaendringene, og at dette skiftet vil være viktigere under scenarioer med større klimaendringer. Likevel estimerte vi med bruk av hybrid SDM at muligheten for begge artene til å spore egnede habitater vil være begrenset. Det skyldtes hovedsakelig begrenset spredningsevne og/eller fragmentering av landskapet. Forsinkelsen *Dolomedes* viste i forhold til å følge endringene i habitatutbredelsen understreker behovet for en oppdatering av deres rødliste-status, samt behov for planlegging av forvaltningen av arten for å bevare den. Å bevare forbindelsen mellom leveområder er avgjørende, samt å utforske Dolomedes sin vinteroverlevelse.

Nøkkelord: Pisauridae, Dolomedes, klimaendringer, generalist arter, spesialist arter, mulig utbredelse, oppnåelig rekkevidde.

Abstract

Understanding the dynamic of the range of a species is important for its conservation and management planning. Theoretical models predict poleward expansions of the suitable habitat of species under climate change. Some species are able to adapt to their new climatic conditions, others species will decline and others are able to track their suitable habitats. These three responses are not mutually exclusive along the range of a species. This thesis aimed at evaluating the abilities of the two European fishing spiders to track their suitable range in the future. *Dolomedes plantarius* and *Dolomedes fimbriatus* are widespread in Europe but the former has scarcer populations and is classified as vulnerable by the IUCN red list of species. Both species are semi-aquatic and consequently inhabit wetlands, which are threatened by climate change and human activities. The main goal of this thesis was to explore the habitat requirements, the propensity for dispersal and the cold tolerance of both species to efficiently predict their range of habitat suitability and reachability in Fennoscandia.

We reviewed scopes and ways species distribution models (SDMs) are used in arthropods studies and provided approaches to mitigate the biases of SDMs predictions. We showed that using hybrid species distribution models (hybrid SDMs) should be favoured over simple correlative SDMs by including process-based information in correlative models. We decided to develop hybrid SDMs to predict the impact of climate change on *Dolomedes*. To do so, we sampled occurrence data on both species and ran physiological and experimental tests to explore their habitat requirements, cold tolerance and propensity for dispersal.

We found narrower habitat requirements for *D. plantarius* compared to *D. fimbriatus*; sympatric sites were indeed more similar to *D. plantarius* sites than to *D. fimbriatus* sites. Deciduous forest, (slow-flowing) water, and low altitude are needed for *D. plantarius*, whereas *D. fimbriatus* tolerate lower pH (coniferous forest), absence of water, and can occupy higher altitudes. Regarding cold tolerance of juveniles fishing spiders, we showed that *D. fimbriatus* from northern (continental) populations were more tolerant than from southern (temperate) populations. Moreover, *D. plantarius* was slightly less cold tolerant than *D. fimbriatus* in Fennoscandia. *D. fimbriatus* had a higher propensity for long-distance airborne (ballooning) and waterborne (sailing) dispersal, while the propensity for short-distance airborne dispersal (rappelling) did not differ between species. However, we found contrasting results for short-distance waterborne dispersal, with a higher propensity for rowing and a lower propensity for running for *D. plantarius* than for *D. fimbriatus*.

Finally, with correlative SDMs we showed that climatic suitability and habitat suitability will expand northward with climate change and that this shift will be more important under stronger climate change. Nonetheless, with hybrid SDMs we predicted that the ability for both species to track their suitable habitats will be limited due to limited dispersal abilities and/or fragmentation of the landscape. The lag of *Dolomedes* behind their suitable range underscores the urgent need for an update of their red-listed status, as well as the needs for planning of conservation and management strategies. Conserving the connectivity between sites is crucial, as well as exploring winter survival of *Dolomedes*.

Keywords: Pisauridae, *Dolomedes*, climate change, generalist species, specialist species, suitable range, reachable range.

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Mammola, Stefano, Julien Pétillon, Axel Hacala, **Jérémy Monsimet**, Sapho-Lou Marti, Pedro Cardoso, and Denis Lafage. 2020. ‘Challenges and Opportunities of Species Distribution Modelling of Terrestrial Arthropod Predators’. Under review at *Diversity and Distribution*.

Paper II

Dickel, Lisa, **Jérémy Monsimet**, Denis Lafage, and Olivier Devineau. 2020. ‘Characterization of Habitat Requirements of European Fishing Spiders’. *Manuscript*

Paper III

Monsimet, Jérémy, Hervé Colinet, Olivier Devineau, Denis Lafage, and Julien Pétillon. 2021. ‘Biogeographic Position and Body Size Jointly Set Lower Thermal Limits of Wandering Spiders’. *Ecology and Evolution* 00: 1–10.
https://doi.org/10/gh7fz8

Paper IV

Monsimet, Jérémy, Julien Pétillon, Olivier Devineau and Denis Lafage. 2021. ‘Contrasted propensity for waterborne dispersal, lesser for airborne dispersal, between two closely related semi-aquatic spider species’. *Manuscript*

Paper V

Monsimet, Jérémy, Olivier Devineau, Julien Pétillon, and Denis Lafage. 2020. ‘Explicit Integration of Dispersal-Related Metrics Improves Predictions of SDM in Predatory Arthropods’. *Scientific Reports* 10 (1): 1–12.
https://doi.org/10.1038/s41598-020-73262-2

1 Introduction

1.1 The concept of ecological niche and species distribution

The niche has been conceptualised numerous times and in many ways. Grinnell (1917) defined the niche as the environmental factors influencing the range of a species. Later on, Elton's vision of the niche was more functional by considering the role and interactions of a species in its ecosystem, namely in relation to food chains (Elton 1927). Hutchinson (1957) combined these two visions of the niche and defined it as a multidimensional hypervolume. The different dimensions represent all the factors, environmental and resources, that a species need to grow and persist. The concept of fundamental and realised niche was also introduced in Hutchinson (1957). The fundamental niche is the entire set of dimensions of the hypervolume where animals can survive and reproduce (close to the Grinnellian niche concept), whereas the realised niche is the part of the volume actually used by a species after accounting for interactions with other species, i.e. accounting for Eltonian niche.

More recently, Soberón and Peterson (2005) and Soberón (2007) defined the concept of BAM, standing for Biotic, Abiotic and Movement. The intersection of these three factors is used to define the distribution of a species. The definition of the realised niche was lacking information on dispersal to define the distribution of a species (Pulliam 2000). Indeed, the distribution of a species function as a population of populations (metapopulation, see Hanski and Gilpin 1991). Functional connectivity is required to sustain species distribution. This connectivity is influenced by dispersal behaviours of organisms in the landscape (Van Dyck and Baguette 2005; Baguette and Van Dyck 2007). Following the BAM concept, the distribution combines suitable environmental conditions of a species (abiotic factors), not too deleterious inter- and intraspecific interactions (biotic factors), and areas that the species can reach (mobility, e.g. dispersal). Defining the realised niche, and more precisely the range of a species is important for conservation planning (Guisan and Zimmermann 2000).

1.2 Distribution and climate change

Due to the increasing rate of environmental changes with human activities (Pimm et al. 1995), considering climate change is nowadays recurrent in ecological studies. It impacts directly and indirectly different scales of the biodiversity (Vitousek 1994) and it is not limited to global warming but also affects the frequency of extreme weather events (Pereira et al. 2010; Garcia et al. 2014). Besides climatic changes, human-induced factors like industrialisation, deforestation and agriculture result in habitat fragmentation, which impacts both biodiversity dynamics and ecosystems functioning (Haddad et al. 2015). Three main responses to climate change are adopted by species (Parmesan 2006). i) The risk of population extinction can increase through the combined action of biology of species, geography and temperature (Collen et al. 2011). This has already caused a decline of various species depicted by a shrink of their distribution and by the loss of some local populations (Parmesan 2006). These local extinctions are the first steps towards species loss at the global scale. Nonetheless, ii) some species can adapt to the new climatic conditions via genetic evolution and phenotypic plasticity (i.e. the ability of one genotype to produce one or several phenotypes) (Radchuk et al. 2019). iii) Few species can shift their distribution (both in altitude and/or in latitude) in order to track their optimal environmental conditions (Huntley et al. 2010). This can result in whole range displacements, or in range expansions but require sufficient dispersal abilities (Stevens et al. 2014). Moreover, these three responses to climate change are not mutually exclusive.

Ecology studies need to address the abilities of species to expand their range (Wiens 2011) and modelling tools need to further develop to achieve it.

1.3 Modelling the distribution of a species

Soberón and Nakamura (2009) shows the importance of knowing which part of the BAM diagram we are modelling, and Kearney (2006) underscores the importance to consider niche, habitat and environment as different concepts when modelling distribution of a species. Methods to describe species distribution are called species distribution models (SDMs, this term will be used hereafter), environmental niche models (ENMs), habitat suitability models or climatic/bioclimatic envelope models.

There are two methods to model the distribution of a species, i.e. correlative or mechanistic models. The mechanistic approach models the fundamental niche as defined by Hutchinson. This method uses physiological, behavioural and/or morphological data to predict the geographic range providing suitable fitness in the environment (Kearney 2006; Kearney and Porter 2009).

The association between environmental conditions and species occurrences to estimate the habitat suitability of the environment is estimated with correlative models. These models correlate the species occurrences to environmental variables like bioclimatic variables (e.g.

the widely used WorldClim dataset, see Fick and Hijmans 2017). The choice of environmental variables should be carefully done because they characterise the biotic part of the BAM, i.e. the environmental part in the Hutchinson hypervolume (Ovaskainen and Abrego 2020). These models predict the range of suitable habitats by providing a probability of occurrence of a species in its geographical environment (Kearney 2006). A wide range of algorithms are available to make this correlation, from the early use of BIOCLIM (for a review on BIOCLIM method, see Booth et al. 2014), to simple logistic regressions and to more recent use of machine learning methods (e.g. MaxEnt, see Elith et al. 2019). Because no algorithms are considered better than others (Qiao, Soberón, and Peterson 2015), all of them are widely used, and predictions from single model are sometimes combined in ensemble models (Araújo and New 2007). Correlative SDMs are based on the niche conservatism idea, i.e. species preserve their ecological traits over time (Wiens et al. 2010). Consequently, distribution and its explanatory variables are considered in stable relation with the environment and the niche is maintained across space and time (Elith and Leathwick 2009).

Mechanistic models require extensive knowledge on key limiting physiological processes (Kearney, Wintle, and Porter 2010). Therefore, using mechanistic SDMs is limited for not well-studied taxa. A solution is to combine correlative and mechanistic processes to understand observed patterns (Hijmans and Graham 2006; Kearney and Porter 2009; Briscoe et al. 2019). Hybrid SDMs are used to include dynamic patters in simple correlative SDMs and they should be preferably used over simple correlative SDMs to predict distribution of species (Zurell et al. 2016; Briscoe et al. 2019). This approach conciliate ecology and biogeography studies and lead to the emergence of the field of "functional biogeography" (Violle et al. 2014). Because of the possibility to model past, current and future range, SDMs are useful tools for conservation and management of species (Guisan et al. 2013).

1.4 Specificity of research and conservation on arthropods

Bias vertebrates/invertebrates in conservation

In conservation and research, the term “invertebrates” is used in opposition to vertebrates and encompassed a highly unbalanced number of species (Table 1). Mainly vertebrates (large mammals or birds) are used as umbrella species (Roberge and Angelstam 2004) or surrogate taxa (Lewandowski, Noss, and Parsons 2010) and it is supposed that other species could benefit from their protection. In turn, a lower number of invertebrates have been evaluated to establish

Taxa	Nb of described species	Nb of species evaluated by the IUCN in 2014	% of species evaluated among species described
VERTEBRATES	66 178	39 223	59
Birds	10 425	10 425	100
Reptiles	10 038	4 414	44
INVERTEBRATES	1 305 250	17 218	1
Insects	1 000 000	5 304	0.5
Arachnids	102 248	209	0.2

Table 1: Number of species evaluated by the IUCN as of 2014 (IUCN 2014). Nb: number

IUCN red lists compared to vertebrate species. The proportion of invertebrates/vertebrates protected reflects this gap even more (1% and 59% respectively, see Table 1). Recent studies with high societal repercussions alarmed on the general decline of invertebrates (Hallmann et al. 2017; Sánchez-Bayo and Wyckhuys 2019). Consequently, the efficiency of the current conservation methods is questionable, especially because the importance of invertebrates in the ecosystem functioning and equilibrium should not be underestimated (Wilson 1987). More research and collaboration between researchers are needed to understand and to counteract this collapse (Cardoso and Leather 2019; Eisenhauer, Bonn, and Guerra 2019). Ways to counteract it are to raise awareness on invertebrates collapse (Branco and Cardoso 2020) and balance the unconscious biased research, which may affect publications on invertebrates negatively (Bonnet, Shine, and Lourdais 2002; Clark and May 2002; Titley, Snaddon, and Turner 2017).

Biases in SDMs studies on arthropods (reviewed in Paper I)

In Paper I, we reviewed the researchers subjective preferences for certain taxa over others in SDM studies (see 3.5.1 for the method used). We showed that there are fewer SDMs studies on arthropods than on vertebrates, both in number and proportion. Moreover, there is a discrepancy between taxa among studies on invertebrates, e.g. there are a lot of studies on butterflies which are easier to identify and more data are available on them than on other arthropods (Brereton et al. 2011). There are also significantly more studies on species with an economic impact, e.g. species vectors of diseases, crop pests or pollinators. However, we observed increasing efforts to map the diversity of invertebrate life in the last 10 years. Researchers on invertebrates are beginning to incorporate SDMs as tools for their studies. SDMs are indeed useful tools to fill the knowledge gap that prevents efficient conservation of arthropods. Despite the difficulty to use mechanistic approaches on arthropods due to limited data available (Viterbi et al. 2020), we provided in Paper I solutions to include process-based elements in hybrid SDMs.

Using hybrid SDMs on arthropods (Paper I)

In Paper I we provided three solutions to include process-based elements in hybrid SDMS, despite the scarcer knowledge on them.

i) Integrating traits in SDMs can influence their outcomes either by influencing species distribution directly or by informing how complete or biased the known distribution is. Modelling approaches that directly incorporate phenotypic plasticity and functional traits into correlative modelling have been developed for trees and vertebrates (e.g., see Garzón, Robson, and Hampe 2019). Increasing the knowledge on arthropods traits (e.g., on spiders see Lowe et al. 2020) would allow to apply these tools on them in a near future.

ii) Integrating genetic data with occurrences data in SDMs improve the predictions of the abilities of species to adapt locally to the new conditions provided by climate change (Marcer et al. 2016). SDMs can also complement landscape genetic studies (Manel et al. 2003; Manel and Holderegger 2013) to understand the spatial dynamic of species.

iii) Despite the difficulty to account for the complexity inherent to dispersal (Clobert et al. 2009) in SDMs (Thuiller et al. 2013), including dispersal can improve SDMs fit (Dormann 2007). Methods have been used on arthropods to account for it, from integrating buffer of long-distance dispersal (Mammola and Isaia 2017) to incorporating more complex dispersal kernel distribution (Singer et al. 2018).

1.5 Case study: the European fishing spiders

Background

According to the World Spider Catalog (2021), there are 102 species of *Dolomedes* (Latreille, 1804) described in the world. However, *Dolomedes* species have been unequally described. *Dolomedes triton* has been well studied as the most common *Dolomedes* in North America (Deshefy 1981; Bleckmann and Lotz 1987; Spence, Zimmermann, and Wojcicki 1996; Spence and Zimmermann 1998; Frost, Graham, and Spence 2013), and Tanikawa and Miyashita (2008) studied the phylogeny of Japanese *Dolomedes*. There are only two species of *Dolomedes* in Europe, *Dolomedes fimbriatus* and *Dolomedes plantarius*. Both species are widely distributed in Europe but the latter is red-listed as vulnerable at the European scale (Baillie et al. 1996) because of its scarcer distribution (see Figure 1A for the distribution in Fennoscandia). A reintroduction plan took place in the United Kingdom to sustain weakened populations of *D. plantarius* (Smith 2000; Smith et al. 2013).

Biology of European fishing spiders

Published knowledge on both species has been mainly based on valuable naturalist observations (Duffey 1958, 1995, 2012; van Helsdingen 1993). Based on their observations, these authors made the assumption that *D. fimbriatus* is more generalist than *D. plantarius*. However, *D. plantarius* and *D. fimbriatus* have relatively similar life cycles. Females lay their eggs into a large silk eggsac, which they carry for about a month and regularly dip into water to keep the eggs moist. Then, they build a nursery in the vegetation like other members of the family Pisauridae (Stratton, Suter, and Miller 2004). Spiderlings hatch in the nursery and stay there for about a week while the mother stands guard. Spiders usually require about two years to reach maturity, but it varies from one to three years.

Due to their semi-aquatic life, they present adaptation to water. They are covered by unwettable, hydrophobic hairs and can stand or run on the water; using the surface tension (Suter et al. 1997; Suter and Wildman 1999). The water surface acted as a silk web and they hunt from a hide and hunt on the water surface itself. Their preys are mayflies or aquatic insects, small fishes like stickleback (Nyffeler and Pusey 2014) but they are not specialist predators and can also hunt on lands (Gorb and Barth 1994; Duffey 2012).

Two species inhabiting wetlands

Wetlands are particularly important ecosystems for climate change mitigation, for biodiversity by providing breeding and feeding grounds for many species, and for hydrology through flood regulation, water holding bodies, and nutrient retention. Thereby, wetlands are crucial to human existence (De Groot et al. 2006). However, since the beginning of the 18^{th} century, approximately 87% of wetlands have been lost mainly because of expansion of agriculture and urbanisation (Davidson 2014). A growing interest towards *Dolomedes*' threatened wetland habitats (Finlayson et al. 2019) might have resulted in an interest towards these spiders. Opportunistic observations of *Dolomedes* were reported during sampling of other species (Bellvert et al. 2013).

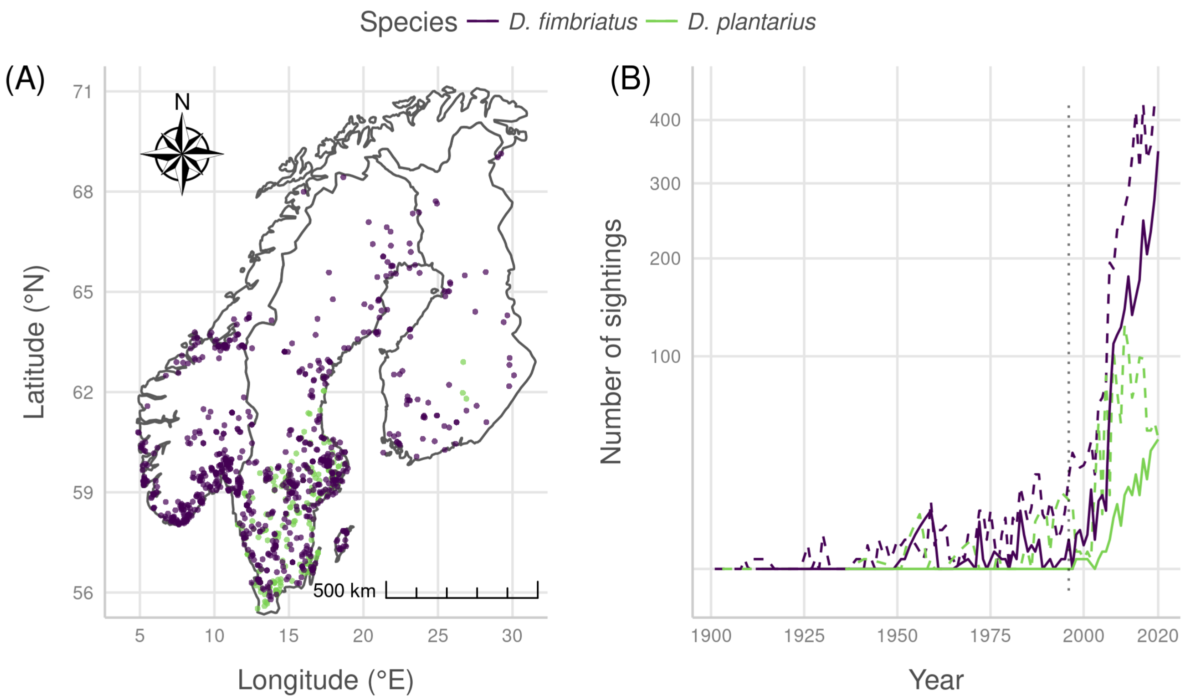

Figure 1: (A) Map of fishing spiders presences in Fennoscandia and (B) evolution of the number of sightings on the GBIF in Europe (dashed) and Fennoscandia (plain) as of February 2021 (GBIF.org 2021).

Increasing number of sightings: expansion?

The separation of European *Dolomedes* in two distinct species was made by Bonnet (1930) but the number of sightings increased only recently (Figure 1B). New observations of *D. plantarius* were reported in northern part of its range (e.g., in Belarus and Norway: Ivanov, Prishepchik, and Setrakova 2017; Fjellberg, Løvbrekke, and Olsen 2018). This could be in line with a predicted expansion of *D. plantarius* suitable climatic range towards Fennoscandia (Leroy et al. 2013; Leroy et al. 2014). However, the increasing number of sightings of both *Dolomedes* started when *D. plantarius* was red-listed (Figure 1B).

This thesis tried to disentangle the effect of an increasing interest on both species and a real expansion. Indeed, Leroy et al. (2013) and Leroy et al. (2014) studied the habitat suitability but not the abilities of *Dolomedes* to track their suitable climate. For instance, their models predicted a shrink of the distribution in South of Europe but nevertheless new sightings were reported from Spain or Italy (Bellvert et al. 2013; Milano et al. 2018, respectively)

2 Objectives

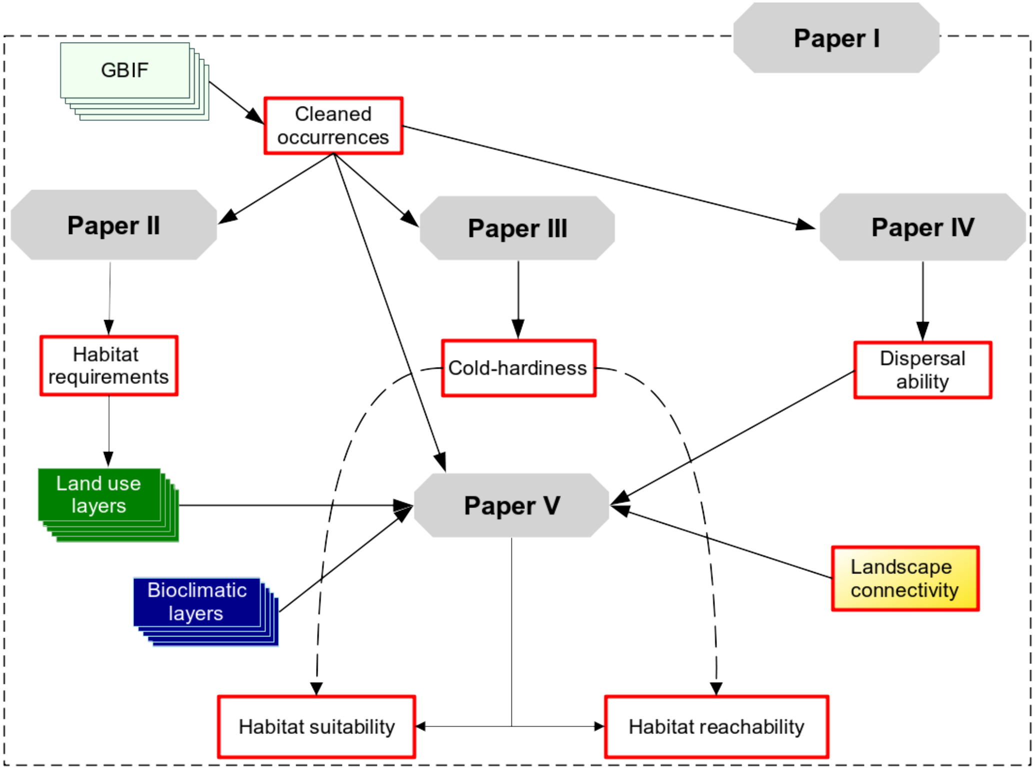

Figure 2: Workflow and connection between papers to predict the current and future suitable and reachable habitats for fishing spiders in Fennoscandia

This PhD project aimed at predicting the current and future distributions of the two European fishing spiders to facilitate their conservation. An increasing number of sightings in Fennoscandia and predictions of the future suitable climatic range (Leroy et al. 2013; Leroy et al. 2014) show a potential expansion of the distribution of *D. plantarius* towards Fennoscandia but the abilities to expand of both species has yet to be verified. Moreover, *D. fimbriatus* has been less studied but might be threatened because its wetland habitats are threatened. Our main hypothesis was that the range of suitable habitats would expand northward for both species as a response to climate change. We also expected that *D. plantarius* would be more specialised in its habitat requirements. It would also lag more behind its suitable habitats than *D. fimbriatus* in the future, due to lower propensity for dispersal. The workflow used in this PhD thesis, explaining the connection between the papers, is presented in Figure 2.

In Paper I, we synthesised trends in the use of SDMs in arthropod research. We explored the literature on SDMs to review their main applications on arthropods and the main ecological patterns driving distributions. We discussed tools and opportunities to improve

SDMs predictions in the context of climate change. We used this information to build our models in Paper V.

Defining habitat requirements of both species, how they differ and how much they are similar is crucial to provide guidance on their conservation and management. Moreover, sites with *Dolomedes* co-occurrences have never been characterised in the literature. **In Paper II, we investigated the habitat requirements of the two European *Dolomedes* and their nursery web placements**. To do so, we sampled data at the site scale and studied detectability and placement of nursery webs at the micro-habitat scale.

If *Dolomedes* spread northward, they will have to survive harsher and colder winter conditions. Even though their suitable habitats shift northward, winter temperature of fishing spiders habitat might not increase, contrary to the mean annual temperature. Indeed, the subnivean layer is becoming colder because of the unsuitability of the snow density and the unstable length of the snow season (Wipf and Rixen 2010; Pauli et al. 2013). For these reasons and because various cold resistance are found in ectotherms (see Bale 1996, 2002) defining the cold resistance of *Dolomedes* is critical. **In Paper III, we estimated the cold hardiness of *D. fimbriatus* along a latitudinal gradient and compared both species cold hardiness at the northern latitudes.**

As semi-aquatic species, fishing spiders are potentially able to use both waterborne and airborne abilities for dispersal. These abilities would be essential to cope with a suitable range moving northward. Indeed, high dispersal is associated with better survival, higher longevity and more chance to track a shifting suitable climate (Stevens et al. 2014). **In Paper IV, we investigated and compared the propensity for long- and short-distance dispersal of *Dolomedes* both in the air and on the water**.

The information collected in Papers II, III and IV was used to build a hybrid species distribution models. **In Paper V, we predicted the future range of both species by considering habitat suitability, landscape connectivity and their propensity for dispersal.** Consequently, we provided a range of suitable but also a range of reachable habitats by means of dispersal for the two *Dolomedes* under current and future climate.

Finally, we used all the accumulated information to provide guidance for the conservation of the European *Dolomedes* in Fennoscandia.

3 Material and Methods

3.1 Study area

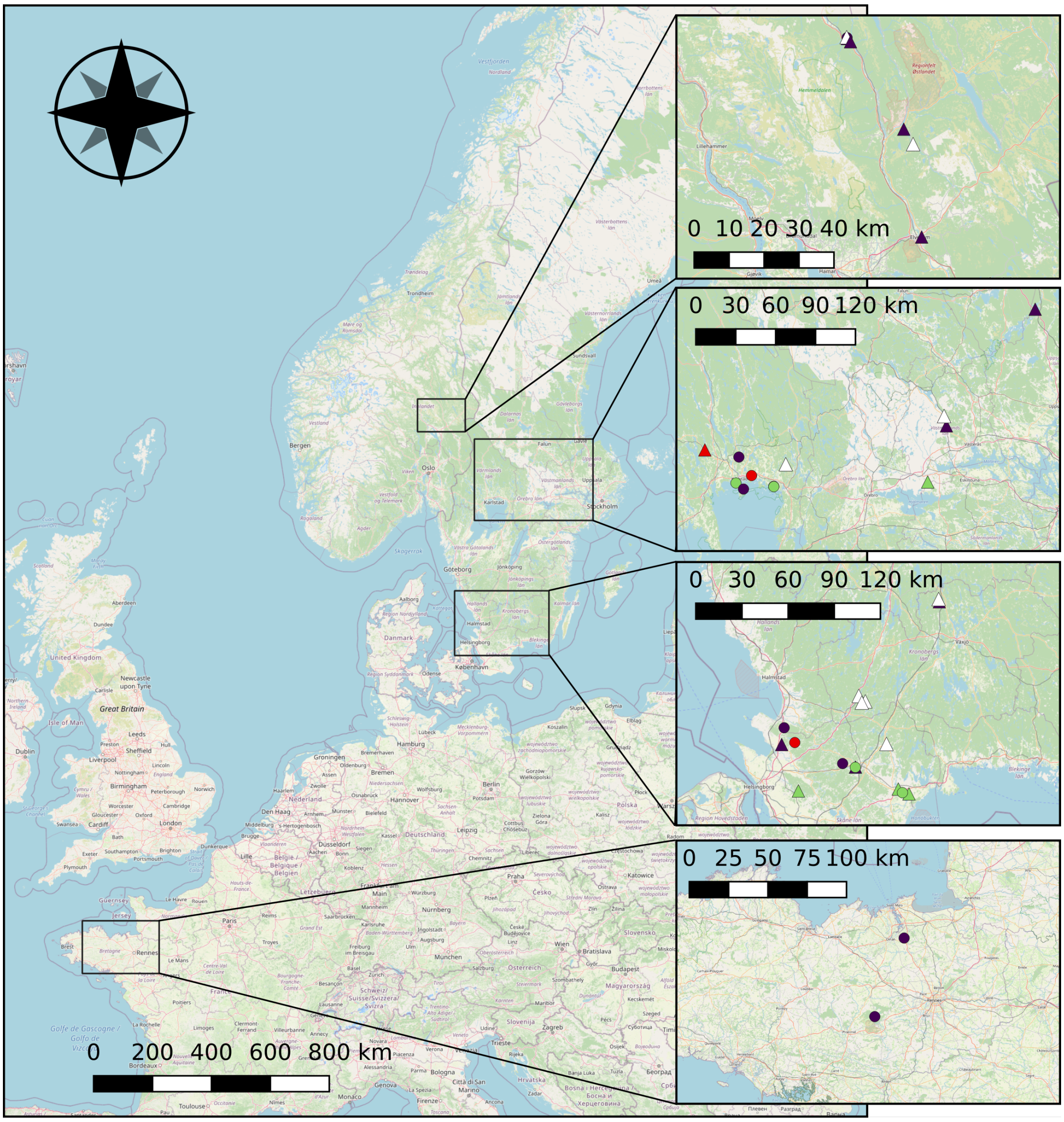

Figure 3: Location of the sites used in Papers II, III and IV. Triangles are sites used only in Paper II. Purple: *D. fimbriatus*; Green: *D. plantarius*; Red: both species; white: absence sites.

We focused the data sampling in South and central Sweden and in South-East of Norway (Figure 3). We searched for *Dolomedes* populations based on GBIF: The Global Biodiversity Information Facility (2021) from which we also retrieved occurrences used in Paper V (see 3.5.2). Paper II was a pilot study regarding the selection of sites used in Papers III and IV. We considered the populations from south of Sweden as from the core of species range and populations from central Sweden and Norway as from the edge (Figure 1A). Moreover, populations from Sweden were subjected to continental climate and were compared to spiders exposed to temperate climate in France to study the impact of bioclimatic regions on cold-hardiness (Paper III, Figure 3). We sampled some sympatric sites, i.e. with co-occurrences of both species, to see the impact of *Dolomedes* sympatry on habitat requirements and propensity for dispersal (Papers II and IV)

3.2 Sampling and identification of *Dolomedes* (Papers II, III and IV)

Like for most spider species, only adults *Dolomedes* can be identified at the species level by observing the epigyne and pedipalps of females and males respectively (Roberts 1995). Because adults tends to flee on and under the water surface when disturbed (Gorb and Barth 1994), the adults sampled were mainly females. For example, females guarding their nurseries flee less than other adults. We identified adults at the species level using a non-invasive "sponge-box" method (see Paper II). In this method, sampled adult spiders are gently squeezed between the glass-container and a sponge, identified by observing epigyne/pedipalp, and released without injuries.

We sampled spiderlings directly in their nursery web by gently opening it with tweezers and sucking up about ten spiderlings with an insect aspirator. These spiderlings were identified by capturing and identifying their mother which was guarding the nursery. With this method we were able to identify spiderlings at the species level, therefore we included the effect of sympatry on tests based on spiderlings (see 3.4.2).

We sampled *D. fimbriatus* juveniles mainly via sweep-netting the tall vegetation surrounding water, when water was present in the site. Whereas *D. plantarius* juveniles were sampled mainly on the water surface or in the vegetation at the water-edge by means of landing net or sweep-net respectively. Because juveniles already spread out of the nurseries, it is impossible to identify them at the species level. They were sampled only in sites with single *Dolomedes* species present. Consequently, we were not able to account for the effect of sympatry on tests based on juveniles (see 3.4.1 and 3.4.2).

3.3 Defining habitat requirements of *Dolomedes* (Paper II)

We sampled 12 sites with *D. fimbriatus*, 6 sites with *D. plantarius*, 4 sites with both species and 9 absence sites (Figure 3). To define habitat requirements of *Dolomedes*, we collected information at the site scale and at a narrower microhabitat scale.

At the microhabitat scale, we used transects in a wet to dry gradient, to model the presence/absence of nurseries in sites with *Dolomedes*. We focused on nursery web placement because they are easy to detect and are good proxies for reproduction success and survival. We characterised the microhabitat by collecting information on the environment such as humidity, vegetation height, vegetation abundance; and by estimating the range of cover of five plant species that are representative of wetlands, i.e. *Carex spp.*, *Juncus spp.*, *Typha spp.*, *Phragmites spp.* and *Sphagnum spp.*. We also characterised nurseries by measuring their height, proximity to other nurseries and their "host-plant".

We modelled the presence/absence of nurseries by fitting a binomial Generalized Additive Model (GAM) by component-wise boosting (Hofner et al. 2018) and the above mentioned microhabitat characteristics as predictors. We also pooled data on both species to predict the detection probability of nurseries with a single-season occupancy model (MacKenzie et al. 2002).

At the site scale, we identified females to characterise *D. plantarius*, *D. fimbiatus*, sympatric and absence sites. We collected information on vegetation type; water speed and water type (standing vs running water); land use, surrounding forest and surrounding landscape to characterise these sites. We characterised the habitats occupied by only *D. fimbriatus*, only *D. plantarius*, both species or none of them with a flexible discriminant analysis (FDA, see Hastie, Tibshirani, and Buja 1994) with the above mentioned characteristics of the site as predictors.

3.4 Experimental tests

3.4.1 Test of cold hardiness (Paper III)

We assessed the cold hardiness of *Dolomedes* by measuring the supercooling point (SCP) of juveniles. SCP is the temperature at the onset of the freezing exotherm produced by the latent heat. We tested the variation of *D. fimbriatus* cold hardiness between two different biogeographic locations. We sampled two sites under continental climate in Fennoscandia and two sites under temperate climate in France. In order to test the difference between species subjected to continental climate, we sampled one *D. plantarius* site and compared the cold hardiness from this site to the cold hardiness of the two *D. fimbriatus* sites.

We fitted generalised linear mixed models in a Bayesian framework to investigate the SCP of the *D. fimbriatus* from the two different biogeographic locations. We considered the time between capture and SCP measurements; sampling site; climate (continental/temperate, as defined by the biogeographic location), sex and body size (approximated by measuring carapace length) as predictors. We also considered the interaction between climate and body size and/or the interaction between body size and site.

We also fitted generalised linear mixed models in a Bayesian framework to investigate the SCP of sites from both species subjected to continental climate . We considered the time between capture and SCP measurements; sampling site; species; spider sex and body size. We also considered the interaction between species and body size and/or the interaction between body size and site.

For both models (biogeographical location and species), we did a model selection based on leave-one-out-cross-validation value (Vehtari, Gelman, and Gabry 2017).

3.4.2 Propensity for long- and short-distance dispersal (Paper IV)

We compared the propensity for short- and long-distance dispersal both for airborne and waterborne dispersal.

Because only smaller spiders use airborne dispersal, we tested the propensity for airborne dispersal in spiderlings. We sampled them in four *D. fimbriatus* sites, four *D. plantarius* sites and three sympatric sites, all located in Sweden (Figure 3). They were tested individually to prevent the influence of another individual's silk on the frequency of aerial dispersal (De Meester and Bonte 2010).

We used the following behaviours to characterise short- and long-distance airborne dispersal:

- **Ballooning:** when spiders release silk threads to catch the wind to become airborne. It is a passive and uncontrolled behaviour and a proxy of long-distance dispersal (Bonte et al. 2009).

- **Rappelling:** when spiders use silk threads as "bridges" and climb these threads to move from plants to plants. This behaviour is associated with a so-called "spanning" behaviour where *Dolomedes* drop themselves from a substrate while producing a silk thread (Frost, Graham, and Spence 2013). It is a proxy of short-distance dispersal.

We fitted generalised linear mixed models in a Bayesian framework to investigate the presence / absence of ballooning and rappelling behaviours separately. We considered the species, ecological characteristics of the nursery (distance to water, its height in vegetation), and sampling date as predictors. We did a selection on the random intercept and tried either the nursery, the site of origin or both nursery and site as random intercepts.

Because smaller *Dolomedes* can be constrained by hydrodynamics on the water, we tested the propensity for waterborne dispersal in juveniles. We sampled them in four *D. fimbriatus* sites and in three *D. plantarius* sites, all located in Sweden. Unlike the effect of wind speed on airborne dispersal (e.g. Bonte and Lens 2007; Pétillon et al. 2012; Frost, Graham, and Spence 2013), the effect of wind and water speeds on waterborne dispersal has been poorly studied. Consequently, juveniles were tested individually under different wind and water speeds.
We used the following behaviours to characterise short- and long-distance waterborne dispersal:

- **Sailing:** when spiders raise legs, abdomen or the whole body alternatively to catch wind and slide on the water (Deshefy 1981; Hayashi et al. 2015). It is a proxy of long-distance dispersal (Suter 1999).
- **Running:** when spiders walk or run on the water surface. It is a proxy of short-distance dispersal (Suter 2013).
- **Rowing:** when spiders use their second and third pairs of legs to propel themselves on the water surface (Suter and Wildman 1999). It is a proxy of short-distance dispersal.

We fitted generalised linear mixed models in a Bayesian framework to investigate the presence / absence of sailing, running and rowing separately. We considered the species, wind and water speeds, weight of the spider, and sampling date as predictors. To control for a possible habituation to wind/water speed, we included the trial number as a co-variate in all models. We used the spider ID as a varying intercept to account for repeated trials.

3.5 Modelling fishing spiders future distribution (Papers I and V)

3.5.1 Challenges for SDM studies in arthropods (Paper I)

In Paper I, we used a bibliometric analyses. We compared articles predicting distributions of terrestrial arthropod predators (ants, ground beetles and spiders) to articles on other taxa (terrestrial vertebrates and arthropods). We surveyed the predictor(s) and SDM algorithm(s) used as well as the key results of each article. We mapped the production of SDM articles per country for each taxonomical group. We used a co-citation network and a collaboration network to identify the most influential papers and the existence of bridges between disciplines among scientists working on ants, ground beetles and spiders.

3.5.2 Apply hybrid SDMs to *Dolomedes* (Papers I and V)

SDMs models	Variables included				Prediction
	Bioclimatic	land-use	Propensity for dispersal	Landscape connectivity	
Bioc	X				Suitable climate
BLU	X	X			Suitable habitat
Disp	X	X	X		Reachable habitat
DispLC	X	X	X	X	Reachable habitat

Table 2: Details of the four models used in Paper V and how to interpret them

Because the main purpose of the Paper V is to estimate the impact of climate change on the future distribution of both fishing spiders, we used different scenarios of future climate. We predicted current and future suitable/reachable habitats in 2050 and 2070, under two "representative concentration pathways" (RCP) 4.5 and 8.5 (van Vuuren et al. 2011). RCP 4.5 corresponds to medium–low greenhouse gas emissions and air pollution, whereas RCP 8.5 considers high greenhouse gas emission, medium air pollution, and an increase in carbon dioxide (van Vuuren et al. 2011).

Predicting distribution of terrestrial arthropods via SDMs can be taxonomically and geographically biased (see 1.4 and Paper I). However, in Paper I we proposed three solutions to mitigate these biases. In Paper V, we accounted for the following solutions in our hybrid SDMs:

- **Distribution data:** because of the ubiquitous nature of arthropods in space and time (Stork 2018), they are undersampled and their range underestimated. To overcome this issue, we used data originating from different sources and gathered in the GBIF: The Global Biodiversity Information Facility (2021). Combining multiple sources maximised the number of data which were used as presence points in our presences/pseudo-abscences approach.

- **Choice of environmental predictors:** despite recent advances in the development of microclimatic maps (see Zellweger et al. 2019), these data are still too scarce to predict in time. Furthermore, Paper I emphasised that habitat, soil and other land use variables, although rarely used, are key features affecting the distribution of arthropods. However, these are only rarely considered. To overcome this issue, we selected land-use variables based on their relevance in defining the habitat requirements of both *Dolomedes* (Paper II). We also quantified this issue by comparing SDMs including or not land-use variables (Bioc vs BLU, Table 2)

- **Algorithms for SDMs:** SDM studies have used a wide diversity of algorithms (Paper I). Nonetheless, it remains unclear if one algorithm is better than another to model the distribution of terrestrial arthropods. However, MaxEnt is widely used in SDM research. In Paper V, we combined predictions from MaxEnt models, gradient boosting models (GBM) and generalised additive models (GAMs) to make ensemble predictions (see section 1.3).

In Paper I (see section 1.4), we showed the importance of incorporating traits to explain processes in SDMs (Briscoe et al. 2019). In Paper V, we developed models Disp and DispLC to predict more than *Dolomedes* habitat suitability (see Table 2). Based on the dispersal knowledge gained in Paper IV, we included *Dolomedes* abilities to spread in their range of suitable habitats. Moreover, we also accounted for landscape connectivity because short-distance rappelling dispersal is only possible between interconnected habitats (Bonte et al. 2003, see models DispLC in Table 2). In Disp and DispLC, short-distance dispersal was possible between adjacent suitable cells, whereas long-distance dispersal was more variable in distance and direction, as shown by Thomas, Brain, and Jepson (2003).

4 Results and Discussion

4.1 More specific habitat requirements of *D. plantarius* (Paper II)

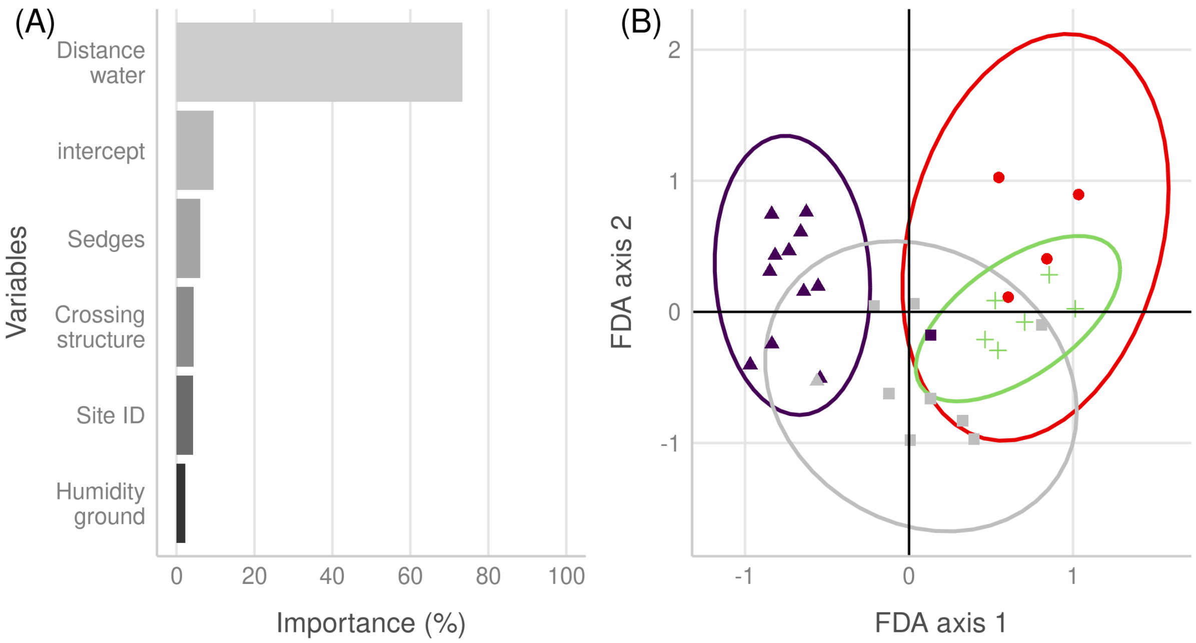

Figure 4: (A) Variables importance for the nursery web placement model (boosted GAM), and (B) results of the FDA to separate sites with both species (red, square), with *D. fimbriatus* only (green, triangle), with *D. plantarius* only (purple, cross), or with no *Dolomedes* (black, square). Colours represent observed species, shapes predicted species, ellipses indicate uncertainty of predicted species (95% confidence intervals)

Impact of the microhabitat on the placement of *Dolomedes* nursery webs

Despite a few papers describing *Dolomedes* based on naturalist observations (van Helsdingen 1993; Duffey 1995, 2012), little comparison of the habitat requirements has been made between the two *Dolomedes* species. In Paper II, we used nurseries as a sampling unit because they are useful to approximate survival and reproduction.

Among all the variables influencing the placement of nurseries (Figure 4A), we found that high humidity and low distance to water increased the probability of presence of nurseries. We made the assumption that *Dolomedes* females stay close to the water when they build their nursery because of their vulnerability at this stage and water provide them a way to escape by diving under water when threatened (Duffey 2012). Moreover, we found that high abundances of sedges (*Carex spp.*) and of crossing structures in the vegetation positively influence the presence of nursery. The stiff stems of the sedges, as well as the complex vegetation structure due to crossing structures are important for wandering spiders (Vasconcellos-Neto et al. 2017). They used this vegetation for hunting (as they do not build hunting silk webs) and to build nursery webs. We confirmed in Paper II the importance of the interactive effect of plant-community and plant-structure on the presence of predatory spiders observed by Woodcock et al. (2007).

Differences and analogies in habitat requirements

In Paper II, we revised and expanded knowledge on the habitat requirements of *Dolomedes*. We found that *D. plantarius* is more specialised in its habitat requirements than *D. fimbriatus*, which confirmed the naturalist observations made by van Helsdingen (1993) and Duffey (1995, 2012). Sites with single species were well segregated along the first axis in Figure 4B, axis loading water type, surrounding landscape and forest type. Moreover, sites with both species were more similar to *D. plantarius* sites (Figure 4B), i.e. *D. fimbriatus* is able to occupy its own specific habitats as well as *D. plantarius* habitats. The impact of forest might be a proxy of an effect of the pH. Coniferous forest, abundant in Fennoscandia, are indeed know to acidify water (Blacklocke 2016), which constrained *D. plantarius* to more alkaline sites. This is in line with the assumption of Duffey (1995) that *D. plantarius* is more sensible to low pH and water acidification. Moreover, we found *D. plantarius* mainly associated with open water and slow flowing water, whereas *D. fimbriatus* was less restricted by water presence and water speed, which depicted the more generalist habitat requirements of the latter.

In Paper II, we characterised sites with co-occurrence of *Dolomedes* for the first time in scientific literature. This co-occurrence was already reported but uncharacterised, e.g. in Lecigne (2016). Our data confirmed the higher degree of association of *D. plantarius* with water compared to *D. fimbriatus*, which restricted the co-occurrence to habitat similar to the former. Based on our results on nursery web placement and on field observations, we made the assumption that co-occurrence is possible by spatial and temporal segregations at the microhabitat scale.

4.2 Higher cold hardiness under continental climate and in *D. fimbriatus* (Paper III)

A higher cold tolerance in *D. fimbriatus*

Spiders are freezing-avoidants, i.e. species body fluids stay liquid below the equilibrium freez-

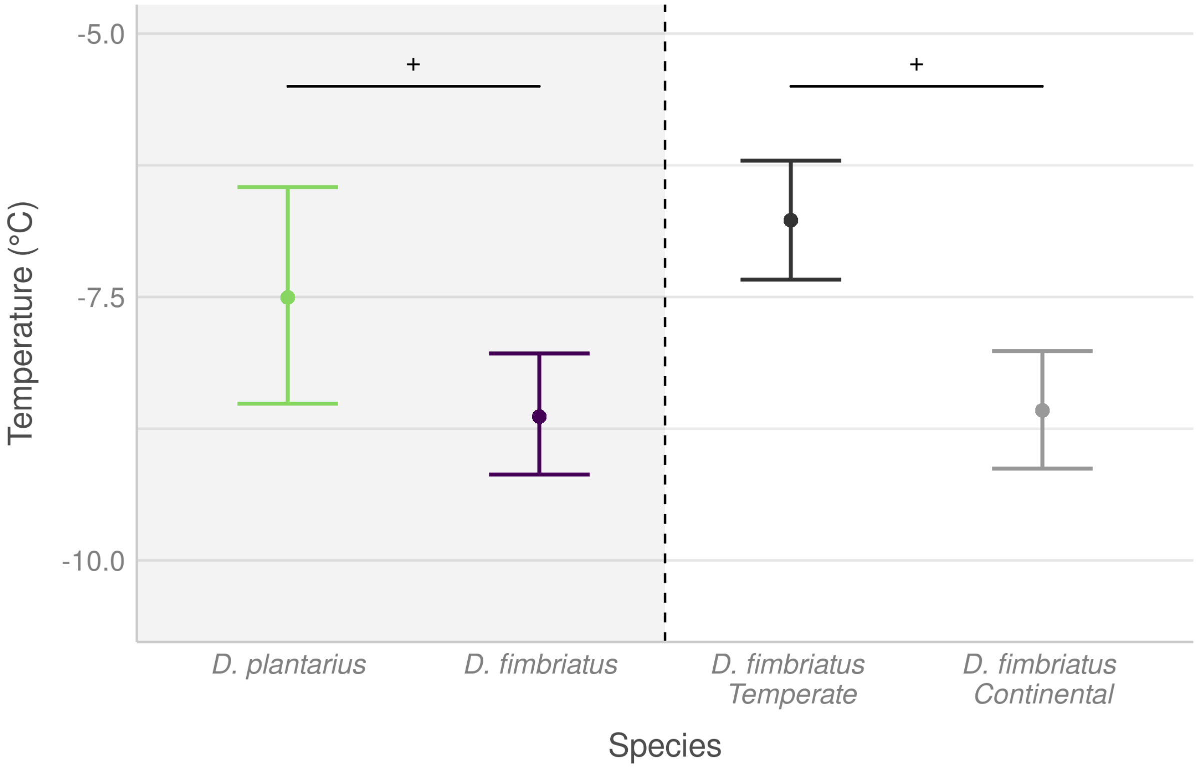

Figure 5: Marginal posterior means of SCP (dots) estimated for the two species (grey backgroud) and for the two climatic areas (white backgroud). Error bars: 95% credible interval.

ing/melting point (supercooling), but none of them survive ice formation (Nentwig 2012). In Paper III, we showed that *Dolomedes* are chill-tolerant and can survive moderately low temperatures but not freezing temperatures (Bale 1996, 2002). A similar observation was made on spiders from a phylogenetically close family (Pardosa, Lycosidae) at northern latitudes (Anthony et al. 2019). Moreover, we found lower supercooling point (SCP), i.e. higher cold tolerance, in *D. fimbriatus* than in *D. plantarius* (Figure 5). This difference might partly explain the wider range of the former, which could have benefit from its higher tolerance to expand and survive under the northern and coldest areas of Fennoscandia. Moreover, specialist spiders are usually larger than generalist ones under similar environment (Ameline et al. 2018). Because of our sampling methods (see section 3.2), we sampled only spiders with similar size. Nonetheless, we can make the assumption that bigger *D. plantarius* are less cold-tolerant because larger spiders are usually less cold tolerant than smaller ones (Almquist 1970; Bayram and Luff 1993).

Clinal latitudinal variation of *D. fimbriatus* cold tolerance

We compared the cold-tolerance of northern juveniles of *D. fimbriatus*, exposed to continental climate with snowy winters (Kottek et al. 2006) at their range limit to juveniles from central latitude of the range and subjected to warmer temperate climate. We found a higher cold tolerance in spiders originating from the two northern sites compared to spiders from the two southern sites (Figure 5). We can make the assumptions that spiders from populations at higher latitude have higher metabolic rate (see the metabolic cold adaptation hypothesis in Clarke 1991, 1993) and higher concentration of enzymes associated with cold tolerance (Sinclair, Addo-Bediako, and Chown 2003). Moreover, an increase of body size was associated with an increase of the SCP in northern *D. fimbriatus*, and the converse effect of the body size on SCP was found in southern spiders. This difference in strategy between two biogeographic areas might be partly due to the shortened breeding season at northern latitudes (Bowden et al. 2015). Smaller *D. fimbriatus* could have an advantage over bigger ones in winter and under continental climate as they can survive colder temperature. After the winter, northern juveniles could accelerate their development because cold-adapted ectotherms have a higher metabolic rate in an environment with limited energy (Sinclair, Williams, and Terblanche 2012). Simultaneously, northern *D. fimbriatus* could benefit from their cold acclimation by being more active during cooler periods in summer (Everatt et al. 2013). The clinal variation might partly explain the latitudinal variation of life duration, from the one-year in *Dolomedes* in the south of their range (in south of France, see Bonnet 1930) to two years and even more under northern latitudes, as hypothesised by Duffey (2012).

Consequences on *Dolomedes* winter habitats

Dolomedes species are inactive during winter (Aitchison 1984). Schmidt (1957) observed *D. fimbriatus* juveniles spending winter in dry vegetation at high strata in Germany, which is probably the overwintering habitat of the southern spiders we tested here. However, the northern *Dolomedes* tested endure temperatures colder than the SCP measured in Paper III. For this reason, we hypothesised that, similarly to *Dolomedes triton* in Canada (Spence and Zimmermann 1998), spiderlings and juveniles overwinter under the snow. Winter survival of *Dolomedes* under northern latitudes might be threatened by the decreasing temperature of the subnivean layer. The air temperature of the subnivean layer is considered as more stable and warmer than the air temperature at the surface (Marchand 1982). This temperature of the subnivean is threatened by climate change which negatively impacts the snow layer (Wipf and Rixen 2010, see section 5 for further discussion).

4.3 Higher propensity for long-distance dispersal in *D. fimbriatus* and contrasted propensity for short-distance dispersal (Paper IV)

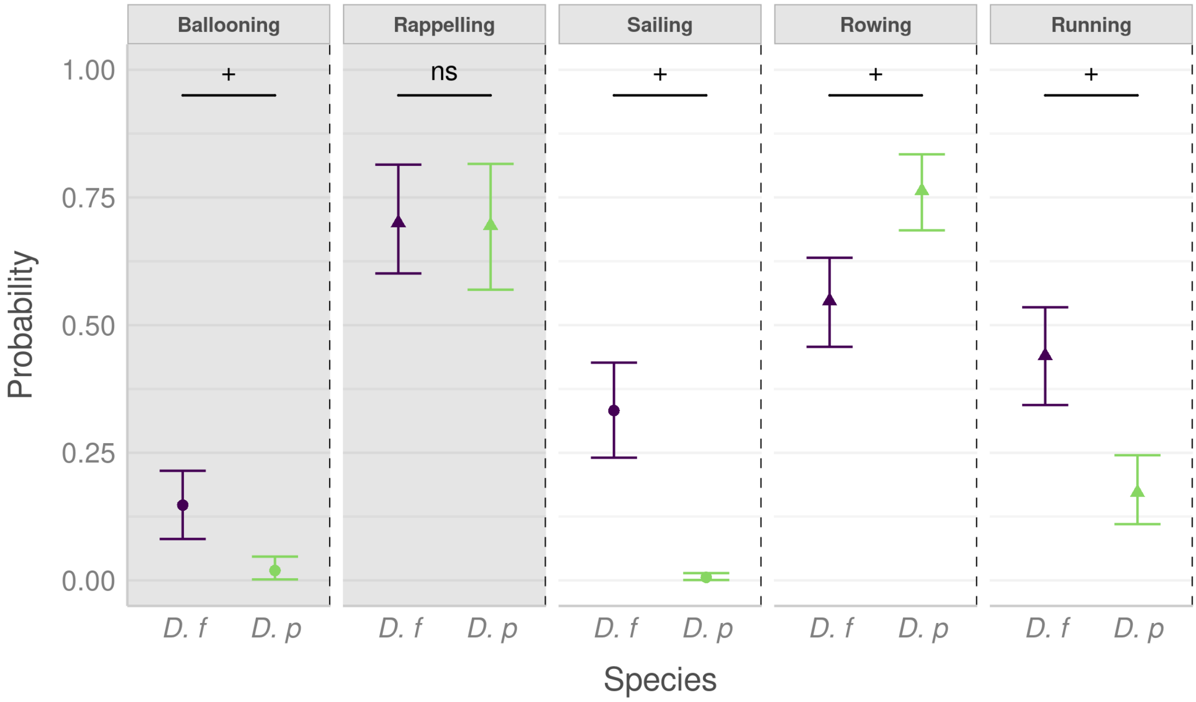

Figure 6: Estimated probability of airborne (grey background) and waterborne (white background) dispersal estimated by the best-fitted model of each behaviour. Errorbars represent the 95% credible interval of the estimated probabilities. D. f: *Dolomedes fimbriatus* (purple); D. p: *Dolomedes plantarius* (green). Circular points: long-distance dispersal, triangular points: short-distance dispersal.

Different propensity for long-distance dispersal between species

As hypothesised, and because *D. fimbriatus* is more generalist than *D. plantarius* (see Paper II and III), we found higher propensity for long-distance airborne and waterborne dispersal in the former (ballooning and sailing respectively, see Figure 6). Passive and uncontrolled long-distance dispersal behaviours of spiders are costly and risky (Bonte et al. 2012). Consequently, the probability to land in a suitable habitat is lower for more habitat-specialist species. Hayashi et al. (2015) observed that spiders than can balloon are also able to move on the water via water repellent legs. In Paper IV, we observed not only similar abilities, but also that higher propensity for long-distance airborne dispersal is associated with higher propensity for long-distance waterborne dispersal. Moreover, we found that sailing was negatively influenced by spiders' weight, indeed smaller spiders can raise their body more easily on water (Suter 1999). We can conclude that, similarly to ballooning, sailing is used by smaller and younger spiders.

Contrasted propensity for short-distance dispersal

We did not find a difference in propensity for short-distance airborne dispersal (rappelling, see Figure 6). Short-distance dispersal is known to be highly influenced by the environment (context-dependency, e.g. sex-ratio, density of spiders; reviewed in Bonte 2013) and not by inherited information (genetically or from congeners) (Bonte et al. 2009). Consequently, propensity for rappelling as estimated in Paper IV might illustrate local movement more than a dispersal behaviour, i.e. not inducing gene flow between populations. Nonetheless, for waterborne dispersal tests we used various wind and water speeds (different context), and we found higher propensity for rowing in *D. plantarius* and higher propensity for running in *D. fimbriatus* (Figure 6). The propensity for running decreased between successive trials and it is consequently more a proxy of stress (Suter et al. 1997; Suter and Wildman 1999; Hu and Bush 2010) than a proxy of short-distance dispersal between populations.

Ecological consequences of propensity for dispersal

The difference in habitat used by the two species might influence their different propensity for rowing. *D. plantarius* lives in habitats with constant presence of water, whereas *D. fimbriatus* is less dependent on water (see section 4.1). Moreover, Lambeets, Van Ranst, and Bonte (2010) found that generalist species use inherited information on water less efficiently than specialist for short-distance movement on water. *D. plantarius* could use both inherited and direct information from the water environment, whereas *D. fimbriatus* could only benefit from direct information provided by the water but not from inherited information, which might explain its lower propensity for rowing.

Lambeets, Hendrickx, et al. (2008) and Lambeets, Vandegehuchte, et al. (2008) found that flooding facilitate the settlement of generalist riparian spiders after flood. Consequently, we can conclude that *D. fimbriatus* is able to use flooding for long-distance waterborne dispersal, whereas *D. plantarius* would hide in the vegetation and use rowing to reoccupy a site occupied before flooding.

The impact of short and long-distance airborne dispersal on species distribution is more detailed in section 4.4.

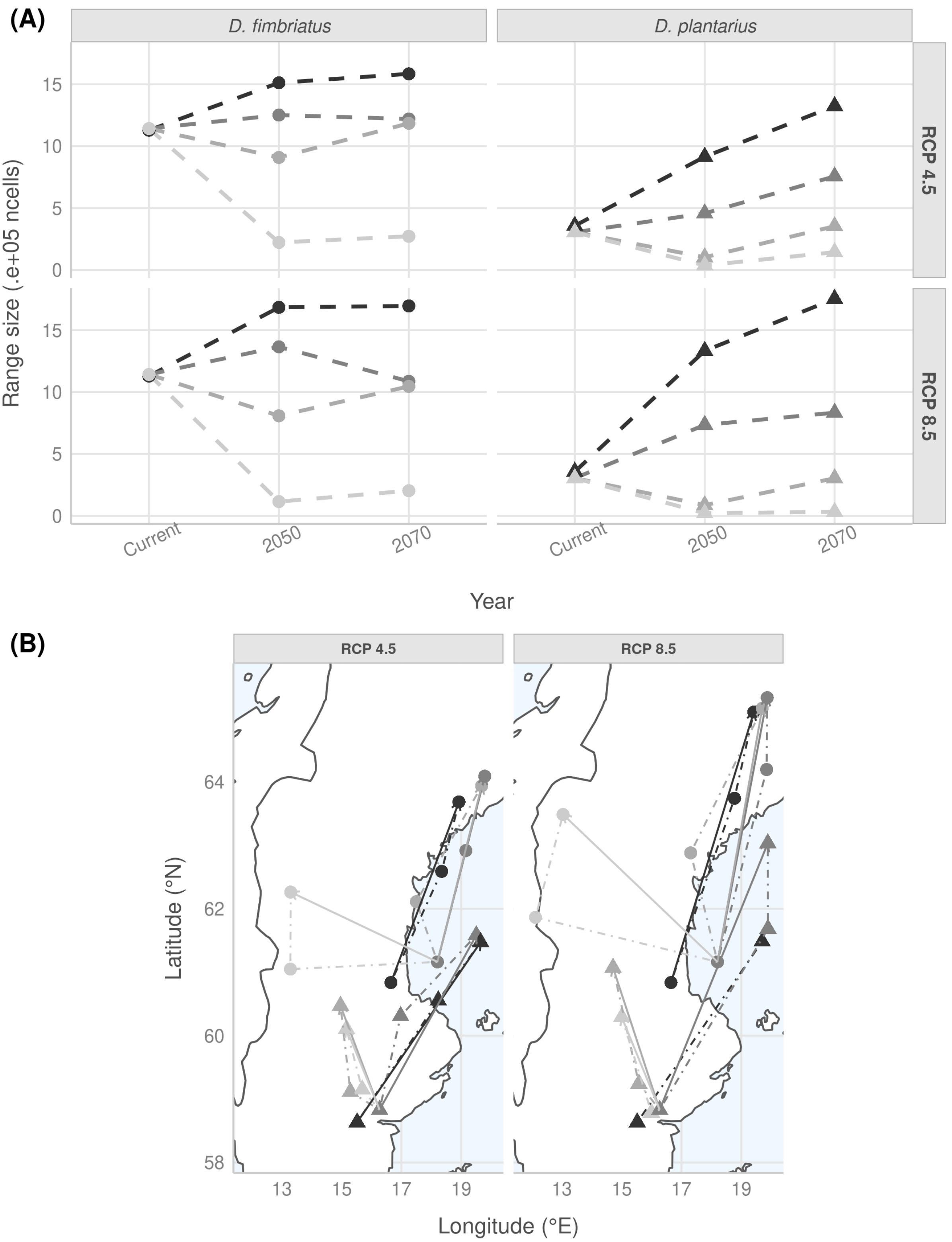

Figure 7: (A) Range size in number of cells of suitable/reachable habitat (see Table 2) predicted by the different SDMs in time per species and scenarios as well as (B) estimated shift of the range (centre of gravity) of the two species distributions predicted by the four SDMs; solid lines: shift from current to 2070; dashed lines: shift from current time to 2050 and from 2050 to 2070. Grey gradient from dark to light: Bioc, BLU, Disp and DispLC. Dots: *D. fimbriatus*, triangles: *D. plantarius*

4.4 Present and future distribution of *Dolomedes* under climate change (Paper V)

Expansion and displacement of the range of habitat suitability

In Paper V, we predicted an expansion and a displacement of the ranges of climatic suitability and habitat suitability (model Bioc and BLU, see Figure 7A). Moreover, including land-use slightly reduced the range of suitability, especially at the range limit, compared to the predictions from Bioc. Under RCP 4.5 scenario, we predicted an expansion of suitable climatic and habitat ranges of both species in 2050 and 2070 compared to their actual suitable range (Figure 7A). For BLU (Table 2), we predicted a proportionally higher expansion under RCP 8.5 for *D. plantarius* than for *D. fimbriatus* compared to their respective current range.

The southern part of the suitable range of both species should shrink, especially in Sweden and, to a lesser extent, in Finland. The general displacement of the suitable range in time is illustrated by a northward shift of the centre of gravity of their suitable range (Figure 7B). This northward expansion is also predicted in other taxa, as climate change promotes an expansion of the range at the colder margin (Parmesan and Yohe 2003; Parmesan 2006).

As hypothesised based on observations of *Dolomedes* habitat requirements and cold hardiness (Paper II and III, see sections 4.1; 4.2), the lifespan might be impacted under northern latitudes in Fennoscandia. This could, in turn, result in a faster life cycle and in a higher chance for *Dolomedes* mothers to have a second brood (second brood observed in September in Fennoscandia, unpublished data).

Contrasted habitat reachability in the future

In the previous paragraph, we discussed the expansion of the suitable range of both species. Nonetheless, models Bioc and BLU predicted only the range of habitat suitability but not the reachability of these habitats by means of dispersal. A lack of abilities to reach some northern areas is indeed expressed by a farther shift of the centre of gravity without dispersal (models Bioc and BLU) than with dispersal (models Disp and DispLC, Figure 7B). Under the Disp model, suitable habitats should be less reachable for *D. plantarius* than for *D. fimbriatus* in 2050. The smaller propensity for long-distance dispersal of *D. plantarius* partly explained the limited reachable range. The species might be trapped in its geographical range due to limited dispersal abilities in the past and current time, similarly to some tree species in Europe (Svenning and Skov 2004). For example, an expansion of *D. plantarius* in Finland seems unlikely, due to scarcer populations and limited propensity for long-distance dispersal. Nevertheless, the size of the area reached by both species under the Disp model should be smaller than their current suitable area.

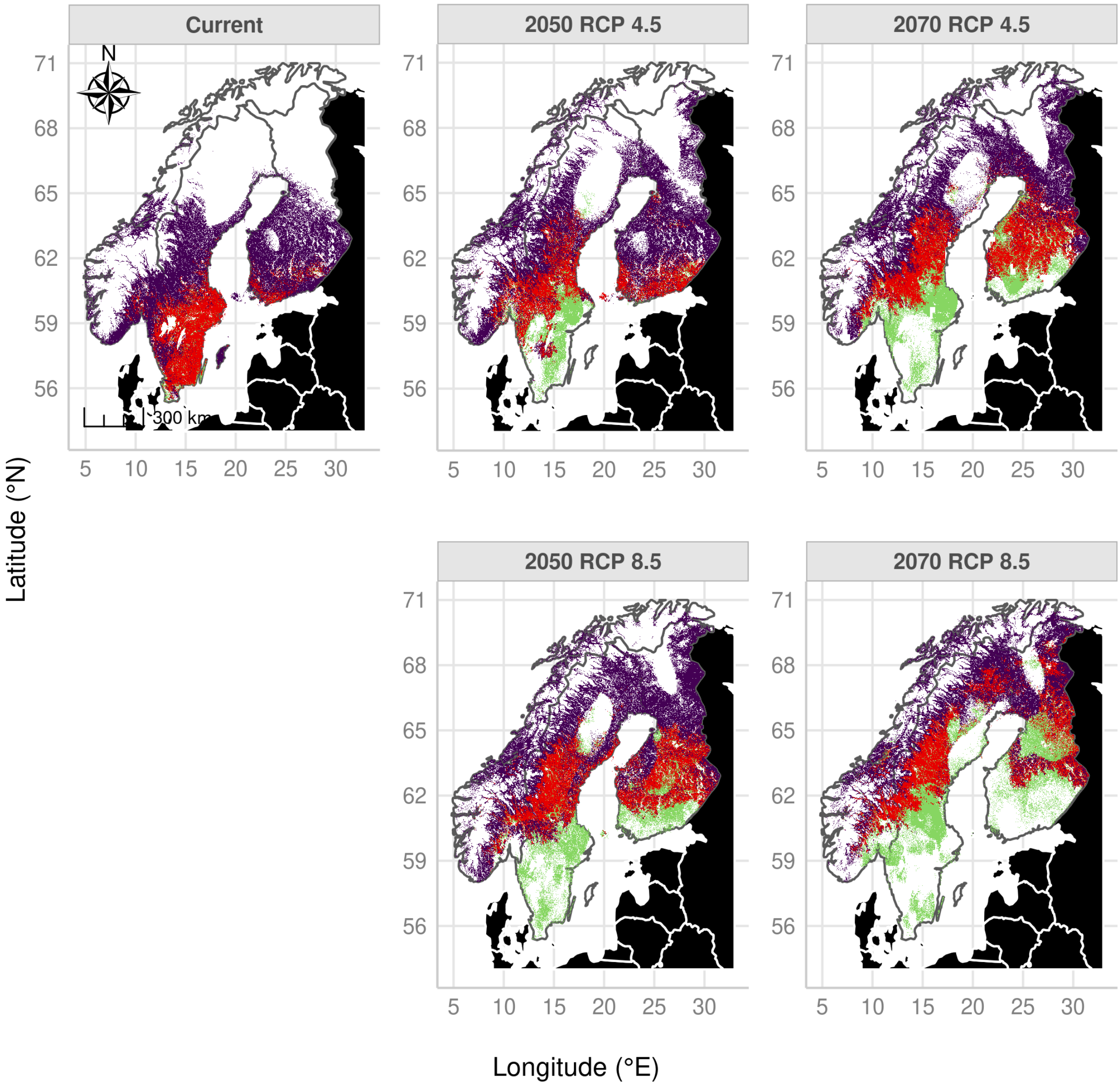

Figure 8: Range overlap and suitable habitat of both species predicted by model BLU from current time to 2070 under scenario RCP4.5 (top) and RCP8.5 (bottom). Purple: suitable habitat for *D. fimbriatus*; green: suitable habitat for *D. plantarius*; red: suitable habitat overlapping between the 2 species.

Consequences on sympatry and syntopy

In Paper V, we showed that the range of the area of sympatry will increase in time (Figure 8. The overlap should mainly occur at the southern range of *D. fimbriatus*.

Our SDMs did not consider the last phase of dispersal, which is the settlement in the newly colonised location (Clobert et al. 2009). The presence of one *Dolomedes* species in a site might influence the probability for the other species to settle in this site because closely related species co-occur less often than moderately related species (Weinstein, Graham, and Parra 2017). Nonetheless, we did not predict the distribution at meso- or microhabitat scales, which would be too fine scales for SDMs. It was also impossible to predict the range of sympatry under models including dispersal due to the random distance and direction of long-distance dispersal events. We cannot predict yet the positive and/or negative influence of syntopy/sympatry on *Dolomedes* distribution. For example, as shown in spiders from the closely related family of Lycosidae, a difference in timing of their breeding season might appear to avoid intraguild predation (Balfour et al. 2003) and facilitate co-occurrence.

Some alarming results

Despite an expansion of *Dolomedes* habitat suitability, we predicted tighter reachable ranges for both species by including dispersal. Moreover, the results from DispLC questioned even more the abilities of both species to expand northward in response to climate change. Short-distance dispersal will have a high importance for their persistence in the future and needs to be associated with a good habitat connectivity. Indeed, propensity for long-distance dispersal tends to decrease with an increase of habitat fragmentation (Bonte et al. 2006).

The predictions from DispLC are in line with Lenoir et al. (2020) observation of the lag of terrestrial organisms to track their sustainable ranges which is partly explained by human activities preventing or slowing down their shift. For these reasons and based on the results of this thesis, we provide advice for species conservation and management of *Dolomedes* in the following section.

5 Conservation of European *Dolomedes*

Fennoscandia: a refugium against climate change?

Suitable habitat of *D. plantarius* will shift northward at the European scale (Paper V, Leroy et al. 2013; Leroy et al. 2014). In this PhD thesis, we showed that this also true for *D. fimbriatus*. Consequently, Fennoscandia may become a climatic refugium for *Dolomedes*, i.e. an area that can mitigate the effects of climate change by providing suitable conditions for species persistence through time (Keppel and Wardell-Johnson 2012). The stronger the climate change will be, the more likely Fennoscandia will act as a refugium. Nonetheless, the climatic and habitat conditions might become too harsh under stronger climate change and it might switch this refugium area even more North.

The quality of the refugium might be limited if *Dolomedes*, and especially *D. plantarius*, lag behind their suitable range because of limited propensity for long-distance dispersal. Indeed, we did not find any evidence of an increasing propensity for long-distance dispersal behaviours from populations at the edge of the distribution. It is therefore essential to protect both current and future suitable habitats.

Call for an update of their IUCN status

The first red list of species which included the threatened status of *D. plantarius* was Wells, Pyle, and Collins (1983). This species is now red-listed as vulnerable (Baillie et al. 1996). Nonetheless, *D. plantarius* status has not been updated since then and this PhD thesis, among other papers (Leroy et al. 2013; Leroy et al. 2014; Milano et al. 2018; Milano et al. 2021) emphasised the need for a reassessment of its status. Contrary to spiders expanding their range in Europe like the wasp spider *Argiope bruennichi* (Wolz et al. 2020), the recent new observations of *Dolomedes* in Europe (Harms, Dunlop, and Schütt 2009; Bellvert et al. 2013; Ivanov, Prishepchik, and Setrakova 2017; Fjellberg, Løvbrekke, and Olsen 2018; Milano et al. 2018) are most probably due to an increasing interest towards conservation of wetlands rather than an actual expansion.

These new observations unknown and consequently not accounted for in the last IUCN assessment, the lack of consideration of *D. fimbriatus* and the potential lag of both species behind their habitat suitability are criteria that should be accounted for in a new IUCN assessment.

Wetlands/*Dolomedes*: mutual benefits from protection

Arthropods conservation is challenging because of the finer-grain level needed compared to vertebrates and the lower empathy towards them (Samways 2018; Cardoso and Leather 2019). Nature conservation is indeed driven and motivated by how human value the species (Lindenmayer and Hunter 2010), which is one of the major obstacle of spiders conservation (Branco and Cardoso 2020). For this reason, raising awareness on the importance and the conservation of arthropods like *Dolomedes* is fundamental, e.g. with citizen science projects (Troudet et al. 2017). Moreover, because spiders are good indicators of management (Marc, Canard, and Ysnel 1999) and have already been used as bio-indicators (Prieto-Benítez and Méndez 2011), *Dolomedes* could be a good indicator of wetlands health. Our models predict a shrink of *Dolomedes* suitable habitats under more intense climate change, indirectly predict the future disappearance of wetlands and their urgent need for conservation (Davidson 2014; Carson et al. 2019).

Large scale conservation

A conservation with corridors and/or via stepping stones (Noss and Daly 2006) could be useful to promote short- and long-distance airborne dispersal respectively. Maintaining connectivity in the first five kilometres around each presence site, which correspond to the more frequent distance of airborne dispersal events (Thomas, Brain, and Jepson 2003), is crucial to conserve current sites, promote expansion, and conserve gene flow. High propensity for short-distance dispersal in both *Dolomedes* (see section 4.3) could be sufficient to maintain genetic exchange, or a least to prevent detrimental genetic drift (Bell et al. 2005). Moreover, stepping stones might support long-distance dispersal which is of primary importance for the sustainability and conservation of threatened species (Trakhtenbrot et al. 2005). Priority should be given to sites with limited connectivity in southern Finland and central Sweden because we predicted a limited spread of *Dolomedes* in those areas. Since *D. fimbriatus* has higher propensity for airborne dispersal, improving the connectivity in the northern part of its suitable range would make it reachable in the future.

To support waterborne dispersal, the conservation of interconnectivity is necessary (Gibbs 1993). This require the management of hydrological functioning, fundamental for spiders inhabiting wetlands (Lambeets, Vandegehuchte, et al. 2008; Lambeets, Breyne, and Bonte 2010; Lafage and Pétillon 2016). Moreover, the propensity of *D. fimbriatus* to use streams for long-distance dispersal might be limited by dams and the conservation of this species could be considered in the management plan of dams, as done for fishes in Sweden (Lejon, Renöfält, and Nilsson 2009).

Local scale management: landscape and micro-habitat actions

The remarkable and successful reintroduction of *D. plantarius* (Smith 2000; Smith et al. 2013) was applied in few populations in UK but might be too costly at the Fennoscandian scale. Moreover, because the natural relocation of specialist spider species is usually challenging (Hacala et al. 2020), the priority should be to conserve existing populations.

For efficient local management, estimating the local density and distribution of *Dolomedes* is important. We showed in Paper II that the detection probability was higher where abundance of crossing vegetation structures was high and with good weather condition, i.e. with optimal temperature and sunny weather. Days with these weather conditions and repeated visits of each site should be used to estimate *Dolomedes* population size, e.g. to use an occupancy modelling (McFarland et al. 2012). Our non-invasive sponge-box identification should facilitate the identification in the field, especially of mothers guarding their nurseries. The management of population by preserving wet habitat, especially continuous presence of water for *D. plantarius*; preserving a shoreline with abundant crossing structures is essential.

Surviving winter conditions, potential knowledge gap in knowledge for conservation

The subnivean winter habitat of both species will become colder due to climate change and we measured warmer SCPs than the coldest temperature at northern latitude of their range. In the future, the temperature of the subnivean will be fluctuant due to variations of the snow density and length of the snow season (Bale and Hayward 2010; Pauli et al. 2013). It will offer a less efficient isolation which might threaten both species and especially the less cold tolerant *D. plantarius*. Despite our tentative to estimate winter tolerance, we did not estimate cold survival, modelling the temperature of the subnivean in the future is needed and would help predicting the effective expansion of *Dolomedes* and plan its conservation.

6 Conclusion and perspectives

In Paper I we explored ways to provide more than simple correlative SDMs to predict climatic suitability in research on arthropods. Hence, we investigated habitat requirements, cold resistance and propensity for dispersal of European *Dolomedes*, which were later accounted for in hybrid SDMs to predict *Dolomedes* future suitable and reachable ranges. The approach used in this thesis gave valuable insights for fishing spiders conservation at the European and Fennoscandian scales.

In Paper II, we found that *D. fimbriatus* is more of a habitat generalist than *D. plantarius*. The latter had narrower habitat requirements than the former. *D. plantarius* was negatively impacted by the presence of deciduous forest in the surrounding, i.e. by low pH, and requires a constant presence of water with a slow flowing speed. *D. fimbriatus* is less impacted by these ecological factors. Moreover, co-occurrences always occur in sites more similar to *D. plantarius* sites.
In Paper III we showed that *D. fimbriatus* can survive colder temperatures than *D. plantarius* under similar latitudes. The tolerance of the former also increased along a clinal latitudinal gradient, gradient characterising spiders subjected to different bioclimatic areas.
Finally, in Paper IV we showed that, despite contrasted propensity for short-distance dispersal, *D. fimbriatus* has a greater propensity for long-distance airborne and waterborne dispersal.

Using hybrid SDMs, we predicted in Paper V that both climate suitability and habitat suitability of *Dolomedes* will expand northward with climate change. This shift will be more important under stronger climate change. Nonetheless, the abilities of both species to track their optimal habitats might be limited due to limited dispersal abilities and/or the fragmentation of suitable habitat. This lag behind suitable habitats might be even bigger for *D. plantarius*.

An aphorism in ecology and more broadly in statistics states that: "All models are wrong, but some are useful."
The predictions of Paper V, made with our hybrid SDMs, have inherent uncertainties. However, they emphasised the urgent need of conservation of *Dolomedes* habitats threatened by climate change (see also Milano et al. 2021). Increasing research on arthropods and collaboration (Cardoso and Leather 2019), raising awareness (Branco and Cardoso 2020), concretely

changing funding attribution in conservation, from conservation based on species popularity to conservation based on extinction risks (Mammola et al. 2020) would help to conserve *Dolomedes*. Effective conservation of wetlands (Finlayson et al. 2019), of arthropods (Cardoso et al. 2020), and of the environment in general (Ripple et al. 2017), would make our predictions wrong but much more useful.

Perspectives

Hortal et al. (2015) reviewed seven shortfalls on knowledge of biodiversity. We did not explore the Darwinian shortfall of *Dolomedes*, which is the past evolution of species and their traits. The phylogeny of European *Dolomedes* is poorly described (Tanikawa and Miyashita 2008; Piacentini and Ramírez 2019; Macías-Hernández et al. 2020). Moreover, genetic information is important because highly influenced by contemporary climate, even more than past climate, and would provide guidance for decision on population genetic importance (De Kort et al. 2021). Resolving the influence of the environment on fishing spiders gene flow, e.g. by using landscape genetic (reviewed in Manel et al. 2003; Manel and Holderegger 2013), would provide insightful information to understand their current dynamic in Fennoscandia.

The Raunkiaeran shortfall is the lack of knowledge about species traits and their ecological functions. The Hutchinsonian shortfall, the lack of knowledge of species responses to change in their habitats (Cardoso et al. 2011; Hortal et al. 2015), could provide complementary information to the Raunkiaeran shortfall. For example, studying *Dolomedes* fecundity would be useful as it can support the spread of a species. The wasp spider *Argiope bruennichi*, in expansion in Europe, invests more in fecundity and no clinal variation in propensity for dispersal was found (Wolz et al. 2020). Moreover, refining knowledge on ecophysiology of fishing spiders or accounting for all phases of dispersal (i.e. emigration, transfer, settlement; see Travis et al. 2012; Travis et al. 2013) and including them in mechanistic SDMs would give complementary information for a better definition of fishing spiders distribution, fundamental and realised niche. To do so, an efficient way of tracking spiders during dispersal still have to be developed. Developing a technology to track individuals that disperse through ballooning or sailing would give great insights to understand these movements that are considered as long-distance dispersal but still lack understanding.

The last shortfall that we did not totally resolve is the Eltonian. It is related to the Eltonian niche, i.e. the ecological interactions. Because *Dolomedes* are generalist predators, lack of preys should not be a limiting factor. Nonetheless, the effect of the co-occurrence sites on populations inhabiting these sites is still unknown. They might not be affected but temporal delay and/or spatial switch at the micro-habitat scale could prevent competition. This would confirm our observation in two Swedish locations of *D. fimbriatus* females with juveniles in the nursery while *D. plantarius* still carried egg sacs. Nonetheless, this has yet to be tested.

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Paper I

Challenges and opportunities of species distribution modelling of terrestrial arthropod predators

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Author contribution statement

SM, JP, and DL conceived the study. SM, AC, S-LM, and DL mined and extracted information from papers. DL curated data, performed analyses, and prepared figures. SM and DL wrote the first draft of the paper, with substantial inputs by JP, JM, and PC. All authors contributed critically to the paper by means of discussions, comments, and additions to the text.

Conflict of interest statement

None declared

ABSTRACT

Species distribution models (SDMs) are emerging as essential tools in the equipment of many ecologists; they are useful in exploring species distributions in space and time and in answering an assortment of questions related to historical biogeography, climate change biology and conservation biology. Given that arthropod distributions are strongly influenced by microclimatic conditions and microhabitat structure, they should be an ideal candidate group for SDM research, especially generalist predators because they are not directly dependent on vegetation or prey types. However, most SDM studies of animals to date have focused either on broad samples of vertebrates or on arthropod species that are charismatic (e.g. butterflies) or economically important (e.g. vectors of disease, crop pests and pollinators). By means of a systematic bibliometric approach, we targeted the literature published on key terrestrial arthropod predators (ants, ground beetles and spiders), chosen as a model to explore challenges and opportunities of species distribution modelling in mega-diverse arthropod groups. We show that the use of SDMs to map the geography of terrestrial arthropod predators has been a recent phenomenon, with a near-exponential growth in the number of studies over the past 10 years and still limited collaborative networks among researchers. There is a bias in studies towards charismatic species and geographical areas that hold lower levels of diversity but greater availability of data, such as Europe and North America. To overcome some of these data limitations, we illustrate the potential of modern data sources (citizen science programmes, online databases) and new modelling approaches (ensemble of small models, modelling above the species level). Finally, we discuss areas of research where SDMs may be combined with dispersal models and increasingly available phylogenetic and functional data to obtain mechanistic descriptions of species distributions and their spatio-temporal shifts within a global change perspective.

Keyword: bibliometrics; climate change; ecological niche models; MaxEnt; niche-based models; predicted distribution; social network analysis; statistical modelling

INTRODUCTION

A mainstream topic in ecology, biogeography and conservation biology is the extent to which climatic conditions affect species performance (Colinet et al. 2015, Rezende and Bozinovic 2019), which together with geographical and historical constraints ultimately modulates species niches and observed range boundaries (Thomas 2010). Obtaining a nuanced understanding of the factors conditioning species distributions has gained new urgency amid the current climate emergency (Ripple et al. 2020), insofar as changing climatic conditions are determining fast redistributions of species along latitudinal, elevational and other spatial gradients (Chen et al. 2011, Lenoir et al. 2020). As global climate change redefine the geography of life, we are becoming spectators of a large-scale experiment of complex ecological responses (Walther et al. 2002), where interactions among previously isolated species can quickly occur (Krosby et al. 2015), invasions of novel areas by alien species are becoming routine (Hellmann et al. 2008, Liu et al. 2020) and unnoticed extinctions are potentially taking place on a daily basis (Hughes et al. 2004, Barnosky et al. 2011, Cardoso et al. 2020b). Therefore, mapping the diversity of life has never been so urgent.

Over the years, ecologists and statisticians have developed a wide range of methods for modelling the niches and distribution of species in space and time, several of which fall under the umbrella of correlative species distribution models or ecological niche models (defined in Box 1). For simplicity, we will hereafter refer to these as ‘species distribution models’ (SDMs), while redirecting the interested readers to key semantic and theoretical discussions (e.g. Peterson and Soberón, 2012; Sillero, 2011; Warren, 2012). Researchers have used SDM techniques for mapping the distribution of organisms in a variety of systems, although the number of applications across habitats and the tree of life have not been equal. For example, while the use of SDMs has grown exponentially in the terrestrial realm from the early 2000s onward (Lobo et al. 2010, Robinson et al. 2011, Araújo et al. 2019), applications in systems where three-dimensionality is an important feature – e.g. marine ecosystems (Robinson et al. 2017, Melo-Merino et al. 2020), tree canopies (Burns et al. 2020), soils (Schröder 2008) and caves (Mammola and Leroy 2018) – have lagged behind. Also, applications of SDMs in animals have concentrated mostly on vertebrates (Titley et al. 2017), while studies on invertebrate groups remain scarcer, although recently increasing (Figure 1).

The paucity of SDM studies is possibly related to a number of arthropod-specific modelling challenges. First, arthropods often are small organisms that move in small spatial scales, strongly influenced by microclimatic conditions and microhabitat structure (Pincebourde and Woods 2020). These characteristics are hardly captured by the ubiquitous bioclimatic variables derived from remote sensing at relatively large spatial scales (e.g. Potter et al., 2013). Second, arthropods often have short life cycles with wide population abundance fluctuations from season to season and strong metapopulation dynamics, making it difficult to determine what their real, constantly changing, range is. Thus, arthropods pose particular modelling challenges that add to the ones already present for vertebrates, but they should also offer opportunities for future SDM research as data and new methods are made available (Maino et al. 2016).

Here, we conducted a systematic mapping of the literature to synthesize trends in the use of SDMs in arthropod research. We explored these topics through the lens of the literature on dominant terrestrial arthropod predators: ants (c. 30,000 described species; Parr et al., 2017), ground beetles (c. 39,300 species; Lorenz, 2020), and spiders (c. 49,000 species; World Spider Catalog, 2020). We begin by conducting a systematic literature search focused on SDM use in our focal group. Then, to put our survey in perspective, we compare the volume of literature with that on other key terrestrial invertebrate and vertebrate groups. By means of bibliometric analyses, we explore the geography of SDM applications and networks of collaborations among researchers working on terrestrial arthropod predators. Subsequently, we review the main areas of application

of SDMs in terrestrial arthropod research, highlighting which ecological factors emerged as important in driving predicted distribution patterns. Building upon this quantitative evidence, we discuss challenges and opportunities of SDM research on terrestrial arthropod predators and delineate potential future lines of enquiry as well as promising areas of research where SDMs may be combined with other modelling tools and data sources to obtain mechanistic descriptions of species distributions and their shifts within a global change perspective.

Box 1. A general definition of SDMs and their domain of applicability

As a broad and general definition, species distribution modeling implies using some statistical algorithms to explore the relationship between species occurrences (typically geo-referenced localities) and environmental variables (typically spatial rasters whose cells represent bioclimatic and other habitat and environmental conditions). Once this relationship is determined, the model is used to characterize the ecological niche of a given species by projecting a probability surface into a geographical space to represent its potential range of distribution (Guisan et al. 2017). These models can be construed using a wide range of algorithms, from simple logistic regression up to sophisticated techniques based on machine learning (Elith et al. 2011, Ryo et al. 2020) and other artificial intelligence methods (Cardoso et al. 2020a). Given the large variety of life histories and data sources, the best modelling algorithm and approach necessarily changes, with no universal best solutions (Qiao et al. 2015).

Whereas the first paper relying on species distribution modelling is now over three decades old [e.g. the first applications of the algorithm BIOCLIM can be traced back to 1986 (Booth 2018)], there has been an acceleration in the use of these tools in just the last two decades (Araújo et al., 2019; Lobo et al., 2010; Figure 1). This trend was probably due to the increase in data (Zhang 2017, Wüest et al. 2020) and easy to use, often automated, statistical packages that perform species distribution modelling (reviewed in Angelov, 2019). These methods have become popular in the toolkit of many ecologists, being useful to answer a range of questions. Not only are SDMs routinely used to describe species distributions, they have also proved important to assist and complement taxonomic studies (Rödder et al. 2010) and to set conservation agendas (Guisan et al. 2013). Furthermore, given that these models are transferable in space and time (Yates et al. 2018), they find applications in studies on climate change (Dormann 2007, Santini et al. 2020), historical biogeography (Peterson 2009), and invasion biology (Peterson 2003, Liu et al. 2020), among other topics.

METHODS

Systematic search of SDM papers and analyses

Between 20 and 24 November 2020, we searched on the Web of Science (Clarivate Analytics) for articles relying on SDMs to predict distributions of terrestrial arthropod predators (ants, ground beetles and spiders) and, for comparative purposes, other terrestrial vertebrate and invertebrate groups (Table 1). For each taxonomic group considered, we found and extracted papers using the following general query:

TS=("family name(s)" OR "vernacular name(s)") AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "Niche model*" OR "Distribution model*" OR "Habitat suitability model*")

where TS denotes a search for 'Topic' and the asterisk (*) is a regular expression used to match all words including that string of characters (e.g. 'model*' matches 'models', 'modelling', 'modelled', etc.). See Appendix 1 for the list of families and vernacular names.

We exported all results into the online review application Rayyan (Ouzzani et al., 2016) for title, keywords, and abstract screening, whereby we excluded by-catches of papers not actually dealing with SDMs or our model species (e.g. our search for the keyword 'spiders' also captured papers dealing with spider monkeys, genus *Ateles*) (Table 1). Furthermore, for ants, ground beetles and spiders, we manually inspected all papers to extract specific data. We recorded the geographical extent of each study and all the species modelled. We classified the type of predictors used, their resolution, and the SDM algorithm(s) and modelling protocol employed. Specifically, we coded the modelling protocol under three main categories: single algorithm, when studies just applied one modelling technique; ensemble of models, when the authors applied a plethora of algorithms and took the consensus between them (Araújo and New, 2007); and no-silver bullet (Qiao et al., 2015), when the authors applied a number of algorithms and chose the best performing one(s) for projecting the distribution. Finally, we read each study and summarized the key results (see Appendix 2 for a full list of extracted information).

Data analysis

We conducted analyses in R 3.6.3 (R Core Team, 2020) and visualized data using the *ggplot2* R package (Wickham, 2009) and QGIS (Open Source Geospatial Foundation Project, 2020). The complete data set and R code used for the analyses is available on GitLab (https://gitlab.com/DenisLafage/sdm_review).

We analysed bibliometric data regarding ants, ground beetles, and spiders with the *bibliometrix* R package (Aria and Cuccurullo 2017). In order to map the production of articles per country for each group, we assigned articles to a country based on the affiliations of all the authors at the time when each article was published. In order to identify the most influential papers for researchers dealing with modelling of macro-arthropod distributions, we used a weighted co-citation network. Initially introduced for bibliometric research, co-citation networks have proved useful to identify key literature items acting as bridges between disciplines (Trujillo and Long, 2018). A particular article is included in the network when it is cited by at least two papers from the dataset under study (Batagelj and Cerinšek 2013). The number of co-citations is the number of times two articles are cited together. Furthermore, we built a collaboration network to identify the existence of bridges among scientists working on ants, ground beetles and spiders.

Caveats in the interpretation of the survey

Some caveats need to be made when interpreting the results of this research weaving. Due to our search strategy in the Web of Science and selection of keywords (Appendix A), we did not capture all possible studies on SDMs dealing with our focal groups. For example, we missed some studies on taxonomy that used SDMs to assist species delimitations, since these rarely mentioned the methodology in their keywords, title or abstract. Similarly, SDMs have recently begun to be routinely used for assessing terrestrial arthropod risk of extinction against International Union for Conservation of Nature criteria (e.g. Branco et al., 2019; Fukushima et al., 2019; Seppälä et al., 2018b, 2018a, 2018c, 2018d), but most of these studies were missed for the same reason. Furthermore, for many groups, especially vertebrates, the authors may not mention the higher taxonomic ranks included in our query but exclusively the species/genus/family, which will not be captured. We also acknowledge that our search was not exhaustive since we only included articles in English (Konno et al. 2020) and we used a single database, Internet browser, and location for the search (Pozsgai et al. 2020).

As a result, our estimation of the volume of the literature on the focal groups should be taken as an approximation of the real number of studies. While we operated under the assumption that the biases were homogeneously distributed across all taxonomic groups, allowing us to compare them and to draw general inferences, still the comparison of absolute numbers of studies across taxa (Figure 1) should be taken with caution.

SURVEY RESULTS

Volume of scientific production in comparison to other groups

By comparing the volume of SDM literature on vertebrates versus invertebrates, we observed a similar exponential increase in the number of studies for both groups, with an inflection point after 2010 (Figure 1a). However, the total number of studies was greater for vertebrates (67%) than invertebrates, despite vertebrates accounting for a considerably lower number of species. Among invertebrates, the largest fraction of studies focused on Diptera (8.2%). Other well-studied groups were butterflies (6.4%), non-carabid beetles (5.8%), and Apoidea (2.5%). Our three focal groups were comparatively less studied (0.7, 1.7 and 1.9% for ground beetles, spiders and ants, respectively); all three of them began to be the focus of SDM research after 2005, with the number of studies steadily increasing from this point (Figure 1b).

Geography of scientific production

The geography of studies, as inferred from author affiliations, revealed how production of SDM papers on ants, ground beetles and spiders is mostly concentrated in North and South America and Europe (Figure 2). There were, however, some conspicuous differences among groups. For ants, modelled species are mostly in North and South America, and Europe (Appendix C), and 15 studies modelled species distribution worldwide. For spiders and ground beetles, most studies focused on European species (Appendices E and G), and only three and one studies/y, respectively, had worldwide coverage. There were considerably more ant species which have been studied with SDMs than spiders and ground beetles (Appendices D, F, H).

Most influential papers

The co-citation network allowed us to identify key articles co-cited by the studies included in our survey (Figure 3). As expected, most co-cited papers were methodological rather than arthropod-specific papers. The top-cited papers were Phillips et al. (2006) and Hijmans et al. (2005), respectively the reference for the algorithm MaxEnt and for the most widely used global climate database (WorldClim). Among the less co-cited but still influential papers, there were several references to phylogenetic methods, suggesting that a number of articles are potentially integrative research using multiple lines of evidence to deal with species delimitation (Ross et al. 2010, Ferretti et al. 2019) and historical biogeography (e.g., Solomon et al. 2008, Magalhaes et al. 2014, Planas et al. 2014, Mammola et al. 2015).

Collaboration network

Network analysis revealed highly structured collaboration hubs around the three groups of interest (Figure 4). Observed collaboration hubs were strongly bound but limited in size, with only four cases of inter-group collaborations (ants–ground beetles, ants–spiders and ground beetles–spiders). Two cases were the result of multi-taxa studies (Christman et al., 2016; Jiménez-Valverde et al., 2009) and two were related to authors involved in articles dealing with two different groups: Williams S.E. (Steiner et al. 2008, Staunton et al. 2014) and Peterson A.T. (Roura-Pascual et al. 2004, 2006, 2009, Peterson and Nakazawa 2008, Planas et al. 2014).

Paper topics

Articles dealing with ants primarily focused on climate change (33.9% of studies) and invasion biology (30.4%). Many studies often dealt with both topics simultaneously (23.2%) as these topics often go hand-in-hand, with researchers seeking to predict the future spread of alien species in climate change scenarios.

The research spectrum of articles dealing with spiders was more diversified, with studies using SDMs to explore the environmental drivers of species distribution (28.6%), to predict distributions under future climate change (33.4%), to assist species delimitation (26.8%), as well as other miscellaneous topics (19.6%). Contrary to ants, only 7.1% of studies on spiders dealt with invasion biology, probably on account of the reduced number of globally important known invasive spiders (Nentwig 2015).

Finally, the focus of articles dealing with ground beetles was almost entirely climate change (52.6%) and the drivers of species distribution (36.8%), with only two papers dealing with biological invasions.

Algorithms used

A large majority of articles used a single algorithm (for ants, ground beetles and spiders 79.6, 94.7, 80.4%, respectively) or ensemble (24.1, 5.3 and 14.3%, respectively) for modelling species distributions, whereas no silver bullet use was sporadic and only used in spider-related articles (7.1%). A total of 33 different algorithms were used in the studies we reviewed. For all taxonomic groups, MaxEnt was the most used algorithm (Figure 5), as also emphasized by the co-citation network (Figure 3). This is a recurrent pattern in the latest SDM research, as found for the research in other animal groups (e.g. bats; Razgour et al., 2016). This trend is probably due to the fact that MaxEnt is a presence-only technique, thus allowing users to overcome some of the difficulties associated with obtaining reliable absence data in the light of imperfect detection (e.g. Ward and Stanley, 2013). Moreover, MaxEnt has proved to be a robust species distribution modelling technique according to comparative studies [e.g. Elith et al., 2006 – a highly co-cited reference in our dataset as shown in Figure 3 (Phillips and Dudík 2008)].

Surprisingly, the simple technique of logistic regression (i.e. a Bernoulli generalized linear model) was sporadically used, even before MaxEnt release in 2004. This may be a true pattern but also an artefact resulting from our keyword search. In fact, the idea that logistic regressions based on distribution records are *de facto* an SDM is relatively recent (Peterson 2006, Elith and Leathwick 2009).

Variables used in the models and their importance in explaining distribution patterns

Bioclimatic variables were by far the most used predictors to model and explain species distributions (Table 2) for the three focal groups. The mean variable resolution was rather similar for ants and ground beetles [respectively 314.9 arc.sec (max = 1.4 arc.sec) and 414.7 arc.sec (max = 0.05 arc.sec)]. The mean resolution was higher for spiders (171.7 arc.sec (max = 1.4 arc.sec). This is partly due to broad availability of free high-resolution climatic variables [e.g. CHELSA (Karger et al., 2017), CliMond (Kriticos et al., 2012) and WorldClim 2 (Fick and Hijmans, 2017)], and partly reflects the true importance of climate as a limiting factor for species distribution (Muñoz and Bodensteiner 2019), especially climatic extremes (Román-Palacios and Wiens 2020). Climatic variables, in fact, were systematically selected as important in virtually all analysed studies (Table 2).

Topography, soil and land use, and habitat variables are used less often, possibly due to greater limitations in their availability (the mean resolution of these predictors in the data set is c. 4.6 km at the equator, much higher than that of bioclimatic variables). Nevertheless, when used, these non-climatic factors were often selected as important in modelling the distribution (>65% for ants and >80% for spiders and ground beetles, table 2), suggesting that fine-scale habitat structure plays a critical role for the ecology of terrestrial arthropods .

The integration of SDM use with species functional traits and ecophysiological data was scarce. For ants, 10.2% of articles used traits and 6.2% ecophysiological data. For spiders, 2.4% of articles used functional traits and none ecophysiological data. For ground beetles, no articles used functional traits or ecophysiological data. In the few instances where similar variables were considered, these were not directly incorporated as predictors in the model but rather discussed in comparison with the modelled distribution. For the three groups, between 20 and 25% of papers used phylogenies, but as previously they were not incorporated into the models.

CHALLENGES FOR SDM RESEARCH IN TERRESTRIAL INVERTEBRATES

Taxonomic and geographical biases

While SDM studies based on comprehensive samples of vertebrate species are becoming routine (e.g. Liu et al., 2020; Thuiller et al., 2019), our survey emphasizes how just a small fraction of terrestrial arthropod predators have been subjected to the attention of modellers. The total volume of SDM articles was higher for vertebrates than for arthropods, and this difference would be even greater if these numbers are relativized to the total number of known vertebrate and arthropod species. This is a typical pattern that is partly explained by the fact that there is more available information on vertebrates (e.g. distribution data; Troudet et al., 2017) and partly the result of a cognitive bias in terms of researcher' subjective preferences for certain taxa over others (Clark and May 2002) – what has been termed by entomologists 'institutional vertebratism' or 'taxonomic chauvinism' (Leather 2009a, b). The few available studies on arthropods are drops in the ocean when considering the number of described and as yet undescribed species of insects (Stork 2018) and spiders (Agnarsson et al. 2013). However, taxonomic bias towards certain groups exists also among articles dedicated to arthropods (e.g. Cardoso, 2012; Leandro et al., 2017). For example, butterflies are among the most studied in SDM studies, which once again may be due to a greater availability of information (Thomas 2005, van Swaay et al. 2008, Brereton et al. 2011), and which in turn might be driven by aesthetic characteristics. Other well-studied groups are those relevant from an economic point of view, such as vectors of diseases (Diptera, 8.9%), crop pests (other beetles, 6.6%) and pollinators (Apoidea, 3.2%).

As for our focal groups, we found that despite spiders and ground beetles outnumbering ants in terms of described species, the number of species studied was considerably higher for ants. This may be linked to the topic of articles, with most papers focusing on one of the numerous invasive ant species – it is likely that a few globally relevant invasive ant species (e.g. Argentine ant, fire ant) allow myrmecologists to obtain research funding, thus attracting most research attention (Holway et al. 2002, Silverman and Brightwell 2008).

Inevitably, the few studies on ants, ground beetles and spiders have often been opportunistic, largely reflecting the specific interests of the few authors who have ventured to explore the potential of SDMs in terrestrial arthropod research (Figure 4). For example, this is evident when looking at a sample of papers on spiders – most studies focused on large-sized, taxonomically unique, and/or charismatic species (e.g. Decae et al., 2019; Jiménez−Valverde et al., 2011; Wang et al., 2018), taxa of medical importance (Planas et al. 2014, Wang et al. 2018, Taucare-Ríos et al. 2018) or taxa inhabiting peculiar habitats that are the interest of certain authors, like caves (Mammola et al. 2018, 2019, Pavlek and Mammola 2020).

The paucity of multi-taxa studies also suggests a general lack of data for less common species. In fact, and this is true also for vertebrates, most SDM applications are set in geographical areas that hold lower levels of diversity but greater availability of data (Europe and North America; Figure 2). The scarcity of data has been pointed out as one of the key limitations to our understanding of the drivers of biodiversity change in invertebrates (Cardoso and Leather 2019), as summarized in eight so-called ‘biodiversity shortfalls’ (Cardoso et al. 2011, Hortal et al. 2015, Ficetola et al. 2019). SDMs may help us to combat some of these impediments by identifying unexplored regions of high environmental suitability for improving the geographical gaps in species distributions (i.e. tackling the Wallacean shortfall), by identifying the environmental drivers of these distributions (Hutchinsonian shortfall), and even by suggesting suitable sites for further sampling (Linnean shortfall). However, the SDM construction in itself requires robust and high-quality distribution data, creating a loop that is difficult to break.

Solutions to alleviate data limitations

Distribution data

A quick search for any bird species in the Global Biodiversity Information Facility (www.gbif.org) reminds us that it is unlikely we will ever possess for arthropods the same amount and quality of data available for vertebrates. Arthropods are simply too ubiquitous in space and time (Stork 2018), while natural scientists are simply too few (Tewksbury et al. 2014). However, some recent technical and technological advances may help us to overcome some impediments related to data limitation and getting close to the goal of modelling the distribution of arthropods with more confidence.

Foremost, there have been recent technical advances in SDMs that may be significant when it comes to modelling the distribution of poorly known taxa. The emergence of ensemble of small models has proved promising to optimize the modelling of species for which few occurrences are available; this is achieved by combining a set of small bivariate models to create a consensus model that avoids overfitting (details in Breiner et al., 2018, 2015).

Second, modelling above the species level (Smith et al. 2019), for example by integrating data from related species when their niche overlap is large (Qiao et al. 2017), may be a useful shortcut to overcome a lack of distribution data in many circumstances.

Furthermore, the information age is characterized by the emergence of a myriad of types of digital data (summarized in Jarić et al., 2020) that may help to fill distribution data gaps, especially for easy-to-identify species. It was shown that photo-sharing platforms and smartphone applications such as iNaturalist are valuable sources of species occurrences (e.g. Unger et al., 2020), even in the case of our focal groups (Wang et al. 2018, Jiménez−Valverde et al. 2019). Citizen science programmes are also a valuable source of distribution data, for example about swarms of ants (Hart et al. 2018a) or common species of spiders (Hart et al. 2018b). Recent modelling exercises based on similar alternative data sources have demonstrated their utility in obtaining realistic representations of niches and distributions for easy-to-identify arthropods (Wang et al. 2018, Peña-Aguilera et al. 2019).

Finally, the recent advances in metabarcoding and especially environmental DNA is of major interest to overcome the issue of species detectability (Muha et al. 2017) and lack of invertebrate taxonomists (Hebert and Gregory 2005). Metabarcoding consists in identifying species using small DNA sequences that are highly variable between species and weakly variable within a given species. It is the basis of the environmental DNA approach which consists in the identification of the species present in a given environment using the DNA left by individuals. Despite the many technical challenges, environmental DNA and metabarcoding face becoming standard survey tools (Deiner et al., 2017), including in our focal groups (Toju and Baba 2018, Piper et al. 2019, Kennedy et al. 2020). Their ability to provide reliable absence data and to produce a massive amount of presence data is predicted to improve the efficiency of SDMs in the near future (Muha et al. 2017). Recently, for example, the use of environmental DNA has proved useful to forecast the spread of invasive species (Zhang et al. 2020) or to monitor reintroduction programme success (Riaz et al. 2020). Large-scale projects including metabarcoding of terrestrial arthropod communities [e.g. LIFEPLAN (https://www.helsinki.fi/en/projects/lifeplan) and the Insect Biome Atlas (https://www.insectbiomeatlas.com)] are currently taking place and will provide an unprecedented data baseline for SDMs. This will likely trigger the parallel development of tools to handle the big data era (Hallgren et al. 2016).

Lack of micro-scale environmental predictors

The second impediment that limits our ability to model the distribution of terrestrial arthropods is the scarcity of relevant environmental predictors at the correct spatial resolution. Most environmental rasters used today for SDMs [e.g. CHELSA (Karger et al., 2017) and WorldClim 2

(Fick and Hijmans, 2017)] achieve a maximum resolution of 30 arcsec (cell size c. 1 km^2 at the equator), which is excellent but might not be enough in the case of invertebrates that are known to respond to microclimatic characteristics over spatial scales of millimetres to metres (Potter et al. 2013, Suggitt et al. 2018). On a positive note, gigantic leaps forward are being made in the development of microclimatic databases (e.g., Kearney et al., 2014), as well as approaches for downscaling temperature data at high resolutions from thermal images (Senior et al., 2019) or airborne light detection and ranging data (George et al. 2015). It is predicted that in the following years, the use of remote sensing derived data will become the standard for modelling and mapping the microclimate (Zellweger et al. 2019), especially in invertebrate research where the use of similar high-resolution data has already proved useful to achieve realistic conservation prioritization (e.g. Bombi et al., 2019).

Furthermore, our literature survey emphasizes that habitat, soil and other land use variables, although rarely used, are key features affecting the distribution of invertebrates. However, these are only rarely considered. As in the case of climatic variables, there is a general paucity of raster data at a meaningful spatial resolution. Once again, statistical downscaling and remote sensing may come to help; for example, the use of high-resolution habitat variables has proved fundamental in modelling the distribution of spiders in spatially complex alpine rocky lands (Mammola et al. 2019).

Testing new algorithms

Despite the large number of algorithms tested (33), even per article (up to 14), it remains unclear if one algorithm rather than another is more suitable for modelling the distribution of terrestrial invertebrates. At the moment, MaxEnt hegemony in SDM research is obvious in our data set. More empirical comparisons of the performance algorithms in the context of terrestrial invertebrates research would be needed (Qiao et al., 2015; Araujo et al., 2019).

OPPORTUNITIES FOR SDM RESEARCH IN TERRESTRIAL INVERTEBRATES

SDMs are often used as a simple, correlative way to estimate species ranges based on the realized niche, having large uncertainties and often over- or underfitting the real distribution. In an influential paper published 15 years ago, it was foreseen that SDMs may offer ‘more than simple habitat models’ (Guisan and Thuiller 2005), for example by tackling biotic interactions, migration processes, dispersal limitations, and (meta)population dynamics.

The challenges faced by conservation biologists today call for the development of more of these process-based models (or mechanistic models), providing causal explanations for the observed patterns (e.g. Briscoe et al., 2019). These can be defined as any model that mechanistically links model predictions and species fitness, measured either directly or indirectly using functional traits or environmental and biological (e.g. competing or mutualistic species) interactions (Kearney 2006). This idea was reinforced by a seminal paper by Kearney and Porter (2009) calling for explicitly integrating physiological data in mechanistic niche modelling, but also life history traits (including dispersal abilities, fitness, eco-physiological tolerances) and biotic interactions (competition, parasitism).

There are proportionally more such studies for plants and marine invertebrates (see e.g. Chardon et al., 2020; Webb et al., 2020) than animals, because large spatial data sets needed for integrating physiological trait variation are available (Chown and Gaston 2016). While all these applications are still rare when it comes to terrestrial arthropods (see Maino et al. 2016), recently there have been studies that have successfully addressed biotic interaction (Mammola and Isaia 2017), dispersal limitations (Monsimet et al. 2020), and metapopulations (Giezendanner et al. 2020), thereby showing promising directions for future research. Studies including probability of survival to different stresses such as cold (Cuddington et al. 2018) or desiccation (Barton et al. 2019) were also performed for particularly well-known groups like lepidopterans and pests.

However, whereas mechanistic models are increasingly available, they have high data demands and thus cannot be routinely used for invertebrates (Viterbi et al. 2020), especially in terrestrial arthropods where, as previously discussed, the scarcity of data on natural history and the large number of species are a clear challenge. Some ideas towards a more mechanistic understanding of arthropod distributions are discussed in the following.

Integration of species attributes and traits in SDMs

Species traits influence the outcome of SDMs in two ways. First, they themselves influence the distribution of species. Either in the present, past or future, the ability of species to adapt to certain conditions, their history, their relation with other species or their ability to disperse, all influence species distribution and its change in time. Second, their traits may influence how complete or biased the known distribution data are and hence how adequate the modelled distributions for the different purposes are. Taking into account trait data before, during and after SDMs is therefore crucial for correct interpretation and to be aware of possible limitations.

The recent upsurge in open source trait databases and projects [ants (Parr et al., 2017), ground beetles (Homburg et al., 2014) and spiders (Lowe et al., 2020)] offers an unprecedented data baseline to integrate trait variability in modeling exercises and develop mechanistic descriptions of species distributions and their changes through time. Accordingly, the integration of correlative distribution analyses and functional approaches has recently been advocated (Mammola et al., 2019; Thuiller et al., 2009; Wittmann et al., 2016), as it would make it possible to bridge the differences in biogeography and functional ecology and move towards the novel field of ‘functional biogeography’ (Violle et al., 2014).

Accounting for trait variability

There are various ways to link correlative SDMs and traits (Kearney and Porter 2009). The most obvious one is a simple comparison between model outputs and trait variability, including the formulation of hypotheses about why these may concur or not. Example in invertebrates is the positive relationship between predicted habitat suitability and body size found in spiders (Mammola et al. 2019), phenotype−environment associations observed in butterflies (Zaman et al. 2019), or the use of thermal physiology tests to define thermal safe zones in ants (Coulin et al. 2019).

With the aim of obtaining more meaningful and realistic prediction of biodiversity change, recently new modelling approaches that directly incorporate phenotypic plasticity and other functional traits into correlative modelling are being scrutinized (e.g., AdaptR; Bush et al., 2016; ΔTraitSDM; Garzón et al., 2019). Following these examples, which are respectively based on dipterans and plants, and considering the recent increase in availability of traits for invertebrates, it is possible to predict a vast potential for developing trait-based SDMs in invertebrates.

Linking genetic data and distributions

SDMs have been criticized, among other things, for not taking into account heterogeneity in the genetic structure of populations within the species range (Hampe and Petit 2005, Smith et al. 2019). Indeed, SDMs generally assume uniformity of responses to climate but local adaptations and intraspecific variations have been documented (e.g. Franken et al., 2018; Hereford, 2009). Several recent studies have demonstrated that genetically informed SDMs improve climate change predictions because they incorporate possible local adaptations (Marcer et al. 2016, Ikeda et al. 2017). Instead of building SDMs based on species occurrence defined using standard taxonomy, one can model the distribution of each genetic unit of the population. The identification of these units can be achieved using traditional molecular markers such as amplified fragment-length polymorphisms, micro-satellites, and even Single Nucleotide polymorphisms (see below). For example, in their study, Marcer et al. (2016) built SDMs for each haplotype *Arabidopsis thaliana* (Brassicacae) and found that even though most haplotypes distribution ranges will shrank with global climate change, two of them will expand. Some authors also advocate the use of genetic data because it allows production of real absence data (absence of a given genetic cluster), making it possible to fit logistic regressions and incorporation of endogenous spatial autocorrelation (Gotelli and Colwell 2011). The recent advances in high-throughput sequencing techniques allow ecologists to collect single nucleotide polymorphism data (Peterson et al., 2012) for cluster identification at reasonable costs. Single nucleotide polymorphism provides fine-scale resolution of population genetic structure, which can then be incorporated into SDMs. To our knowledge this has rarely been done on animal populations (but see Razgour et al., 2018) and has never been done on terrestrial arthropod species.

Accounting for dispersal

Using a correlative approach makes the inclusion of complex processes like dispersal more difficult. While the inclusion of dispersal can improve model fit (Dormann 2007), dispersal processes are rarely accounted for in the studies on arthropods. The only such studies either considered dispersal via the calibration area (Anderson and Raza 2010, Barve et al. 2011), by including a buffer of reachable areas around presences based on species-specific dispersal abilities [e.g. long-distance dispersal via ballooning for spiders (Mammola and Isaia 2017)], or relied on more sophisticated approaches based on kernel distribution [e.g. model of butterfly accounting for both demography and dispersal via a kernel distribution (Singer et al. 2018)].

In general, these are rough estimations, given that dispersal is a complex phenomenon that is not trivial to integrate into SDMs (Thuiller et al. 2013). Indeed, dispersal is characterized by three phases (Clobert et al. 2009), i.e. departure, transfer and settlement, that the model should theoretically account for. Moreover, several factors can influence each of these phases (e.g. inbreeding, temperature development, body condition or starvation; on spiders see Bonte et al., 2009, 2008b, 2008a), often acting synergistically.

Different methods, with varying complexity levels, have been developed to integrate dispersal into SDMs. The use of mechanistic models, which is highly data demanding, is not easily feasible for mega-diverse arthropod groups. Moreover, while models that include dispersal often outperform simpler models, an increase of the model complexity usually increases the uncertainty of the prediction (Zurell et al. 2016). Integration of dispersal is thus still largely ignored in SDMs, not only in the case of arthropods, but even in most studies on vertebrates and plants. It should be considered, for example in conservation or invasive species studies, to improve predictions in time by predicting the range of potentially suitable habitat that can be reached.

CONCLUSIONS

Efforts to map the diversity of invertebrate life have been mostly concentrated in the last 10 years, emphasizing how more and more entomologists and other scientists are beginning to incorporate SDMs into their research. In the light of our ignorance about the diversity, distribution and life history of most arthropods, these versatile tools are proving useful to fill some major knowledge gaps regarding arthropod diversity. The importance of similar endeavours becomes apparent when considering the accumulating evidence about the silent extinctions of invertebrates (e.g. Cardoso et al., 2020; Eisenhauer et al., 2019), the limited conservation efforts that are directed towards them (e.g. Cardoso, 2012; Mammides, 2019; Mammola et al., 2020), and the calls for solutions to these problems (Harvey et al. 2020, Samways et al. 2020).

Apart from the conservation implications of using SDMs to map arthropod diversity, we have shown how terrestrial arthropods may provide opportunities for advancing SDM research.

Given that terrestrial arthropod distributions are strongly influenced by microclimatic conditions and microhabitat structure, they represent ideal candidates for testing novel modelling approaches. So far this potential is still largely unexploited and thus we have discussed some recent avenues of research where the integration of different data sources may lead to mechanistic descriptions of key processes associated with species distributions. We are certain that our suggestions are a drop in the ocean when compared with what is currently available in terms of modelling possibilities – methodological advances in SDM-related theory are so quick that often it is difficult to keep pace. As brand new solutions to describe patterns and processes associated with species distribution are becoming available, we hope that this review will succeed in highlighting the potential of arthropods in SDM research and, in the future, that we will more often see them involved as protagonists in these developments.

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SUPPLEMENTARY MATERIALS

Appendix S1. Queries on the Web of Science.

Appendix S2. List of information collected for ant, ground beetle and spider papers selected.

Figures S1–S5. Spatial distributions of studied species.

DATA AVAILABILITY

The complete dataset and R code used for the analyses is available on Gitlab (https://gitlab.com/DenisLafage/sdm_review).

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TABLES

Table 1: Number of articles returned by the queries on Web Of Science (WOS) and number of articles kept after title, keywords and abstract screening.

Group	# papers WOS	# papers kept
Spiders (Araneae)	74	55
Ground beetles (Carabidae)	32	24
Ants (Formicidae)	108	51
Other arachnids	37	34
Mites and ticks (Acari)	159	110
Molluscs (Gasteropoda)	164	121
Flies (Diptera)	454	320
Grasshoppers and crickets (Orthoptera)	59	34
Beetles other than Carabidae (Coleoptera)	313	183
Butterflies (Lepidoptera)	391	253
Dragonflies and damselflies (Odonata)	50	42
Bees (Apoidea)	116	81
Reptiles (Reptila)	529	347
Amphibians (Amphibia)	652	412
Mammals (Mammalia)	854	617
Birds (Aves)	1411	930

Table 2: Percentage of studies predicting distribution in the past, present and future, using different types of predictor variables and where a given predictor variable type was selected in the best models (values in brackets).

		Ants	Ground beetles	Spiders
Projection	Past	10.7	22.2	21.4
	Present	87.5	61.1	96.4
	Future	28.6	22.2	19.6
Predictor variables	Climate	92.9 (100)	77.8 (100)	98.2 (100)
	Soil	19.6 (65)	27.8 (100)	10.7 (80)
	Geology	5.4 (0)	11.1 (0)	10.7 (33.3)
	Topography	25.0 (73.6)	27.8 (100)	41.1 (80)
	Habitat	28.6 (73.9)	38.9 (100)	21.4 (80)
Mechanistic explanations	Species traits	8.9	0.0	3.6
	Ecophysiology	5.5	0.0	0.0

FIGURE CAPTIONS

Figure 1: Cumulative number of articles per year. a) Comparison between arthropods and vertebrates; b) comparison between main arthropod groups.

Figure 2: Production of studies per country for the three groups. Papers were attributed to a country based on the affiliations of the authors using the *bibliometrix* package.

Figure 3: Weighted co-citation network for the top 30 cited papers in the entire data set (ants, ground beetles and spiders). The size of the vertex is proportional to the number of articles citing a given reference. The colours of the links and vertex reflect citation clusters. The colour of the text corresponds to the paper theme.

Figure 4: Collaboration network between authors. Colours represent clusters of collaboration and pictograms the group targeted. For readability, the network is restricted to those papers with at least one author having two articles in the data set. This represents 64 articles (out of 103) and 211 authors (out of 355).

Figure 5: Number of articles using a given algorithm for species distribution models by year and group. To improve readability, only algorithms used at least five times in the entire data set are shown. ANN: artificial neural network; CT: classification tree; FDA: flexible discriminant analysis; GAM: generalized additive model; GARP: genetic algorithm for rule-set production; GBM: generalized boosting model; GLM: generalized linear model; MARS: multiple adaptive regression spline; MaxEnt: maximum entropy.

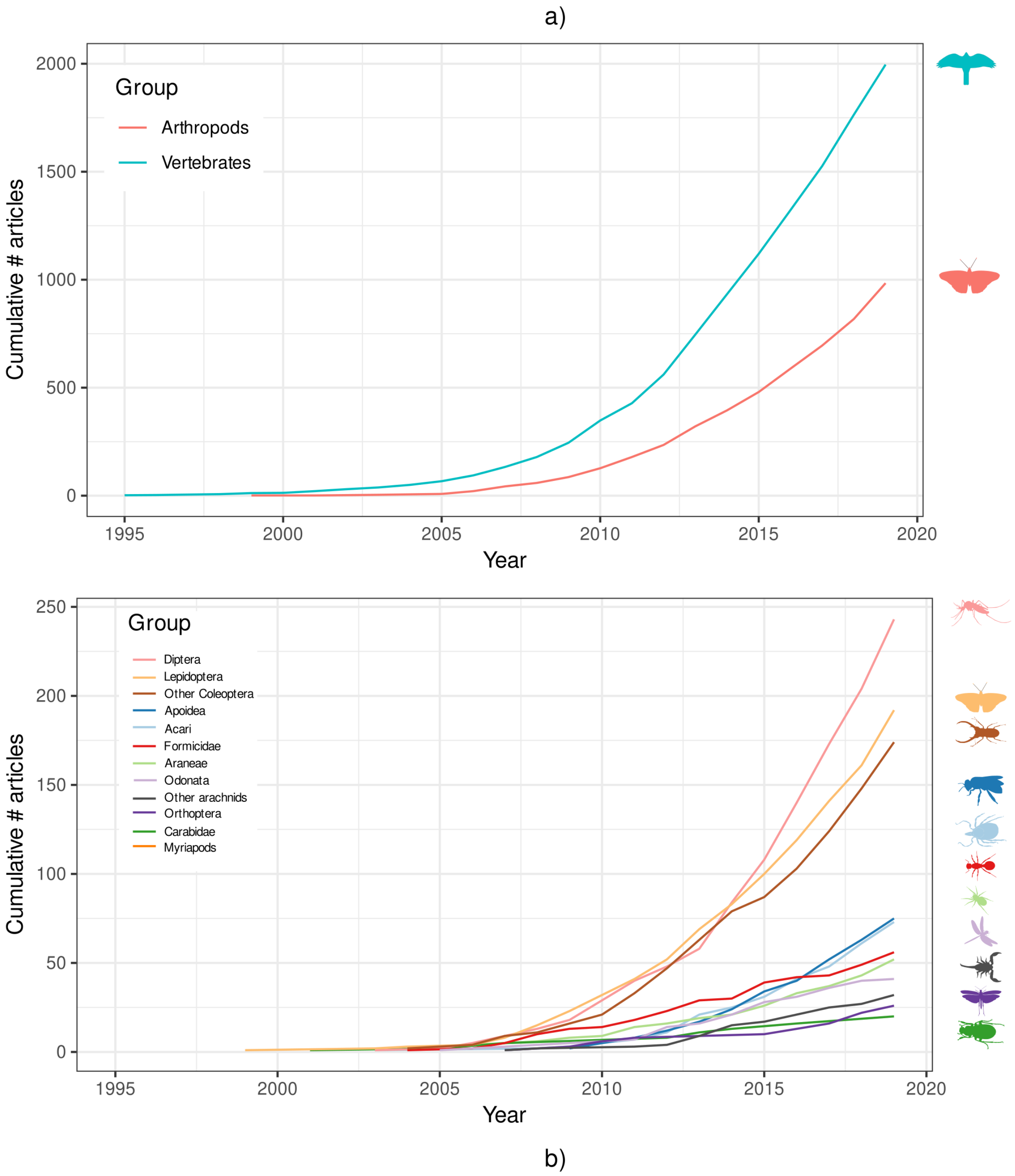
a)
Group
Arthropods
Vertebrates
Cumulative # articles
2000
1500
1000
500
0
1995
2000
2005
2010
2015
2020
Year
Group
Diptera
Lepidoptera
Other Coleoptera
Apoidea
Acari
Formicidae
Araneae
Odonata
Other arachnids
Orthoptera
Carabidae
Myriapods
Cumulative # articles
250
200
150
100
50
0
1995
2000
2005
2010
2015
2020
Year
b)

Figure 1

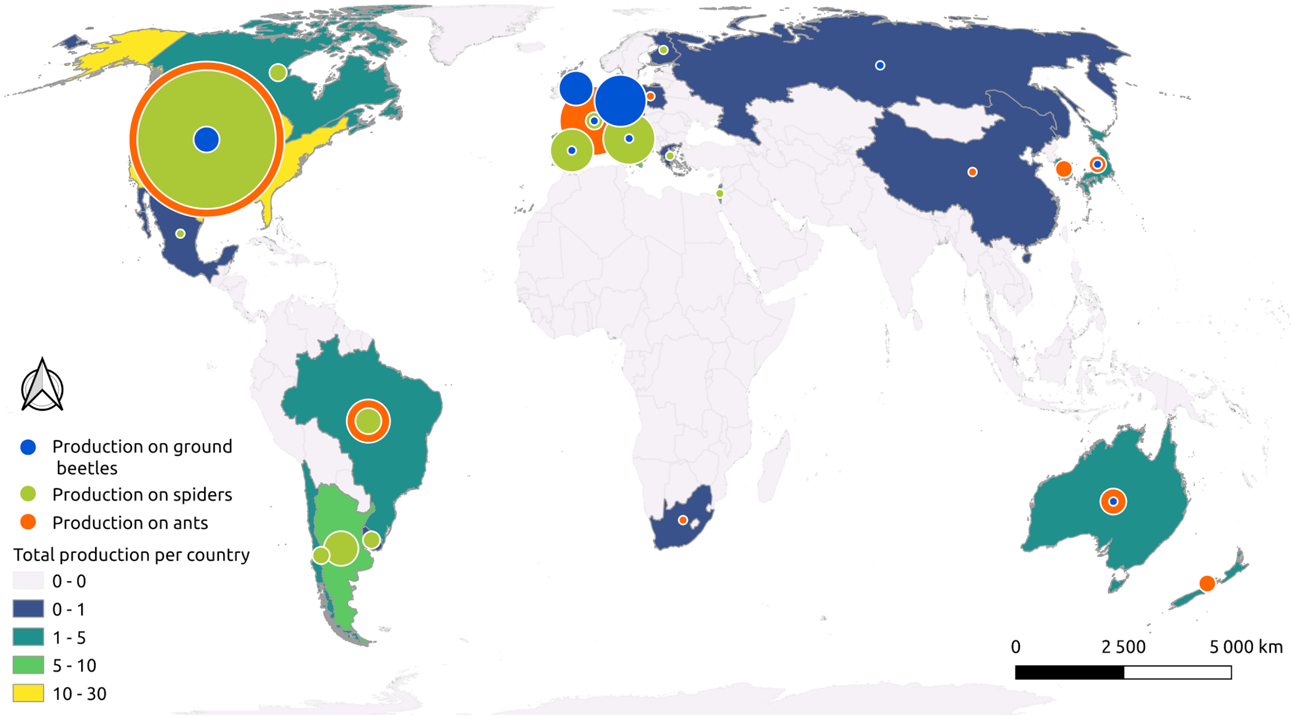
Production on ground beetles
Production on spiders
Production on ants
Total production per country
0 - 0
0 - 1
1 - 5
5 - 10
10 - 30
0
2 500
5 000 km

Figure 2

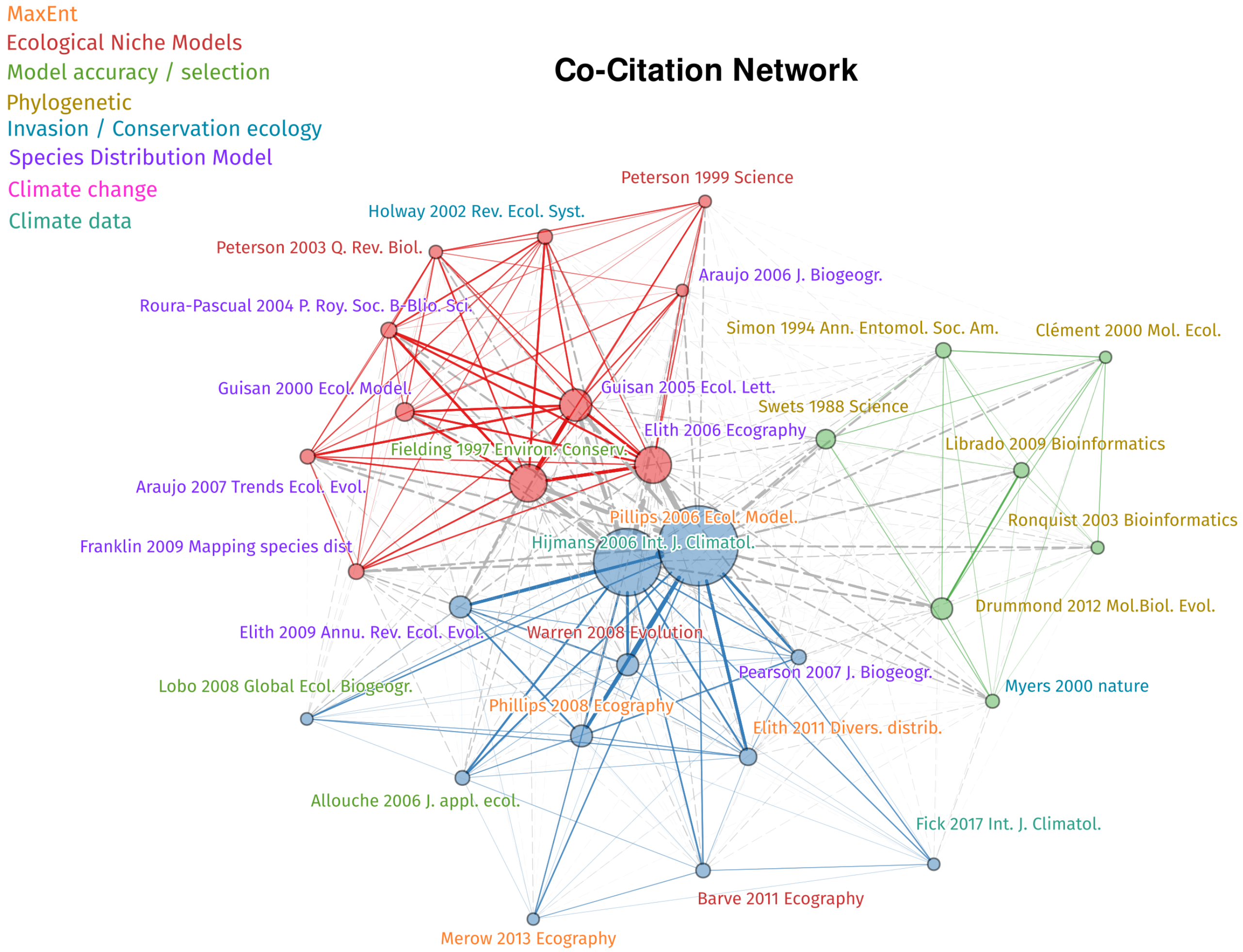
MaxEnt
Ecological Niche Models
Model accuracy / selection
Phylogenetic
Invasion / Conservation ecology
Species Distribution Model
Climate change
Climate data
Co-Citation Network
Peterson 1999 Science
Holway 2002 Rev. Ecol. Syst.
Peterson 2003 Q. Rev. Biol.
Araujo 2006 J. Biogeogr.
Roura-Pascual 2004 P. Roy. Soc. B-Blio. Sci.
Simon 1994 Ann. Entomol. Soc. Am.
Clément 2000 Mol. Ecol.
Guisan 2000 Ecol. Model.
Guisan 2005 Ecol. Lett.
Swets 1988 Science
Elith 2006 Ecography
Librado 2009 Bioinformatics
Fielding 1997 Environ. Conserv.
Araujo 2007 Trends Ecol. Evol.
Pillips 2006 Ecol. Model.
Ronquist 2003 Bioinformatics
Hijmans 2006 Int. J. Climatol.
Franklin 2009 Mapping species dist
Drummond 2012 Mol.Biol. Evol.
Elith 2009 Annu. Rev. Ecol. Evol.
Warren 2008 Evolution
Pearson 2007 J. Biogeogr.
Lobo 2008 Global Ecol. Biogeogr.
Myers 2000 nature
Phillips 2008 Ecography
Elith 2011 Divers. distrib.
Allouche 2006 J. appl. ecol.
Fick 2017 Int. J. Climatol.
Barve 2011 Ecography
Merow 2013 Ecography

Figure 3

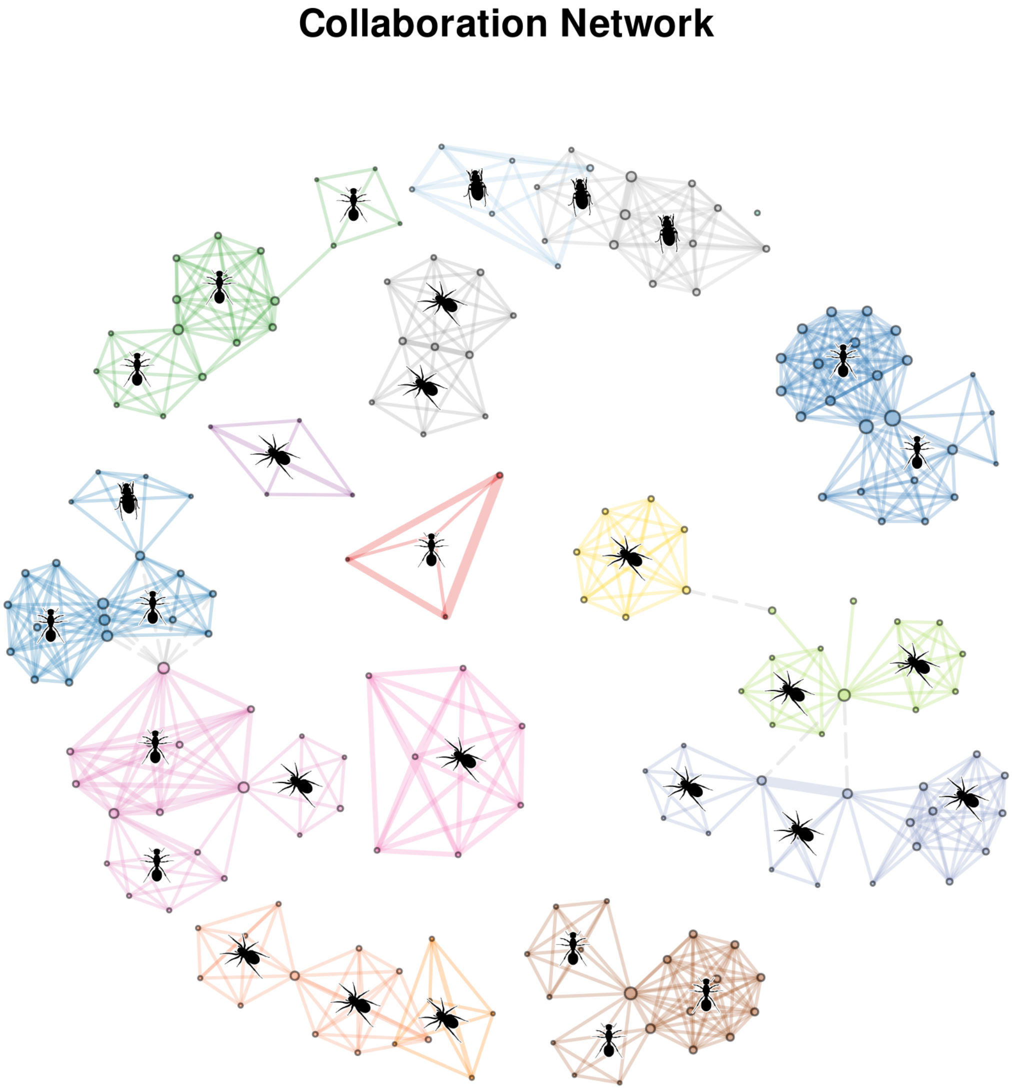

Figure 4

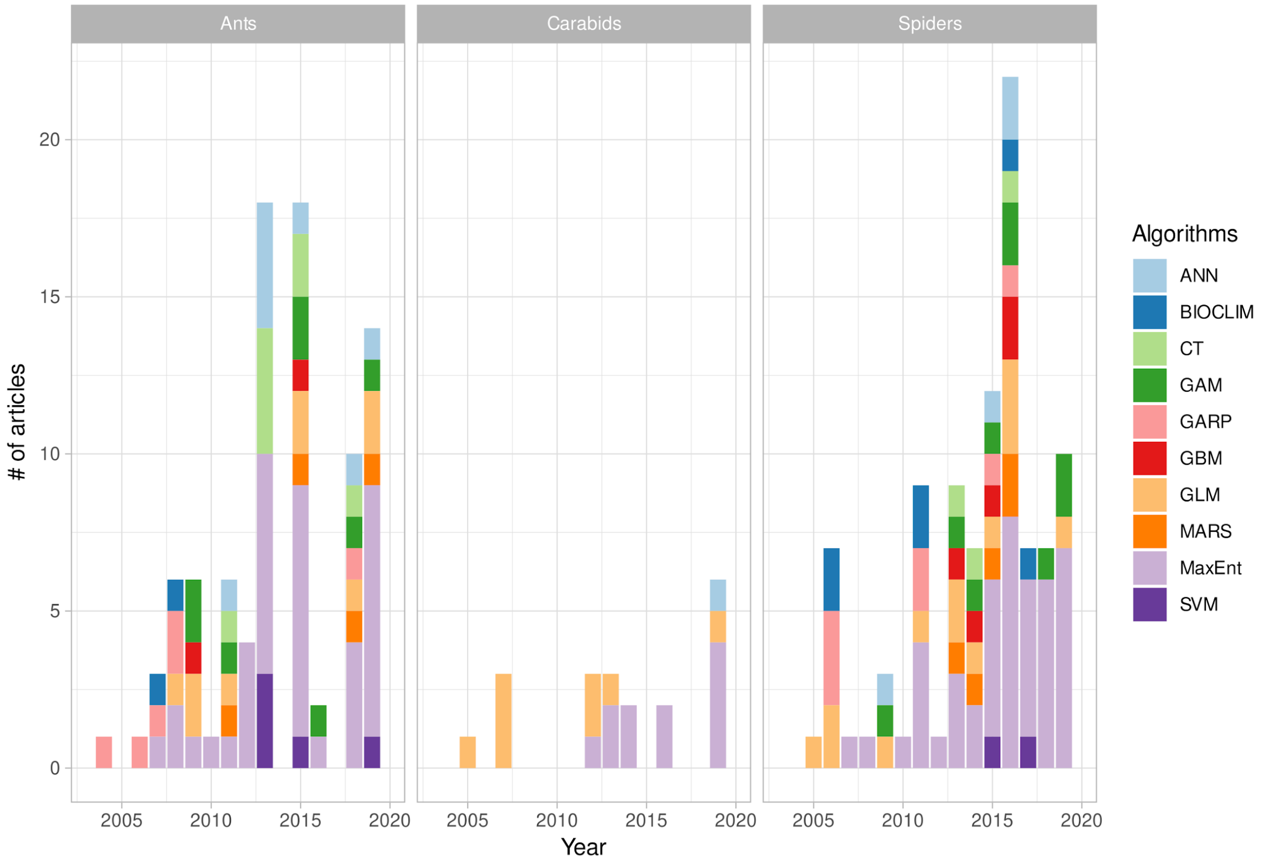
Ants
Carabids
Spiders
# of articles
0
5
10
15
20
2005
2010
2015
2020
Year
Algorithms
ANN
BIOCLIM
CT
GAM
GARP
GBM
GLM
MARS
MaxEnt
SVM

Figure 5

SUPPLEMENTARY MATERIAL FOR

Challenges and opportunities of species distribution modeling in terrestrial arthropods

Mammola et al.

Appendix S1. Queries on the Web of Science. Queries were made between 20 and 24 November 2020. TS denotes search for "Topic" and the asterisk (*) is a regular expression indicating to match all words including that string of characters (for example, "spider*" matches "spider", "spiders", "spiderling(s)", etc.).

- **Acari**: TS= ("Acari" or "tick" or "mites") AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR "Niche model*" OR "Distribution model*" OR "Habitat suitability model*")

- **Amphibians**: TS= ("amphib*" or "anura" or "urodela" or "caudata" or "frog*" or "salamander*" or "newt*") AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR "Niche model*" OR "Distribution model*" OR "Habitat suitability model*")

- **Ants**: TS= ("Formicidae" OR "Ants" OR "Ant") AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR "Niche model*" OR "Distribution model*" OR "Habitat suitability model*")

- **Bees**: TS= ("Apoidea*" OR "bee" or "bees") AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR "Niche model*" OR "Distribution model*" OR "Habitat suitability model*")

- **Birds**: TS= ("bird*" or "aves") AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR "Niche model*" OR "Distribution model*" OR "Habitat suitability model*")

- **Butterflies**: TS= ("butterfl*" OR "lepidoptera*" or "moth*) AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR "Niche model*" OR "Distribution model*" OR "Habitat suitability model*")

- **Coleoptera except ground beetles**: TS= ("beetle*" OR "coleoptera" NOT "Carabidae" NOT "Carab*") AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR "Niche model*" OR "Distribution model*" OR "Habitat suitability model*")

- **Diptera**: TS= ("diptera*" OR "fly" OR "flies" OR "mosquitoe*" or "midge*" or "gnats") AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR “Niche model*” OR “Distribution model*” OR “Habitat suitability model*”)

- **Gasteropoda**: TS= ("Gastropod*" or “snail*” or “slug*”) AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR “Niche model*” OR “Distribution model*” OR “Habitat suitability model*”)

- **Ground beetles**: TS= ("Carabidae*" OR "Carabid*") AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR “Niche model*” OR “Distribution model*” OR “Habitat suitability model*”)

- **Mammals**: TS= ("mammal*" or "Monotremata" or "Dermoptera" or "Chiroptera" or "Primates" or "Pholidota" or "Lagomorpha" or "Rodentia" or "Carnivora" or "Tubulidentata" or "Proboscidea" or "Hyracoidea" or "Perissodactyla" or "Artiodactyla" or "Didelphimorphia" or "Scandentia" or "Paucituberculata" or "Microbiotheria" or "Dasyuromorphia" or "Peramelemorphia" or "Notoryctemorphia" or "Diprotodontia" or "Macroscelidea" or "Afrosoricida" or "Erinaceomorpha" or "Soricomorpha" or "Cingulata" or "Pilosa") AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR “Niche model*” OR “Distribution model*” OR “Habitat suitability model*”)

- **Myriapods**: TS= ("Chilopod*" or "Centiped*" or "Myriapod*" or "Milliped*" OR "Diplopod*" OR Pauropod* OR "Symphyl*" OR "pseudocentiped*") AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR “Niche model*” OR “Distribution model*” OR “Habitat suitability model*”)

- **Odonates**: TS= ("Odonat*" OR "dragonfl*" OR "damselfl*") AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR “Niche model*” OR “Distribution model*” OR “Habitat suitability model*”)

- **Orthoptera**: TS= ("Orthoptera*" OR "Grasshopper*" or "locust*" or "cricket*") AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR “Niche model*” OR “Distribution model*” OR “Habitat suitability model*”)

- **Other arachnids**: TS= ("Opilion*" OR "Scorpion*" OR "Pseudoscorpio*" OR "Amplypyg*" OR "Solifug*" OR "Palpigrad*" OR "whip scorpion*" OR "Microwhip scorpion*" OR "harvestman" OR "camel spider*" OR "wind scorpion*" OR "sun spider*" OR "solifug*") AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR “Niche model*” OR “Distribution model*” OR “Habitat suitability model*”)

- **Reptila:** TS= ("reptil*" or "snake*" or "lizard*" or "turtle*" or "crocodyl*" or "squamata") AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR “Niche model*” OR “Distribution model*” OR “Habitat suitability model*”)

- **Spiders**: TS= (“Araneae” OR “Spider*”) AND TS=("Species distribution model*" OR "Ecological niche model*" OR "Bioclimatic envelope model*" OR "MaxEnt" OR “Niche model*” OR “Distribution model*” OR “Habitat suitability model*”)

Appendix S2: List of information collected for ant, ground beetle and spider papers selected.

Article information	CODE	Arbitrary code relating paper to taxa information
	TITLE	Article title
	JOURNAL	Journal in which the paper was published
	DOI	Digital Object Identifier
	AUTHORS	List of authors
	YEAR	Year of publication
	GEOGRAPHIC AREA	Area covered by the SDM
	PURPOSE	Purpose of the paper
	MODELLING_ALGORITHM	Modelling algorithm used in the SDM
	MODELLING_APPROACH	Single, ensemble, or no silver bullet approach for algorithm
	PAST_PROJECTION	Past projection of the distribution (0/1)
	PRESENT_PROJECTION	Present projection of the distribution (0/1)
	FUTURE_PROJECTION	Future projection of the distribution (0/1)
	CLIMATIC_VAR	Climatic variables used as predictors (0/1)
	GEOLOGICAL_VAR	Geological variables used as predictors (0/1)
	SOIL_VAR	Soil variables used as predictors (0/1)
	HABITAT_VAR	Habitat variables used as predictors (0/1)
	TOPOGRAPHIC_VAR	Topographic variables used as predictors (0/1)
	HISTORICAL_VAR	Historical variables used as predictors (0/1)
	BIOTIC_INTERACTIONS_VAR	Biotic interactions effect included in the SDM (0/1)
	VAR_RESOLUTION	Predictor variables resolution
	TRAITS	Species traits included in the SDM
	PHYLOGENETIC_DATA	Phylogenetic data used in the paper
	ECOPHYSIOLOGICAL_DATA	Ecophysiological variables used in the paper
	NOTES	Remarks
Taxa information	CODE	Arbitrary code relating paper to taxa information
	FAMILY	Family of the species studied
	GENUS	Genus of the species studied
	SPECIES	Species studied
	ENDEMIC	Is the species studied endemic of the area (0/1)
	ALIEN	Is the species studied considered by the authors as alien
	HABITAT	Species habitat
	PAST_SHIFT	Is the past distribution larger/shifted than the present (0/1)
	PAST_SMALLER	Is the past distribution smaller than the present (0/1)
	FUTURE_DECLINE	Is the future distribution smaller than the present (0/1)
	FUTURE_SHIFT	Is the distribution forecasted to shift compared to the present (0/1)
	FUTURE_EXPANSION	Is the future distribution larger than the present (0/1)
	CLIMATIC_VAR_SEL	Were climatic variables selected among the best predictors (0/1)
	GEOLOGICAL_VAR_SEL	Were geological variables selected among the best predictors (0/1)
	SOIL_VAR_SEL	Were soil variables selected among the best predictors (0/1)
	HABITAT_VAR_SEL	Were habitat variables selected among the best predictors (0/1)
	TOPOGRAPHIC_VAR_SEL	Were topographic variables selected among the best predictors (0/1)
	HISTORICAL_VAR_SEL	Were historical variables selected among the best predictors (0/1)
	BIOTIC_INTERACTIONS_VAR_SEL	Were biotic variables selected among the best predictors (0/1)
	NOTES	Remarks

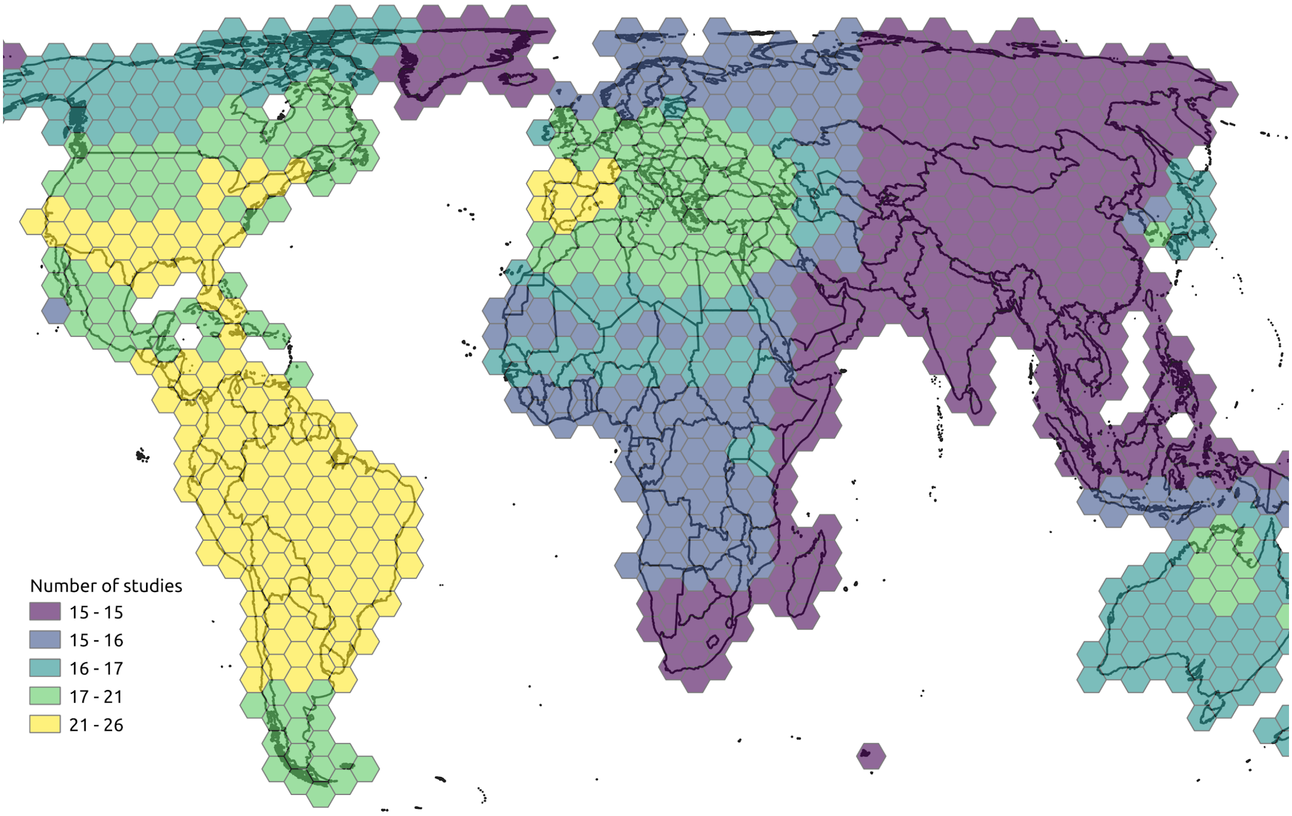

Figure S1. Distribution of the number of ant studies (for 250 km side hexagon). For each study the distribution of each species resulting from SDM were mapped on the hexagon grid.

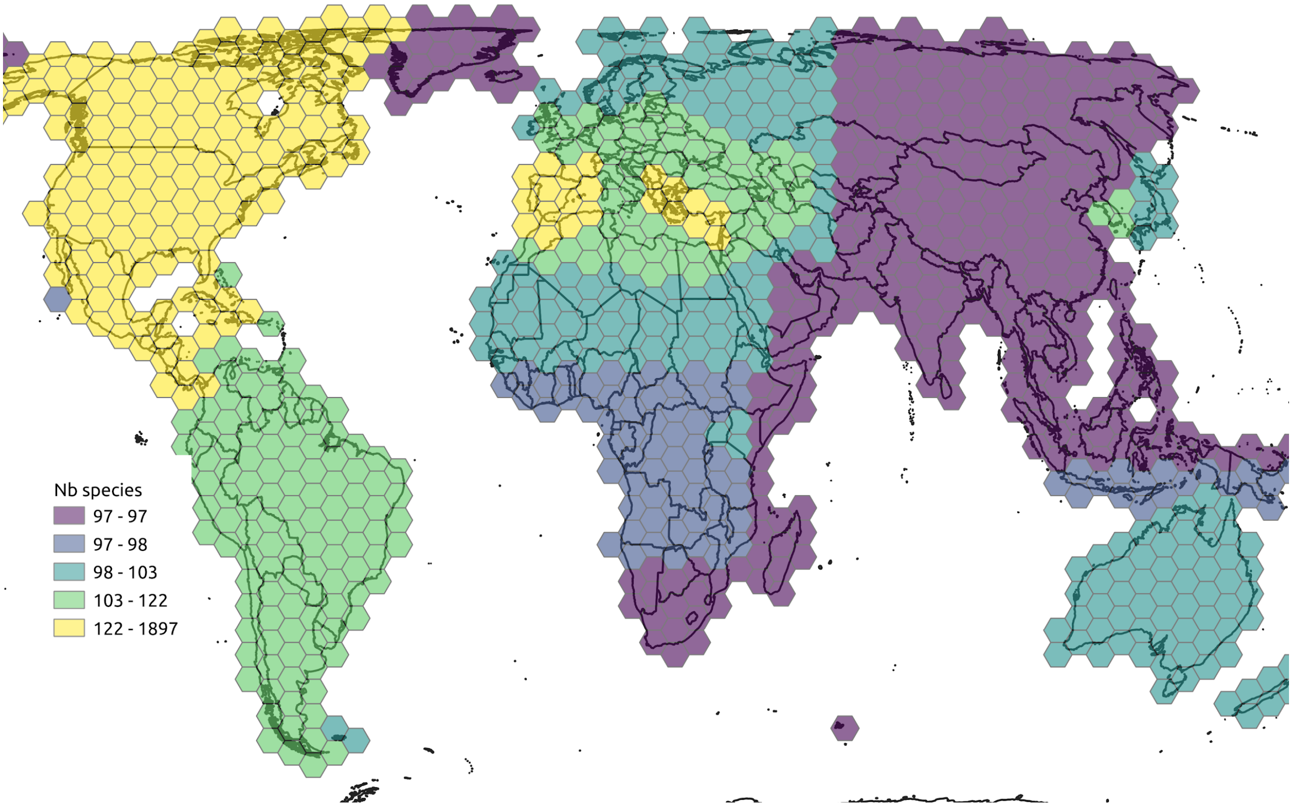

Figure S2. Distribution of the number of ant species (for 250 km side hexagon). For each study the distribution of each species resulting from SDM were mapped on the hexagon grid.

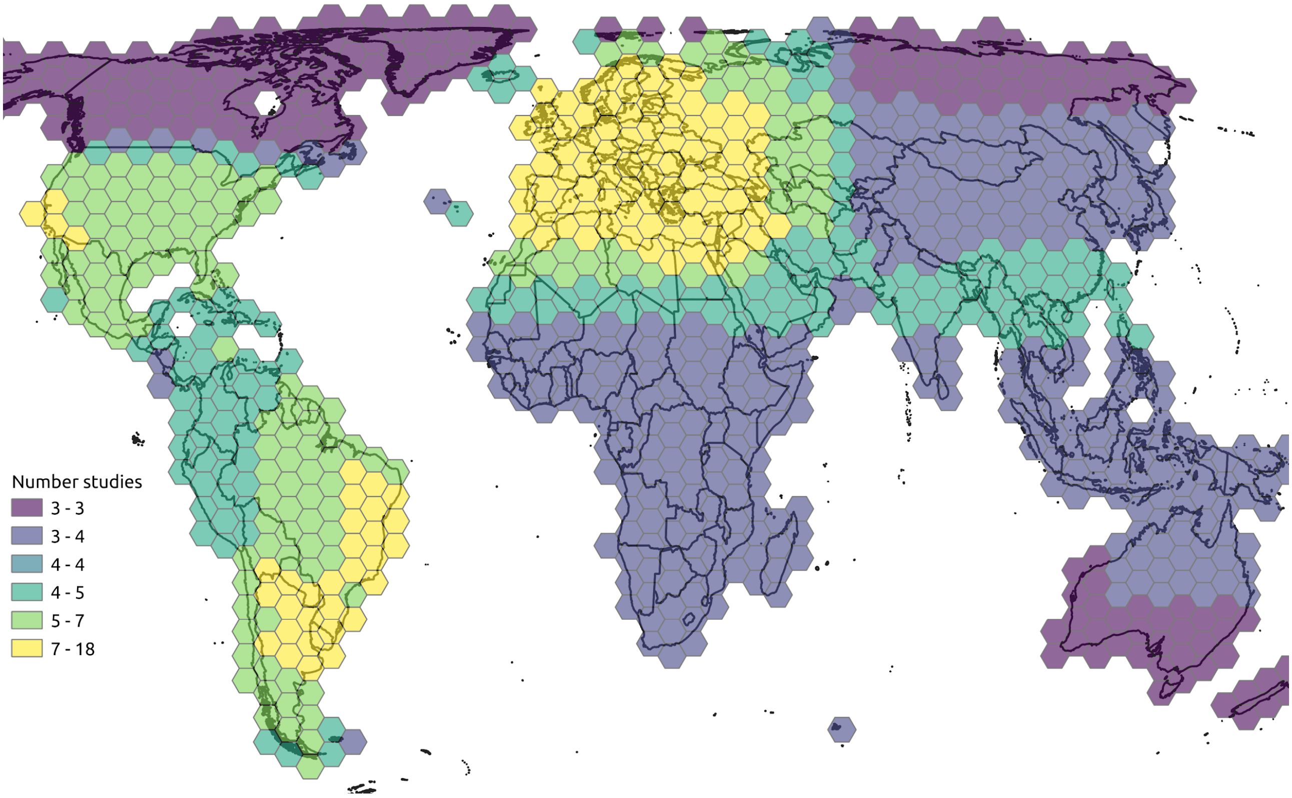

Figure S3. Distribution of the number of spider studies (for 250 km side hexagon). For each study the distribution of each species resulting from SDM were mapped on the hexagon grid.

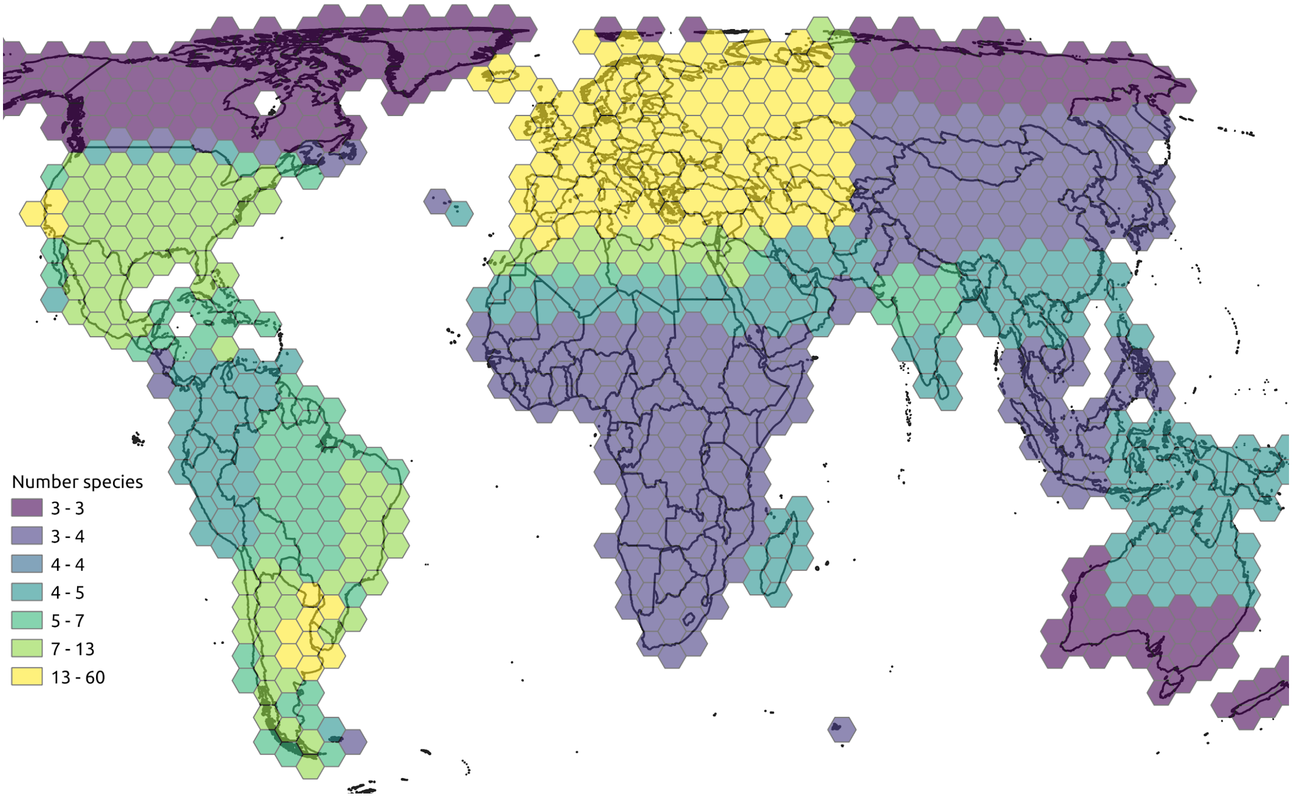

Figure S3. Distribution of the number of spider species (for 250 km side hexagon). For each study the distribution of each species resulting from SDM were mapped on the hexagon grid.

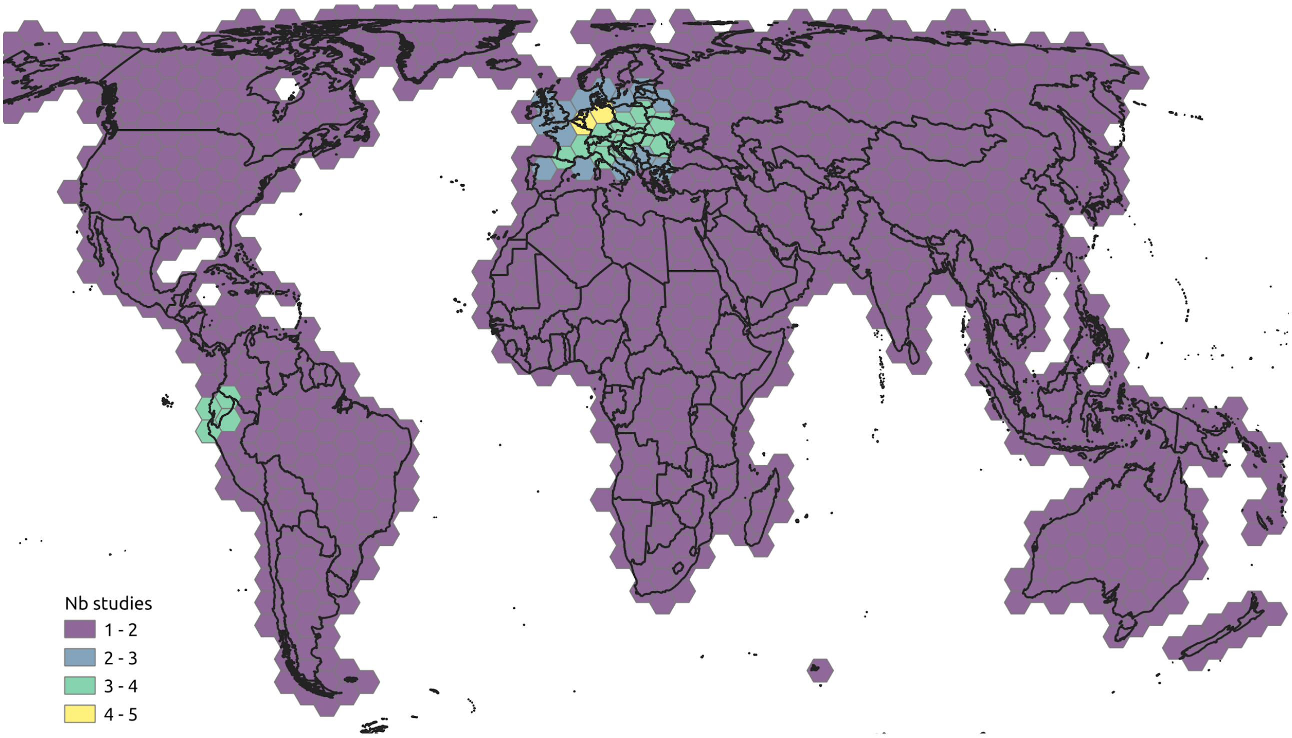

Figure S4. Distribution of the number of ground beetles studies (for 250 km side hexagon). For each study the distribution of each species resulting from SDM were mapped on the hexagon grid.

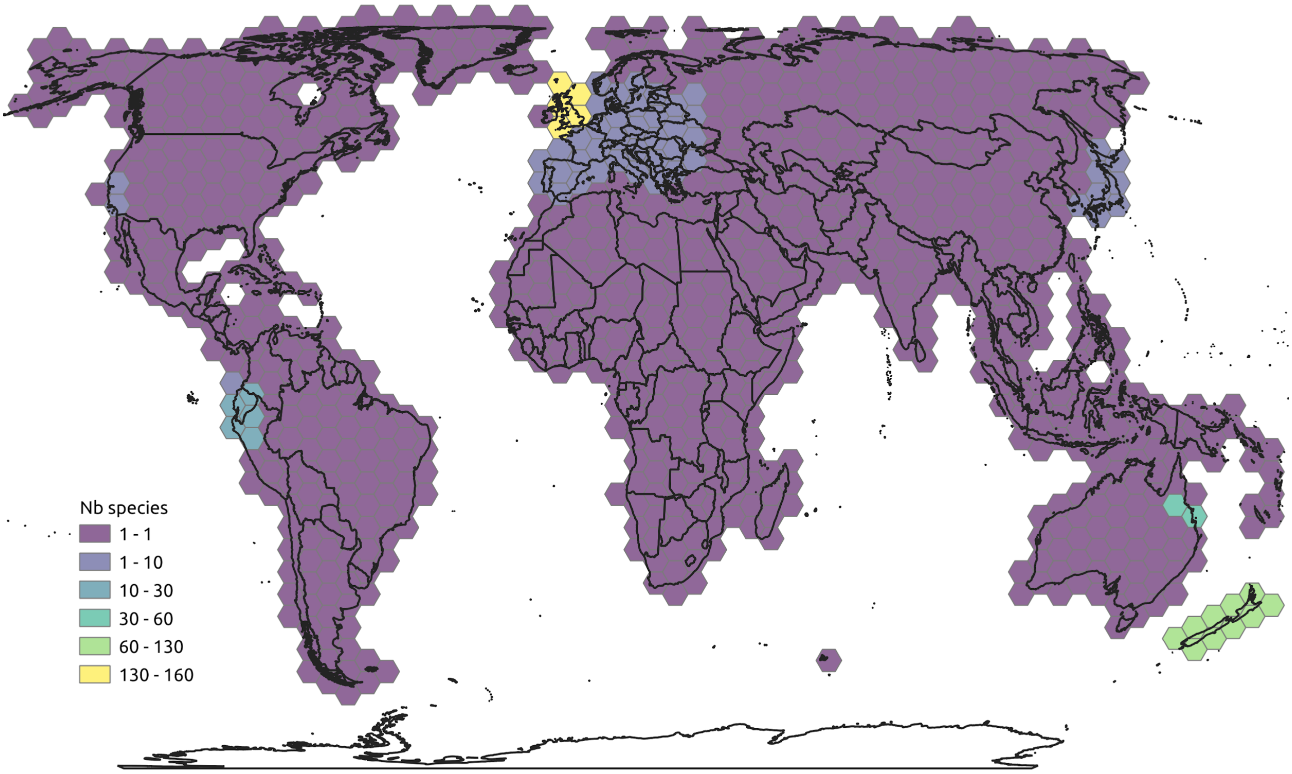

Figure S5. Distribution of the number of ground beetles species (for 250 km side hexagon). For each study the distribution of each species resulting from SDM were mapped on the hexagon grid.

Paper II

Characterization of habitat requirements of European fishing spiders

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Abstract

Wetlands are among the most threatened habitats in the world, and so are their species, which suffer habitat loss due to climate and land use changes. Freshwater species and arthropods receive little attention in research and conservation, and the goals to stop and reverse the destruction of wetlands published 25 years ago in a manifesto by the Union of Concerned Scientists have not been reached. In this study, we investigated the occurrence and habitat requirements at two spatial scales of two species of European fishing spiders *Dolomedes*, which rely heavily on declining wetland habitats in Sweden and southern Norway. We collected occurrence data for *Dolomedes plantarius* and *Dolomedes fimbriatus*, using a live-determination-method. We modelled the placement of nursery webs to describe fine scaled habitat requirements related to vegetation and microclimate. Using a machine learning approach, we described the habitat features for each species, and for co-occurrence sites, to provide insight into variables relevant for the detectability of *Dolomedes.* We found that habitat requirements were narrower for *D. plantarius* compared to *D. fimbriatus*; that the detection of nursery webs can be affected by weather conditions and that nursery placement is mostly dependent on the proximity to water, the presence of *Carex sp.* (Sedges) and crossing vegetation structures, and on humidity. Furthermore, co-occurring sites were more similar to *D. plantarius* sites than to *D. fimbriatus* sites, whereby surrounding forest, water type and velocity, elevation and latitude were of importance for explaining which species of *Dolomedes* was present. We provide a detailed field protocol for *Dolomedes* studies, including a novel live-determination method, and recommendations for future field protocols.

Keywords: *Dolomedes*, Pisauridae, detectability, red listed species, conservation

Introduction

Biodiversity is threatened by anthropogenic land use and climate changes (Sala et al., 2000), and especially wetlands species are declining rapidly together with their habitats. Yet wetlands are particularly important ecosystems in terms of climate change mitigation, biodiversity by providing breeding and feeding grounds for many species, and hydrology through flood regulation, water holding bodies, and nutrient retention. Thereby, wetlands are crucial to human existence (De Groot et al., 2006). The Ramsar Convention (Ramsar, 2013) and the first world's scientists warning to humanity (Kendall, 1992) formulated wetland conservation as a global goal. However, Finlayson et al. (2019) stated that not only wetland protection and restoration goals were not reached, but that wetlands destruction and loss have proceeded. Conservation priorities are mostly determined through variable and dynamic human values (Lindenmayer & Hunter, 2010), which has led to unequal conservation efforts across habitats and taxa, with groups like invertebrates (Clark & May, 2002; Finlayson et al., 2019) and freshwater/wetland species being particularly neglected (Darwall et al., 2011). Other issues interact with and add to this: the difficult accessibility of wetlands and the low detection of invertebrates (Noreika et al., 2015) cause bias across habitats and taxa. Yet, according to a review by Kellner & Swihart (2014), few studies accounted for imperfect detection, and even less often in invertebrate studies than in studies of other taxa.

Although Clark & May (2002) recognized the taxonomic imbalance of research almost 20 years ago, basic knowledge is still missing to inform conservation of invertebrates inhabiting wetlands. This knowledge is lacking for the two European fishing spiders, namely *Dolomedes fimbriatus* and *Dolomedes plantarius*. Both species are semi-aquatic, forage on land as well as on water, and build their nursery webs close to or even above the water surface (Duffey, 2012; Gorb & Barth, 1994). The detection of both species is difficult due to their lifestyle, which includes fleeing behavior on and under the water surface when disturbed (Gorb & Barth, 1994). *Dolomedes* do not construct webs to capture prey, which makes individuals even more difficult to detect. But like other members of the Pisauridae family, *Dolomedes* build nursery webs (Stratton et al., 2004), which are a convenient sign of presence during the reproductive season, thus facilitating their detection. Females are found close to their nursery webs, which is useful for identification, mainly because only adults can be identified with certainty by inspecting their genitals (Roberts, 1995). Further, the placement of nursery webs functions as an important indicator for *Dolomedes* habitat determining reproductive success and survival.

Habitats of both species are declining because of anthropic transformation and draining of wetlands (Finlayson et al., 2019; Hu et al., 2017; van Helsdingen, 1993). While *D. fimbriatus* is relatively common (Duffey, 2012), *D. plantarius* is much rarer, and is one of the few red-listed spiders in Europe, despite its fairly broad distribution range (Leroy et al., 2013, 2014). Naturalist observations suggest that *D. plantarius* has more specific habitat requirements than *D. fimbriatus* (Duffey, 2012). Habitat loss might have more severe consequences for *D. plantarius*, which has less plasticity, thus making it a species of conservation interest (Smith, 2000). Investigating the population decline is difficult, as historical distribution data of *Dolomedes* are scarce (Duffey, 2012). Some authors suggest that there may be denser populations of *D. plantarius* than known, especially in the less monitored areas in eastern Europe (in Belarus: Ivanov et al., 2017). Additionally, misidentifications of the two species were common in the first half of the 20th century, when body color was used for determination, although it is not a reliable indicator for the discrimination of both species (Bonnet, 1930; van Helsdingen, 1993). Little monitoring combined with potential misidentifications and difficult detection of *Dolomedes* caused an overall lack of knowledge about the distribution and status of the species. Recent observations indicate that co-occurrence, which was considered rare or even impossible, might be more frequent than previously thought (Ivanov et al., 2017).

In this study, we contribute to further characterizing the habitat requirements of the two European Dolomedes species. Based on naturalist observations by van Helsdingen (1993), Duffey (1995), and Duffey (2012), we expect *D. fimbriatus* to be more flexible than *D. plantarius* in its habitat requirements regarding the presence of water, and the specific characteristics of the aquatic habitat. We also expect *D. fimbriatus* to occur at higher altitudes and latitudes due to less restricted temperature requirements, and to tolerate more acidic terrestrial habitats, which would facilitate its presence in mires, bogs, and near coniferous forest.

Material and Methods

Study Area and Site Choice

In order to find potential *Dolomedes* habitats, we chose our study sites based on prior observations extracted from the GBIF: The Global Biodiversity Information Facility (2021) using the R package rgbif (Chamberlain & Boettiger, 2017) and based on the habitat suitability map of *D. plantarius* from Leroy et al. (2014). Because the resolution of the suitability map and the accuracy of the GBIF positions were too low for our purpose, we selected sampling areas within the highly suitable habitat and close to the GBIF positions based on information from the literature.

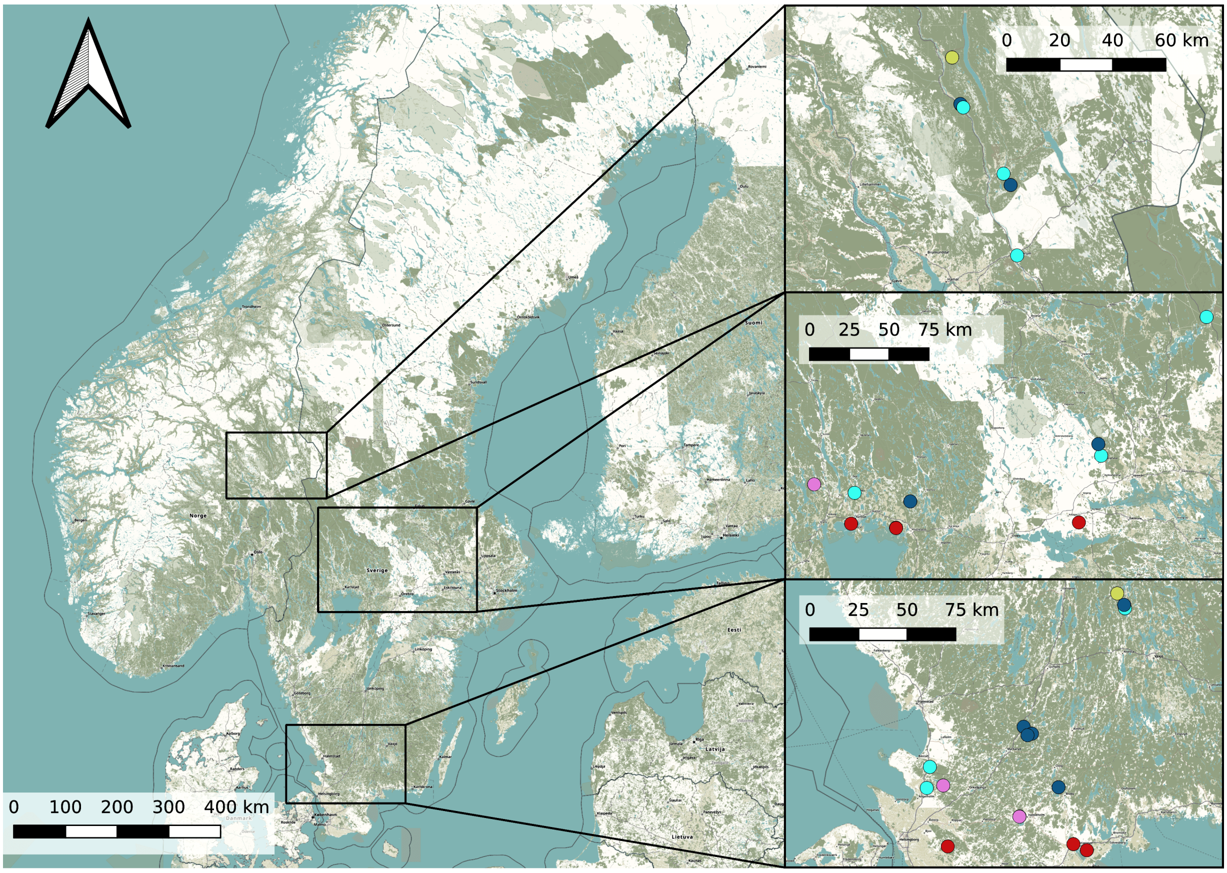

Figure 1: Overview map of the study area in Sweden and Norway (left) with detail maps of the three study areas (right). Dots represents the study sites (Pink: both species; red: *D. plantarius*; green: *D. fimbriatus*; blue: absence sites; light green: *Dolomedes sp.*) The background map is obtained from OpenStreetMap

We chose water bodies with riparian vegetation and other types of wetlands (bogs, fens, meadows) for data collection (Duffey, 1995, 2012; van Helsdingen, 1993). Because the model by Leroy et al. (2014) is only valid for *D. plantarius*, we assessed the potential suitability for *D. fimbriatus* based on the visual impression we had of the wetland during a visit. The selected locations and the detected species are shown in Figure 1.

Data Collection

We collected and geo-referenced all data using the data collection software KoBoToolbox (KoBoToolbox, 2020). We collected habitat data at site and microhabitat scales. We

Table 1: Levels and explanations of variables on landscape / site scale

Variables	Levels
Surrounding	Infrastructure/forest/other
Surrounding forest	Deciduous/coniferous/mixed
Water type	River/bog/lake/creek
Water speed	Standing/slow/fast
Water clearness	Clear/brown/murky
Vegetation type (at site)	Open wet/open dry/deciduous forest/coniferous forest
Latitude	Latitude (continuous), DEM
Elevation	Elevation (continuous), DEM
Clouds (detectability)	Yes/no/partly
Wind (detectability)	Measured with anemometer on Beaufort scale
Reason visit	Suitable habitat/GBIF/other

determined and recorded species of *Dolomedes* at the site scale. We delimited each study site by its natural borders, or, if too big, after five transects; i.e. 40 m along the water body, see transect description below.

Site Scale Data Since the detectability of free-ranging spiders varies with weather conditions (Noreika et al., 2015), we recorded temperature and wind speed, and visually classified rain and clouds at the beginning of each field work session. In case of wind (Beaufort scale > 3, equivalent to 12- 19 km/h wind speed) or rain, we did not attempt to detect the spiders, to keep detection conditions equal.

We searched for nursery webs and spiders for 20 minutes on each site (some spiders/nurseries were also found during the transects, which increased the duration of effective search). If possible, we searched the edge of the vegetation both visually and by sweep-netting, while wading through the water. If entering the water was not possible (e.g., due to quality of the substrate, the strength of stream or water depth), we moved carefully across the riparian vegetation to the contact zone of marginal

Table 2: Braun Blanquet scale and simplification used in this study.

Percentage	Number of occurences	Original Braun Blanquet category	Simplified category
0	0	no	
<1	1	r	0
<1	2-5	+	
<5	6-50	1	
<5	>50	2m	1
5-15	arbitrary	2a	
26-25	arbitrary	2b	
26-50	arbitrary	3	2
51-75	arbitrary	4	3
76-100	arbitrary	5	4

vegetation and water and applied the same search strategy. We found most adult females in nursery webs or in the nearby vegetation, or on the water. We captured the spiders in a glass container. If the spider dived, we caught it with a fishing net (mesh size approximately 0.9X0.3 mm) from the water and transferred it into a glass container.

Once inside the container, we determined the species by pressing the individual gently with a soft sponge against the glass, to inspect the epigyne or pedipalps (A picture of the identification process is available in Appendix S1). We released all spiders after identification. If we detected only nursery webs but no spider on a site, we discarded the data, as the nursery web of *Pisaurida mirabilis* cannot safely be distinguished from the web of *Dolomedes*. We collected variables regarding vegetation type, land use and surroundings at site level (Table 1). As *Dolomedes* are semi-aquatic species, measurements on plot level were concentrated around the water body or in the 'wet center' of study sites without open water, from where we drew transects for further data collection plots.

Table 3: Levels and explanations of variables on microhabitat / nursery scale. BB: Braun Blanquet

Variables	Levels
Spiders detection	Spider/nursery web/no
Aquatic vegetation	Braun-Blanquet scale
Distance to water	No water; 0m; 0.7m; 2m; 7m
Humidity	Measured at ground level and 20cm above ground
Dominant plant group	Dominant group of plants in plot
Horizontal cover	Measured at 10cm; 30cm; 50 cm above ground
Maximum height	Maximal height of vegetation in plot, measured with 10cm accuracy
Average height	Measured 5 times in random location within plot with 10cm accuracy
Tussocs	Tuft of grasses or sedges, measured on BB scale
Large leaves	Yes/no
Litter	Yes/no
Shade	Yes/no/partly
Crossing structures	Abundance of crossing vegetation structures, measured on BB scale
Carex spp.	Abundance measured on BB scale
Juncus spp.	Abundance measured on BB scale
Typha spp.	Abundance measured on BB scale
Phragmites spp.	Abundance measured on BB scale
Sphagnum spp.	Abundance measured on BB scale
Deciduous plants	Abundance measured on BB scale
Aquatic vegetation	Yes/no
Nursery web detected	Yes/no
Nursery height	Height of web above ground or water
Nursery plant	Host plant of nursery web
Number of nurseries/plot	Number of nursery webs detected in one plot

Microhabitat Data Within each site, we placed up to five transects to systematically arrange sampling plots (Figure 2) to collect microhabitat data. If open water was present, we placed the transects perpendicular to the water body and 10 meters apart. If no open water was present, we placed transects along a wet to dry ground gradient. If no gradient was detectable, the transects started (at random) from a habitat edge, to represent the site of interest. We recorded the applied sampling procedure for each site.

Along each transect, we collected plot-scale data for one aquatic plot (if water was present) at the beginning of each transect and terrestrial circular plots (radius = 1.5

m). Terrestrial plots were located at two, seven and twelve meters from the water edge based on test sites to represent the gradient from aquatic to terrestrial habitat. The focus on the shore-area (or the wettest area in the site) is reflected by the higher density of plots close to the water (Figure 2). We collected data in one to three terrestrial plots, depending on the width of the site. When the riparian vegetation was limited to a few centimeters by the water edge, we included a fourth half-circle (r = 0.5m) terrestrial plot with its center at the water edge to represent the vegetation (see tw plot in Figure 2). The shape of the additional plot differed from the others to avoid plots overlapping. We collected percent cover data for the five most relevant plant species according to literature (*Carex spp.*, *Juncus spp.*, *Typha spp.*, *Phragmites spp.* and *Sphagnum spp.*) on the Braun-Blanquet scale (Westhoff & Van Der Maarel, 1978), which we later reduced for modeling purposes (Table 2). Furthermore, we collected structural and microclimate variables (Table 3). We collected the same measurements around the nursery webs, which we searched for in the entire site. We extracted site elevation after data collection from a digital elevation model (EEA, 2018).

Statistical Analysis

We prepared and analysed all data in R (R Core Team, 2020), and R Studio (RStudio Team, 2012). We followed the protocol for data exploration by Zuur et al. (2010) and used the tidyverse framework for data exploration and preparation (Wickham et al., 2019). We standardized all continuous variables to facilitate model convergence and interpretation.

Site Scale Analysis In order to investigate differences among occupied habitats, we compared sites in which only *D. fimbriatus*, only *D. plantarius*, both species or

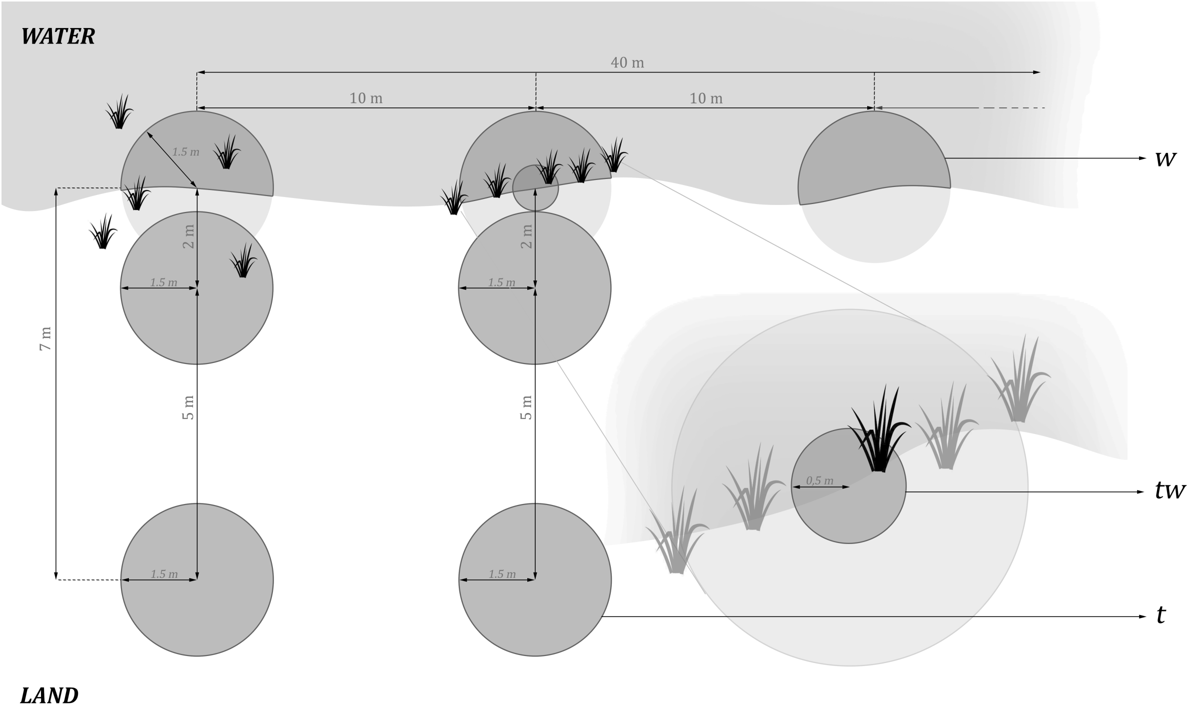

Figure 2: Arrangement of plots transects in a site with open water, i.e. with aquatic plots, a higher density of plots close to the water, and with an additional small terrestrial plot for the narrow riparian vegetation area (middle). w: aquatic plots, tw: plots at the edge of the water, t: terrestrial plots.

no *Dolomedes* and none of both species were detected by using flexible discriminant analysis (FDA, Hastie et al., 1994) using the R package 'mda' (Hastie et al., 2013). We used the *Dolomedes* species detection; i.e. *D. fimbriatus*, *D. plantarius*, both species, or no *Dolomedes* detected, as the response variable in this supervised machine-learning-model. We considered surrounding landscape and forest type, latitude, elevation, water type, water speed, water clearness, and vegetation type as predictors (Table 1).

In addition, we used a single-season occupancy model (MacKenzie et al., 2002) within the unmarked package (Fiske & Chandler, 2011) to predict the nursery detection probability pooled for both species. We used the nursery and plot-scale data as spatial replicates, as an alternative to the usual temporal replicates/detection attempts. We considered weather, microclimatic variables (wind, cloudiness, rain, shade), vegetation structure and sampling related variables as potentially influencing detectability.

Microhabitat Characteristics Around Nursery We modeled nursery presence/absence for sites in which *Dolomedes* presence was verified and in which we found at least one nursery web. Thereby we ensured that the sampling was not temporally unsuitable or the site generally unsuitable, which allowed us to model nursery placement within generally suitable sites.

For variable selection and parameter estimation, we fitted a binomial Generalized Additive Model (GAM) by component-wise boosting, using package mboost (function gamboost, Hothorn et al., 2020). Prior to model fitting, we checked variables correlation and we dropped highly correlated variables accordingly (threshold=0.7, Dormann et al., 2013). We did not consider interactions due to the low sample size. From variables humidity at ground level and humidity at 20 cm above ground level, we kept humidity at ground level. We kept average vegetation height, but we discarded the highly correlated maximum vegetation height. We then fitted a regularized model, following the recommendation in Hofner et al. (2018) using all other predictor variables to identify the most relevant predictors and estimate the model parameters. We validated the model using cross validation and present the final model estimates.

To validate the model, we tested the stability of the selected variables via resampling using the package ‘stabs’ (Hofner & Hothorn, 2017). Stability selection provides a reliable way to find an appropriate level of regularization, to keep variables with high selection probabilities. In our model, we used standard choices of tuning parameters, with a cut-off of 0.75 and the number of falsely selected base learners tolerated of 1 (Meinshausen & Bühlmann, 2010). A conceptual overview of the analyses performed and the data used is presented in Appendix S2-4.

Results

Site Scale Habitat Characteristics – Species Specific

We detected *D. fimbriatus* alone in 12 sites, *D. plantarius* alone in 6 sites, both species together in 4 sites and none of the two species in 9 of the visited sites (total sites: n= 31, Figure 1).

The first axis of the FDA explained 77.33%, the second axis 14.12% (Figure 3). The main variables loading onto the FDA axes, i.e., discriminating best between sites with none/both/each species, were water type and surrounding forest on the first axis, and water speed on the second axis.

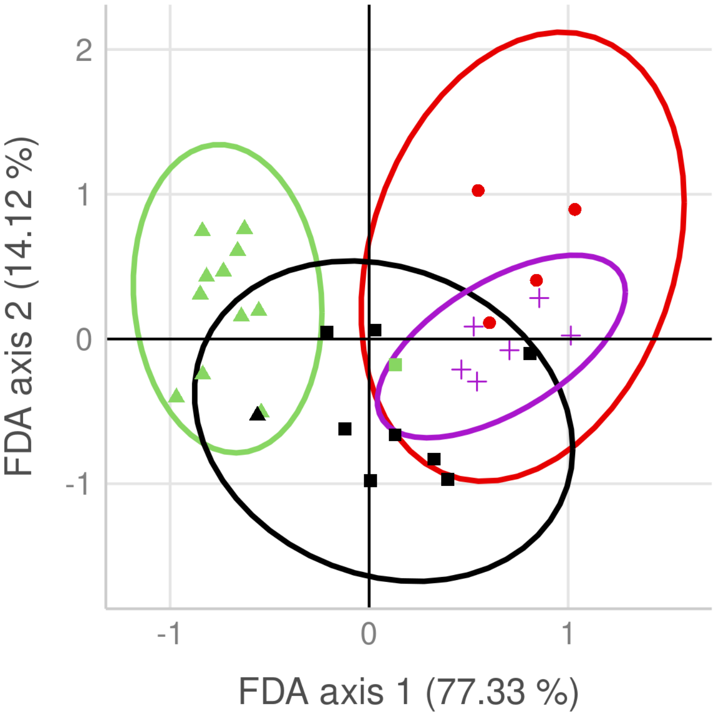

Figure 3: Results of the flexible discriminant analysis (FDA) to separate sites with both species (red, square), with *D. fimbriatus* only (green, triangle), with *D. plantarius* only (purple, cross), or with no *Dolomedes* (black, square). Colors represent observed species, shapes predicted species, ellipses indicate uncertainty of predicted species (95% confidence intervals)

Sites holding either of the two species were well discriminated by the combination of variables loading on the first axis. *D. plantarius* sites were more restricted with respect to the associated habitat variables, and sites with both species overlapped mostly with *D. plantarius* sites (Figure 3).

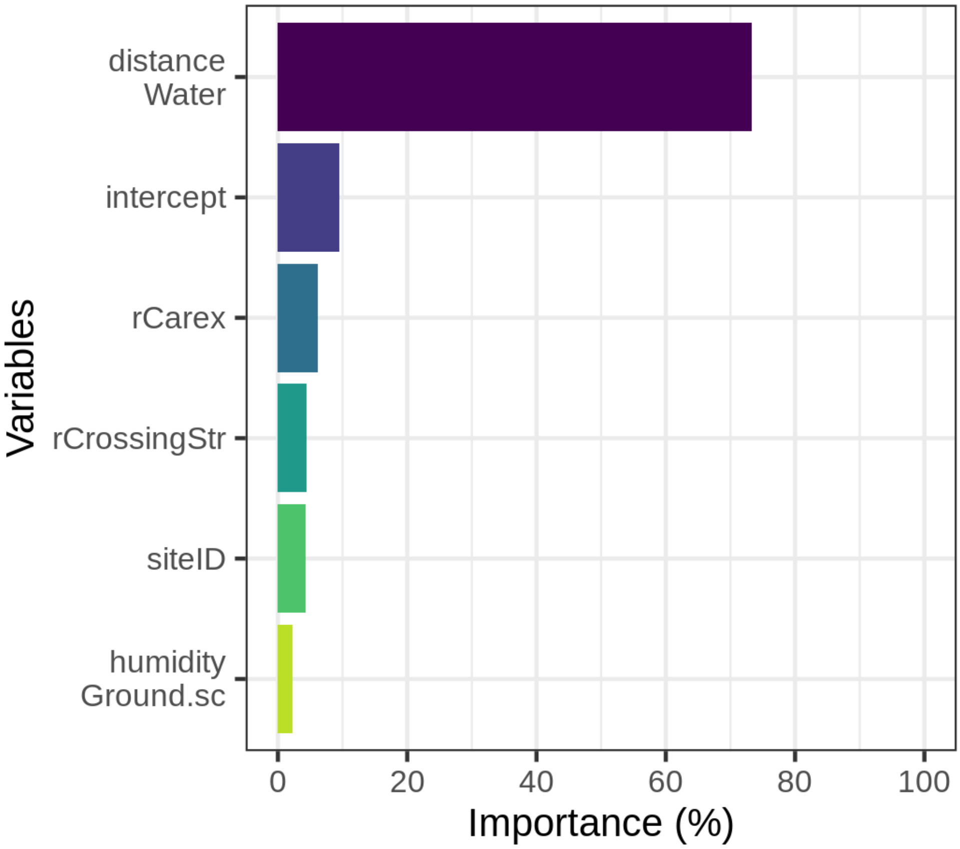

Figure 4: Variables importance for the nursery placement model (boosted GAM). distanceWater: distance to water, rCarex: abundance of *Carex* on simplified Braun-Blanquet scale, rCrossingStr: crossing vegetation structures on simplified Braun-Blanquet-scale, siteID: varying intercept per site ID, humidityGround.sc: humidity at ground level (standardized)

Microhabitat Characteristics Around Nursery

In the field, we found nurseries in 35 plots out of 184. The main variables selected in the boosted GAM model (Figure 4) were distance to water (selection frequency = 0.66), *Carex spp.* cover (selection frequency 0.13), crossing structures (selection frequency 0.09), the random effect site ID (0.08), humidity at ground level (selection

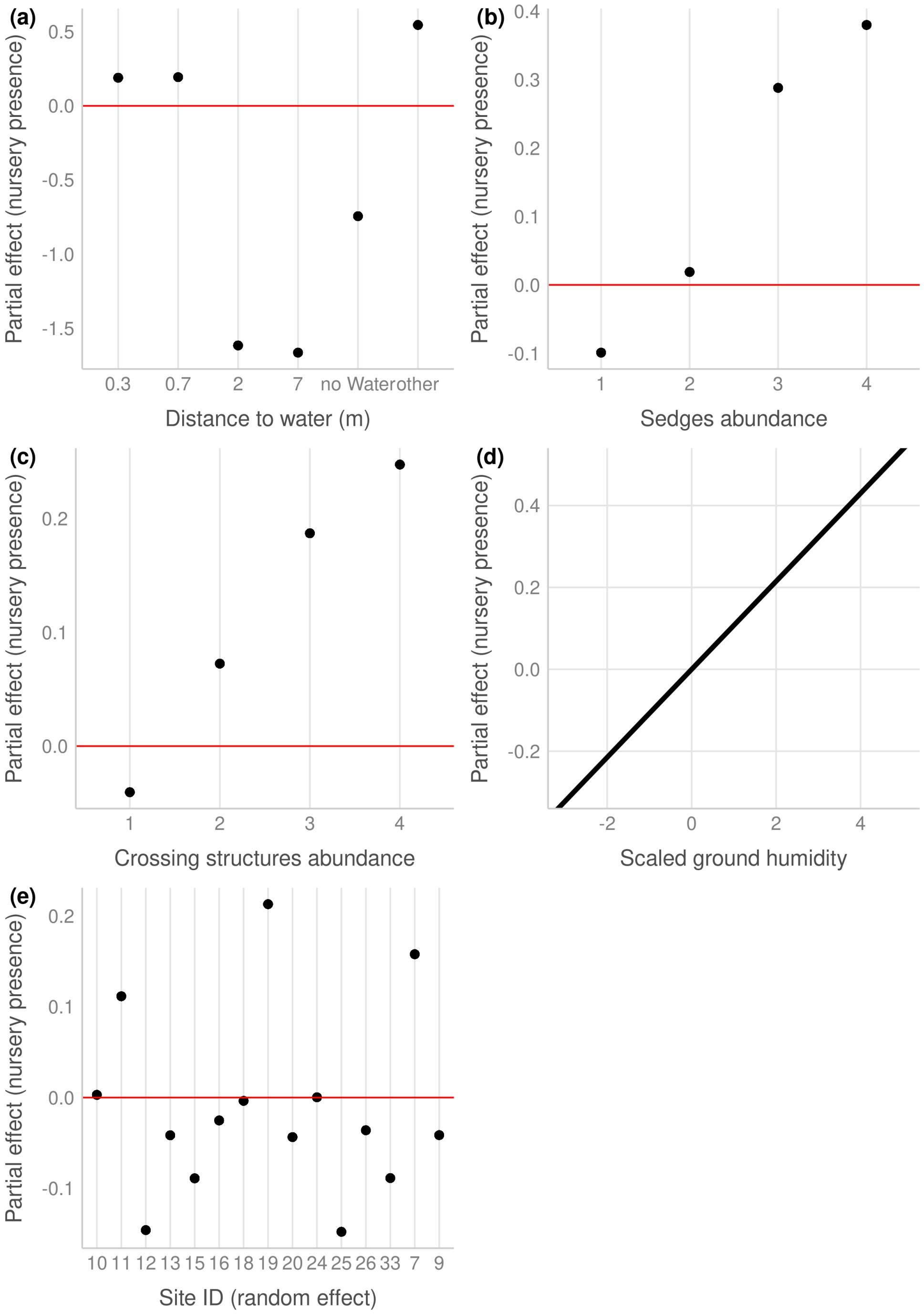

Figure 5: Marginal effects of variables selected in the nursery placement model (boosted GAM): (a) Impact of the distance to water (category 0 meter in the intercept), (b) of the abundance of sedges (intercept: 0), (c) of the abundance of crossing vegetation structures (intercept: 0) and (d) of the ground humidity on the presence of nursery. (e) The effect of sites, considered as random effect.

frequency 0.02) and the intercept (selection frequency 0.01). We found that high abundances of sedges (*Carex spp.*), crossing structures, high values of humidity and low distances to water increased the probability of presence of a *Dolomedes* nursery (Figure 5). If water was present, the probability of encountering nursery webs beyond 70 cm away from the water edge was low. There was variation in the probability of finding nursery webs across sites (Figure 5). However, when testing the stability of the selected variables via resampling, only distance to water, the intercept and the random site ID were found to be stable enough, which was most likely caused by the small sample size (Appendix S3).

The detection probability of nursery webs was higher for plots with a high abundance of crossing structures, higher air temperatures, fewer clouds (at the time of data collection), as well as for sites with open water compared to sites without a water body (Figure 3). Model details can be found in Appendix S4.

Discussion

In this study, we found that the two *Dolomedes* present different habitat requirements. We found that *D. fimbriatus* is more generalist regarding its habitat requirements than *D. plantarius*. Forested habitats, and habitats with low pH (as indicated by the presence of species such as *Carex* and *Sphagnum* and the proximity to coniferous forest, Blacklocke, 2016) or absence of water appear to still be suitable for *D. fimbriatus*. At the microhabitat scale, nurseries were more likely to be located close to water, and where sedge and crossing structures were present.

The habitat requirements of the two fishing spiders were discriminated mainly by water, represented by the water type and speed, and by the site's surroundings, both in terms of landscape and forest. We found that *D. fimbriatus* was more tolerant to forested areas, and especially of coniferous forest. Duffey (1995) hypothesized that *D. fimbriatus* can occupy habitat with lower pH values compared to *D. plantarius.* Surrounding coniferous forest, which are dominant in Fennoscandia, may acidify water streams (Blacklocke, 2016), thus impacting the pH and potentially restricting *D. plantarius.* We found *D. plantarius* most often at sites with slow-flowing rivers, and we found *D. fimbriatus* most often in bogs. *D. plantarius* was also highly associated with open and slow water, whereas *D. fimbriatus* was less restricted by water conditions. *Dolomedes* can use water as a hunting area and benefit from the use of vibrations at the water surface to detect prey (Bleckmann & Lotz, 1987). This close relationship to water, together with the observation of juveniles of *D. fimbriatus* far from the shore, while juveniles of *D. plantarius* are found on the water (Duffey, 2012), might result from different hunting abilities between the two fishing spider species.

We found some overlap in habitat requirements, which reflected a spatio-temporal overlap at the site scale. Holec (2000) hypothesized that co-occurrence of both species might only be observed in transitional habitats between sites suitable for *D. plantarius* (i.e. ponds) and sites suitable for *D. fimbriatus* (i.e. bogs). This observation is validated for one of the sympatric sites sampled (Figure 1), a fen in the forest. Nonetheless, we hypothesize that the conditions for co-occurrence are less restrictive because similar to Lecigne (2016), we found two sympatric populations on the vegetation at the shore of a lake (Finjasjön lake, Figure 1). As already hypothesized by Duffey (1995), Duffey (2012), and van Helsdingen (1993), our data confirmed the higher degree of association of *D. plantarius* with water compared to *D. fimbriatus*, and in general more substantial restrictions in potential habitats for the former. This suggests that *D. plantarius* is more of a habitat specialist than *D. fimbriatus.* The co-occurrence of the two species might be explained by a broader ecological niche of *D. fimbriatus*, which partly overlaps with the niche of *D. plantarius.* The co-occurrence observed hide a possible segregation of both fishing spider species at the microhabitat scale.

At the microhabitat scale, *D. plantarius* might be more dependent on water for its reproductive behavior and nursery placement, which will require further species-specific investigation. Moreover, distance to water and humidity of the ground influenced nursery web placement. This dependency of *D. plantarius* on the water could facilitate cohabitation with *D. plantarius* being spatially segregated towards the shore. We also observed, in two sympatric populations, *D. plantarius* females carrying egg-sac while females of *D. fimbriatus* were already guarding their nursery webs with spiderlings. This might indicate temporal segregation as well, which would also facilitate the co-occurrence of otherwise ecologically close spiders species (Fasola & Mogavero, 1995; Uetz, 1977). Lastly, a segregation for food could occur based on the different diet of the two species, with juveniles of *D. plantarius* being more restricted to water (Duffey, 2012).

Within habitats occupied by *Dolomedes*, we found at the microhabitat scale that abundance of sedges (*Carex sp.*) and crossing structures, together with distance to water and humidity, were the most relevant variables for predicting the presence of nursery webs. Indeed, the architecture complexity of the vegetation, as well as the relation between plant community and architecture, are important for wandering spiders (Vasconcellos-Neto et al., 2017; Woodcock et al., 2007). Here, this is expressed by the positive influence of the presence of crossing structures. We also hypothesize that spiders benefit from the stiff stems of the sedge more than being taxonomically exclusive to them for placing nurseries. De Omena & Romero (2008) showed that some species which are associated with specific host plants are sometimes mostly dependent on the plant's architectural structure for hunting and as dwelling. The structural aspect should be for conservation of fishing spiders, e.g. by managing the mowing season.

In this study, our sample was small due to the rarity of the two species, especially in Scandinavia, and due to a narrow temporal window of data collection. At the landscape scale, this small sample, and especially the lack of co-occurrence sites limits the scope of our conclusions about the characteristics of sympatric populations. At the microhabitat scale, repeated visits of the same sites would provide opportunities to refine the occupancy model and to clarify detection issues for these two species. With a better knowledge of nursery timing, other microhabitat studies would also be facilitated. Further data collection at the landscape level would increase knowledge about potential habitat, and investigating water and soil acidity could be helpful to clarify habitat restrictions for *D. plantarius*. Finally, species-specific occupancy modeling could be helpful, as especially *D. plantarius* is likely to dive when disturbed and might be more difficult to detect than *D. fimbriatus*, which might prevent identification of double-species sites.

The future range of habitat suitability of both species is excepted to shift northward in Europe (Leroy et al., 2013, 2014; Monsimet et al., 2020). This shift might be limited by low dispersal abilities and unconnected habitats in Fennoscandia (Monsimet et al., 2020). It is therefore essential to protect both current and future habitats. Conserving both *Dolomedes* species emphasizes the special importance to protect wetlands, in Fennoscandia and elsewhere (Carson et al., 2019; Davidson, 2014; Sala et al., 2000). The conservation of the red-listed *D. plantarius* might be prioritized as it seems to have narrower habitat requirements than *D. fimbriatus*, which makes it more vulnerable to climate change (Cardoso et al., 2020).

To counteract various threats, which spiders currently face, land protection and the management of both land and species, is important (Branco & Cardoso, 2020). For efficient management, estimating the local probability of presence of the species is important. Occupancy modeling can help to decide which areas could be necessary to protect and where to apply conservation efforts (McFarland et al., 2012). In this study, the detection probability of nursery webs was higher where abundance of crossing vegetation structures was high and with good weather condition, i.e., optimal temperature and sunny weather. Nonetheless, the use of nursery webs as detection units could be improved by specifying the timing and duration of nursery webs with repeated visits (e.g. weekly) to the same sites and nursery webs (Smith, 2000). Monitoring nursery webs also makes it possible to encounter the female spiders, which is especially valuable with the non-invasive sponge-technique we used for identifying the species. Additionally, to estimating the population's abundance dynamic, the management of population by preserving wet habitat, especially continuous presence of water for *D. plantarius*; preserving the shorelines and with abundant crossing structures is essential.

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Appendix S1: Identification method

Figure S1: Sponge determination technique for live species identification of *Dolomedes* spiders.

In order to determine the species of *Dolomedes*, we captured the spiders in a glass box, then removed carefully the lid and inserted the sponge (a soft sponge for normal housework activities, prewashed, but dry at the time of use). We then pushed the spider gently to the bottom of the box, paying attention that the spider was in a correct position, with the legs pointing away from the body (important for not harming the spider and for good conditions for determination). We then used a magnifying class to inspect the epigyne or the pedipalps and compared them with illustrations and descriptions of the *Dolomedes* genitals relevant for species identification.

Appendix S2: Site scale data

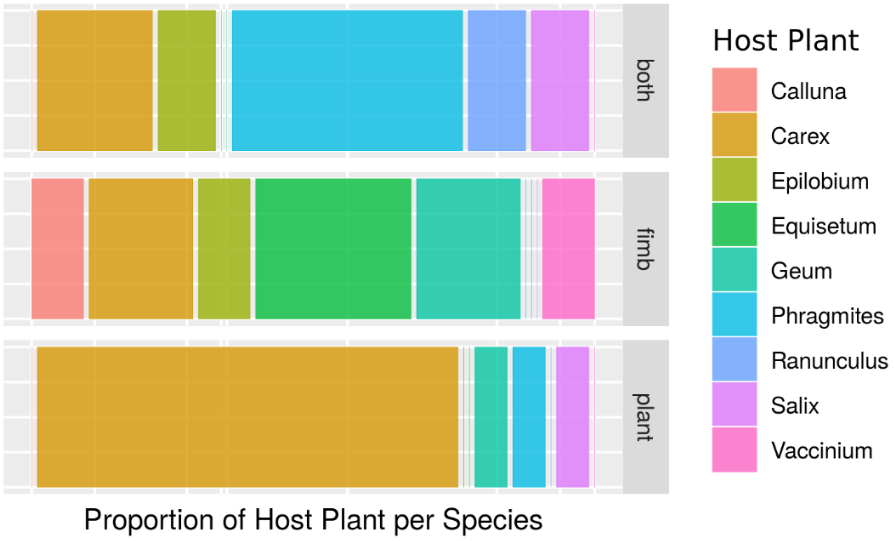

Figure S2: Frequency of nursery host plants in sites where both species were found (top section: ‘both’), and in sites where only *D. fimbriatus* (middle section: ‘fimb’), or only *D. plantarius* (bottom: ‘plant’) was detected.

Appendix S3: Nursery placement model (boosted GAM)

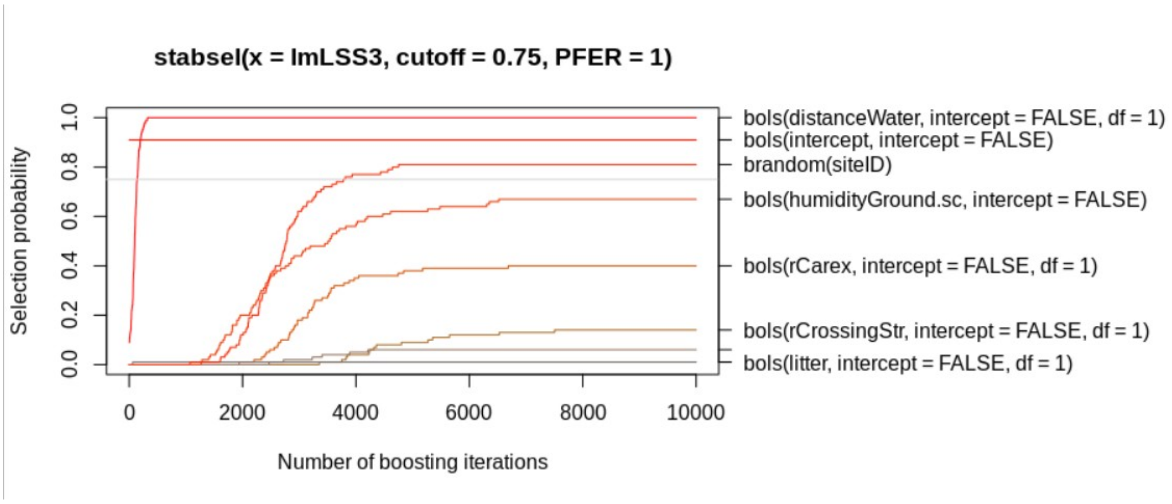

Figure S3: Model validation of boosted GAM for nursery placement, indicating the stability of the selected variables. The steeper the first part of the curve, and the earlier it flattens, the more stable the selection of the variable across resampling, ie the more important the variable. The grey horizontal line indicates the threshold of acceptance.

Appendix S4: Occupancy model

Table S1: Top five models of the model selection for the occupancy model.

Model	negLogLike	delta	AIC	AICwt
`~ sampling_type ~ 1`	89.36	0.00	202.71	0.45
`~1 ~ Cattle_grazing + type`	90.95	1.18	203.9	0.25
`~ rCrossingStr + temperature + cloudyness + sampling_type ~ 1`	92.86	3.00	205.71	0.1
`~ temperature ~ 1`	89.36	4.00	206.71	0.06
`~ shade ~ 1`	92.57	4.43	207.14	0.05

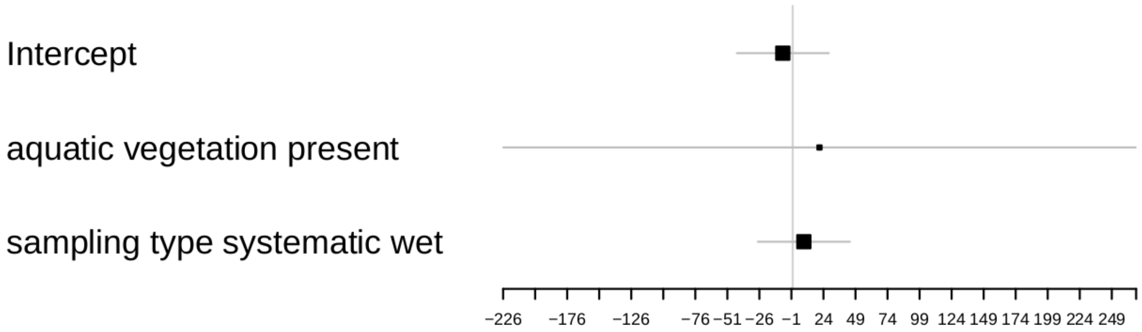

Figure S4: Estimates for occurrence parameters, from the best occupancy model.

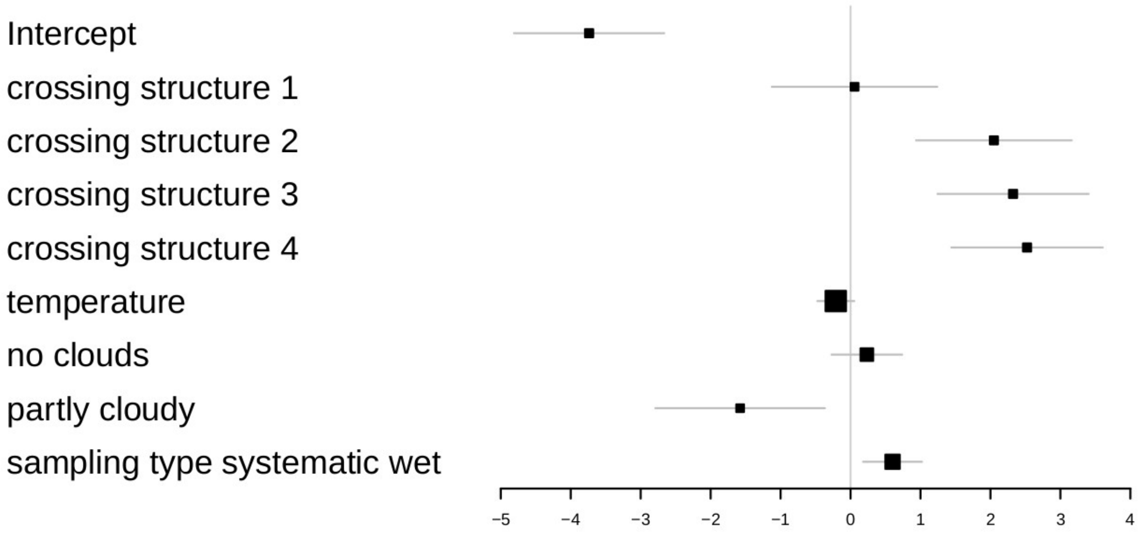

Figure S5: Estimates for detectability parameters, from the best occupancy model.

Paper III

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ORIGINAL RESEARCH

Biogeographic position and body size jointly set lower thermal limits of wandering spiders

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Abstract

Most species encounter large variations in abiotic conditions along their distribution range. The physiological responses of most terrestrial ectotherms (such as insects and spiders) to clinal gradients of climate, and in particular gradients of temperature, can be the product of both phenotypic plasticity and local adaptation. This study aimed to determine how the biogeographic position of populations and the body size of individuals set the limits of cold (freezing) resistance of *Dolomedes fimbriatus*. We compared *D. fimbriatus* to its sister species *Dolomedes plantarius* under harsher climatic conditions in their distribution range. Using an ad hoc design, we sampled individuals from four populations of *Dolomedes fimbriatus* originating from contrasting climatic areas (temperate and continental climate) and one population of the sister species *D. plantarius* from continental climate, and compared their supercooling ability as an indicator of cold resistance. Results for *D. fimbriatus* indicated that spiders from northern (continental) populations had higher cold resistance than spiders from southern (temperate) populations. Larger spiders had a lower supercooling ability in northern populations. The red-listed and rarest *D. plantarius* was slightly less cold tolerant than the more common *D. fimbriatus*, and this might be of importance in a context of climate change that could imply colder overwintering habitats in the north due to reduced snow cover protection. The lowest cold resistance might put *D. plantarius* at risk of extinction in the future, and this should be considered in conservation plan.

KEYWORDS

climate change, *Dolomedes*, fishing spiders, freezing, supercooling ability

1 | INTRODUCTION

The ability of a species to cope with variations in abiotic conditions influences its distribution range (Gaston, 2003). Abiotic factors, and among them temperature, shape the geographic range of ectotherm species, and this is even more relevant in the context of global warming (Addo-Bediako et al., 2000; Somero, 2012). Some ectotherms survive extracellular freezing of their body fluids and are thus freezing tolerant, whereas most ectotherms are freezing intolerant. Instead of having high supercooling abilities (i.e., low supercooling point, SCP), freezing tolerant species, like some alpine species, tend to freeze at relatively high subzero temperatures, a phenomenon that occurs thanks to the synthesis ice nucleators and cryoprotectants that respectively induce and protect against freezing stress

(Bale, 2002; Duman, 2001; Duman et al., 2004). Freezing intolerant arthropods, which include freeze-avoidant, chill-tolerant, chill-susceptible, and opportunistic-survival classes, can exhibit deep supercooling ability, ranging from −15 to −25°C (Danks, 2004), by producing cryoprotectants (e.g., polyols) and antifreeze proteins (Bale, 2002; Duman, 2001).

Body size influences and is influenced by the animal's stage, its body fat content or the concentration of ice-nucleating bacteria, which affect the SCP (Colinet et al., 2007; David & Vannier, 1996; Johnston & Lee, 1990). The size of animals also changes along latitudinal and altitudinal clines. Both an increase and a decrease of body size toward northern latitudes were observed and theorized under the Bergmann and converse Bergmann rules, respectively (Blanckenhorn & Demont, 2004). For ectotherms, these two rules were first opposed (Mousseau, 1997; Voorhies, 1996), but it seems that both larger and smaller individuals at northern latitudes are possible and the two rules are eventually not exclusive (Blanckenhorn & Demont, 2004), possibly coexisting in close species (e.g., in artic wolf spiders, see Ameline et al., 2018). The latitudinal size cline is of importance as body size also influences cold hardiness (Ansart et al., 2014), for example, with smaller arthropods having better supercooling capabilities than larger ones (Colinet et al., 2007; David et al., 1996; Sinclair et al., 2009; Sømme, 1982). Hence, a negative relationship between ectotherms size and the ability to supercool has been reported (Lee & Costanzo, 1998). Consequently, smaller individuals could benefit from colder temperatures under harsher winter conditions at northern latitudes.

Latitude, by influencing winter conditions, also influences the cold hardiness strategies defined by Bale (1996). Indeed, it influences the temperature gap between the SCP and the lower lethal temperature (Addo-Bediako et al., 2000; Vernon & Vannier, 2002), and consequently, opportunistic-survival animals are mainly found in tropical and semitropical regions, chill-susceptible and chill-tolerant in temperate and subpolar regions, and freeze-avoidant in region with severe cold winter conditions.

Despite the importance of latitude on cold resistance, most studies investigating latitudinal clinal changes of arthropods' physiological tolerance focused on differences between species rather than among populations of the same species (Spicer & Gaston, 1999 but see, e.g., Jensen et al., 2019). Basal cold tolerance is a physiological trait that has evolved many times in arthropods (Sinclair et al., 2003). Most of the knowledge on cold tolerance of arthropods comes from the study of insects, and different mechanisms might influence the cold hardiness of insects versus arachnids. Indeed, Anthony and Sinclair (2019) showed divergent cryoprotective dehydration, the action of losing water by evaporation at low temperature, between insects and arachnids, and the presence of coma under hypoxic conditions is also remarkable in spiders (Pétillon et al., 2009). The same cold hardiness classes are used to categorize freezing intolerance of spiders and insects. Indeed, some spiders are freeze-avoidant, others chill-tolerant or chill-susceptible (Anthony et al., 2019; Kirchner, 1973). However, not all spiders are freezing tolerant (Nentwig, 2012).

In this study, we focused on fishing spiders (Araneae, Pisauridae) with contrasted distributions. These spiders are represented by two species only in Europe. Both species are quite widespread but climatic and habitat conditions in the future might negatively impact their abilities to cope with climate change (Monsimet et al., 2020), especially for the red-listed *Dolomedes plantarius*. Estimating the cold resistance is essential to adopt efficient conservation strategies for species having a subnivean winter habitat that might become colder in their northern range, Fennoscandia (Wipf & Rixen, 2010).

The thermal performance of populations could be depicted by a thermal performance curve representing how a temperature gradient influences arthropod activity (Sinclair et al., 2012, 2015). However, the estimation of thermal performances requires many individuals per population. Consequently, measuring an anchor point like the SCP is useful to assess the cold tolerance class of species. The SCP represents the lower lethal temperature (LLT) for freezing-avoidant species and is still a useful indicator for chill-tolerant species as SCP and LLT are almost similar for them (Bale, 1996). Even though the ecological value of the SCP has been debated (e.g., Ditrich et al., 2018; Renault et al., 2002), it is a useful metric to explore and describe the cold tolerance strategy of poorly studied species (Sinclair et al., 2015), such as *Dolomedes*.

In this study, we assessed the variation in cold resistance, estimated through SCP ability of different populations of the most common *Dolomedes fimbriatus* with contrasted distributions. Due to the rarity of *D. Plantarius*, we decided to sample this species only in northern population. We hypothesized that (a) northern populations of *Dolomedes fimbriatus* have lower SCP values than southern populations, (b) the size of spider in the north is positively related to the SCP, and (c) *D. fimbriatus* has lower SCP values than *D. plantarius*, potentially impacting the distribution of the latter one, less spread in Europe.

2 | MATERIALS AND METHODS

2.1 | Case study species and sampling locations

The fishing spiders, *Dolomedes plantarius* and *Dolomedes fimbriatus*, are widespread in Europe with a northern range limit in Fennoscandia. *D. plantarius* has a lower population density and is red-listed at the European scale (Baillie et al., 1996). The latitudinal contrast encompassed two different biogeographic positions, characterizing two different climatic areas (continental, coded C hereafter versus temperate, coded T). The continental climate is annually colder, and colder months are much colder than under temperate climate (Table 1). Moreover, the variation of temperature among seasons is much higher for continental climate (Table 1).

We sampled *D. fimbriatus* individuals of sampled at their range limit and compared them with others from a central latitude of the distribution. We sampled two sites with *D. fimbriatus* in Fennoscandia (C1 and C2; Figure 1), which characterize the northern population, subject to a continental climate. In addition, we sampled two sites in

TABLE 1 Climatic characteristics of the sampling sites

Site	Mean temp (°C)	Diurnal range (°C)	Temp seasonality	Coldest month (°C)	Coldest quarter (°C)
T1	11.62	7.03	457.72	3.30	6.27
T2	11.14	6.30	440.90	3.40	6.07
C1	2.56	9.50	865.37	−12.70	−8.25
C2	5.52	8.54	787.69	−7.90	−4.07
C3	6.05	7.78	741.83	−6.90	−2.67

Note: Mean temp: annual mean temperature; Diurnal range: mean diurnal range (mean monthly (maximum temperature – minimum temperature)); Coldest month: mean temperature of the coldest month; Coldest quarter: mean temperature of the coldest quarter (extracted from Worldclim2; see Fick and Hijmans (2017)).

France (T1 and T2; Figure 1), representing the centrally distributed populations exposed to a temperate climate. Given the conservation status of *D. plantarius* in Europe, the limited knowledge on the species, we chose to limit our sampling of this species to the area where it is most abundant (Fennoscandia) and we sampled only one population later compared to its sister species *D. fimbriatus*.

As the SCP is influenced by the developmental stage (Aitchison, 1984; Anthony et al., 2019), we sampled only juvenile spiders of both sexes. The peak of the breeding season of European *Dolomedes* is in late July (Smith, 2000). Females keep egg sacs several weeks before building a nursery web where eggs will hatch and from which spiderlings will later spread out into the surroundings. Juvenile spiders overwinter, but not adults, similarly to other species in the genus (Guarisco, 2010). We sampled *D. fimbriatus* by sweep-netting the vegetation on sunny and windless days. We sampled *D. plantarius* on the water surface by visual hunting, and active hunting by perturbing the water surface. We sampled, and latter tested the SCP of about 24 spiders at each sampling site (*N* = 24, 24, 21, 26, 24 for C1, C2, C3, T1, T2, respectively, Table 2).

2.2 | Measurement of the supercooling point

To determine the SCP, we placed the spiders in centrifuge tubes, which were submerged in a cryostat bath (Polystat CC3, Huber Kältemaschinenbau AG, Germany) filled with heat transfer fluid (Thermofluid SilOil, Huber, Germany). The temperature of the bath was slowly reduced at a rate of 0.5°C/min to reach a target temperature of −30°C. To monitor the temperature of the spiders, we placed a K-type thermocouple in direct contact with the spider opisthosoma, secured with Parafilm® and connected to a Testo 175T3 temperature data logger (Testo SE& Co., Germany). We recorded the temperature every ten seconds. The SCP was defined as the temperature at the onset of the freezing exotherm produced by the latent heat (see Figure 2 for representative exotherms), and we considered spiders dead if they did not move in the 24 hr after SCP test.

The number of spiders tested per day was limited by the capacity of the instrument (4 spiders at a time). Therefore, we included the time lag between capture and tested it to account for possible acclimation to laboratory conditions in our models (variable Diff).

2.3 | Measurement of spider body size

We measured the spiders' body size after the SCP experiment to avoid injuring the spiders and biasing the results. We took a picture of the spider' back together with a measuring tape for measuring the body size later in the ImageJ software (Schneider et al., 2012). We measured the highest length and largest width of the carapace (prosoma) which are commonly used as proxy for whole body size, fitness, and metabolic rate in spiders (Jakob et al., 1996; Penell et al., 2018).

2.4 | Data treatment

The carapace width and length were highly correlated ($\gamma = 0.83$, Pearson correlation test), so we used the carapace length as a proxy of body size (Jakob et al., 1996) and referred to as body size hereafter. Moreover, all the climatic variables presented in Table 1 were highly inter correlated and correlated to the latitude ($\gamma > 0.9$), so we kept the latitude and categorical climate as a proxy of climatic variables.

We modeled the SCP of the four *D. fimbriatus* (model modClim hereafter) with several candidate linear models including predictor variables Diff (time between capture and SCP measurements), site, climate (continental/temperate, as defined by the biogeographic location), sex, and body size. We also considered the interaction between climate and body size and/or the interaction between body size and site (See Appendix S1 for the list of candidate models). We modeled the SCP of species from Scandinavia (*D. fimbriatus* and *D. Plantarius*, model modSp in the following) to compare the SCP of species from northern populations. We modeled the SCP with several candidate linear models with variables Diff, site, species, sex, and body size, as well as the interaction between species and body size and/or the interaction between body size and site (See Appendix S2 for the list of candidate models).

2.5 | Statistical analysis

We used packages rstanarm (Goodrich et al., 2020), modelbased (Makowski et al., 2020), and bayestestR (Makowski et al., 2019) in

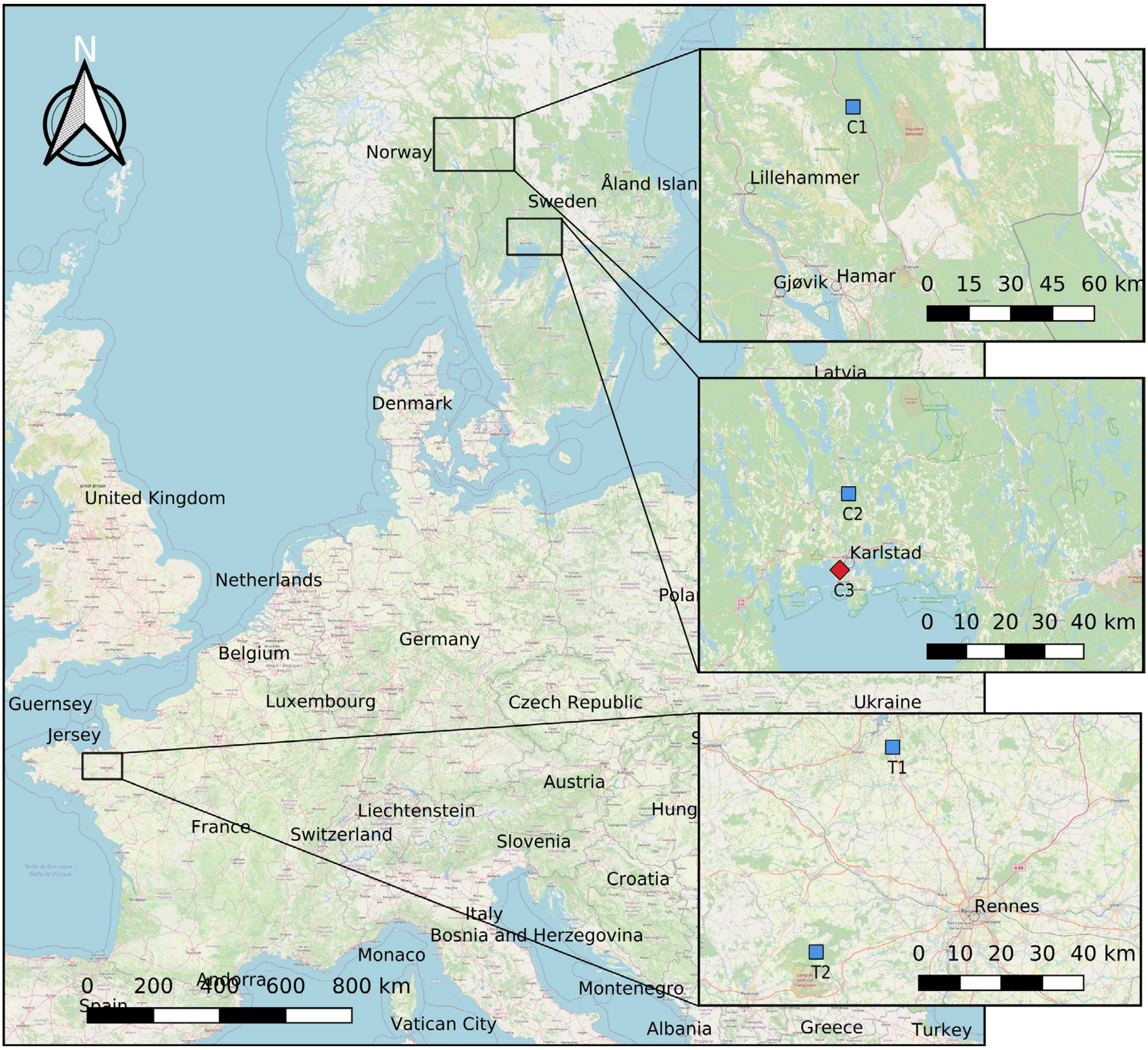

FIGURE 1 Location of sampling sites for *Dolomedes fimbriatus* (blue squares) and *Dolomedes plantarius* (red square) in France and Fennoscandia

TABLE 2 Description of the climatic conditions at the sampling sites, based on the Köppen–Geiger climate classification (Kottek et al., 2006)

Sites	Species	*N*	Country	Climate	SCP (°C)	Body size (mm)
C1	*D. fimbriatus*	24	Norway	Continental	−9.08 ± 0.45	4.13 ± 0.52
C2	*D. fimbriatus*	24	Sweden	Continental	−9.06 ± 0.4	4.43 ± 0.56
C3	*D. plantarius*	21	Sweden	Continental	−7.56 ± 0.32	5.36 ± 0.69
T1	*D. fimbriatus*	26	France	Temperate	−7.78 ± 0.4	4.62 ± 0.46
T2	*D. fimbriatus*	24	France	Temperate	−5.39 ± 0.4	4.44 ± 0.48

Note: N: number of spiders tested; SCP: mean SCP ± *SD*; Body size: mean length of the carapace ± *SD*.

R (R Core Team, 2020) to fit the linear models in a Bayesian framework. We used a normal distribution centered on 0 and a standard deviation of 2.5 as weakly informative priors (rather than using flat priors, see Gelman et al., 2008; Gelman & Shalizi, 2013). We fitted the models using four chains and 4,000 iterations. We used leave-one-out cross-validation value (LOO value) to compare the predictive accuracy of fitted models, and to select the most accurate model (Vehtari et al., 2017). We checked the convergence of the models both visually and by making sure that Rhat value was not larger than 1.01 (Vehtari et al., 2020).

Following Makowski, Ben-Shachar, and Lüdecke (2019 and 2019), we represented the median of the posterior distribution and its uncertainty with a credible interval of 95%. We used both the probability of direction (pd), which is the probability that the posterior distribution of a parameter is strictly positive or negative, and the percentage of the full region of practical equivalence (ROPE). The thresholds beyond which the effect was considered as significant (i.e., non-negligible) were pd > 95% and ROPE < 2.5%.

3 | RESULTS

3.1 | General results

The SCP of the spiders varied from −2.6 to −16.4°C, with an average of −7.8 ± 2.3°C (*N* = 119). Figure 2 shows typical cooling curves of *Dolomedes fimbriatus* (from C2) and *Dolomedes plantarius* (from C3) with exotherms of about 8 and 6.5°C and a SCP of −9.3 and −7.5°C, respectively. None of the spiders tested survived freezing.

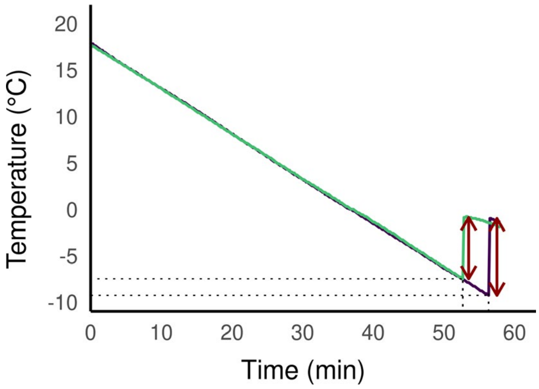

FIGURE 2 Cooling curves of *D. plantarius* (one spider from C3, in yellow) and *D. fimbriatus* (one spider from C2, in purple) recorded during a cooling experiment. The SCP (dotted line) is followed by the exotherm (dark red arrows), a sudden increase in the measured temperature due to the release of latent heat linked to the phase change during freezing

The body size of the sampled juveniles of *D. fimbriatus* was 4.28 ± 0.56 mm in the south and 4.53 ± 0.47 mm in the north and did not significantly differ between sites (ROPE > 2.5%). The body size of juveniles of *D. plantarius* was on average 5.36 ± 0.69 mm and did not significantly differ from *D. fimbriatus* juveniles (pd > 95% but ROPE > 2.5%).

3.2 | Validation and selection of models

All of our candidate models converged (Rhat < 1.01). According to LOO values, some models were considered equivalent (Appendices S1 and S2). The modClim model with the lowest LOO value and therefore the highest predictive power included variables Diff (time between capture and test), climate, body size, and the interactive effect of climate and body size (Table 3). For modSp model, the best model included Diff, species, body size, and the interactive effect of body size and species.

3.3 | Comparison of SCP across latitudes and between species

Regarding *D. fimbriatus* (modClim; Table 3), the SCP of individuals of southern and northern populations significantly differed (pd > 95%, <2.5% in ROPE, Figure 3) and was −6.6 ± 2.3°C (min. −11.5°C, max. −2.6°C; *n* = 50) and −9.05 ± 2.31°C (min. −6.30°C, max. −2.30°C, *n* = 48), respectively. The effect of spiders' body size on the SCP was significantly different between the two climatic areas (pd > 95%, <2.5% in ROPE; Figure 4). Namely, the SCP increased with the body size of spiders in the northern climate (median = 6.88 [−2.18; 16.05]) while the SCP decreased with the body size in the South (median = −8.52 [−19.06; 2.40]), which means that larger spiders had, in the northern and southern climate, respectively higher and lower SCP than smaller spiders.

Regarding ModSp (Table 4), the SCPs of individuals of *D. plantarius* and *D. fimbriatus* of northern populations significantly differed (pd > 95%, <2.5% in ROPE, Figure 5) and were higher for *D. plantarius* (−7.56 ± 0.32 min. −9.4°C, max. −4.4°C; *n* = 21; for

TABLE 3 Parameter estimates of the most accurate model explaining the SCP values between different climatic areas for *D. fimbriatus* (modClim, see Appendix S1)

	Estimate	CI low	CI high	pd	ROPE (%)	Rhat
(Intercept)	−8.10	−12.40	−3.92	1.00	0.01	1.00
Diff	−0.26	−0.40	−0.12	1.00	35.80	1.00
Temperate	8.58	2.44	14.51	1.00	0.10	1.00
Body size	6.88	−2.20	16.05	0.93	1.26	1.00
Temperate:Body size	−15.37	−28.90	−1.82	0.99	0.11	1.00

Note: CI, 95% credible intervals; Diff, time difference between date of capture and date of test; pd, probability of direction; ROPE, percentage of the full region of practical equivalence; Temperate, climate variable (continental climate in the intercept); Temperate:Body size, interactive effect of the climate and body size.

D. fimbriatus, see above). Nonetheless, the effect of body size on the SCP was not significant (pd < 95%) and we did not find a significant effect of Diff for modSp (pd < 95%).

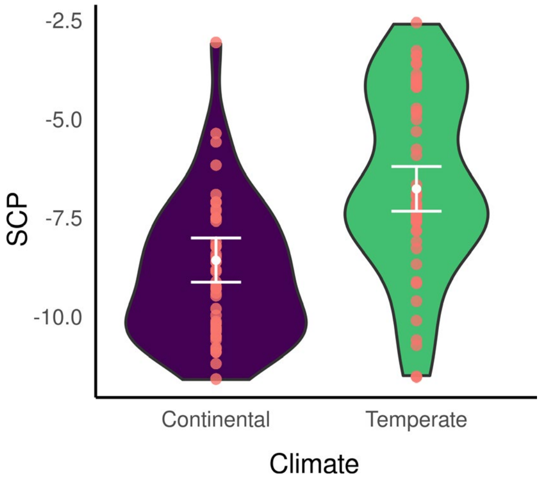

FIGURE 3 Marginal posterior means of SCP (white dot) estimated under modClim for the two different climatic areas and its 95% credible interval (white bar). Red dots represent the original data, and the violin distributions represent a density plot

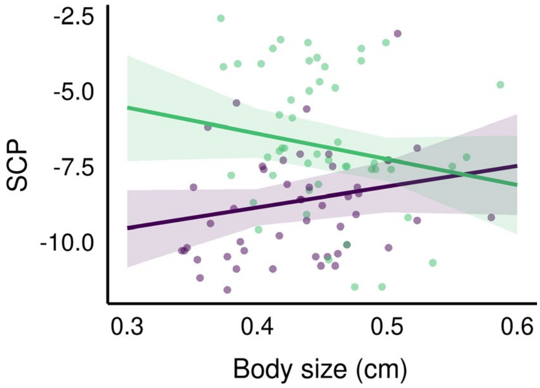

FIGURE 4 Predicted effect of *D. fimbriatus* body size on the SCP, and its 95% credible interval, for the two different climatic areas under modClim. Purple: predictions for the continental climate, green: predictions for the temperate climate; dots represent original data

4 | DISCUSSION

Our study showed that the SCP of northern *D. fimbriatus* from a continental climate was lower than the SCP of southern populations from a temperate climate. The SCP was positively related to body size in the north, and the opposite effect was observed in southern population of *D. fimbriatus*. Finally, we found that the SCP of *D. fimbriatus* was lower than that of *D. plantarius*, even though the juveniles tested did not differ in size.

The SCP of *D. fimbriatus* decreased with increasing latitude, while juveniles of the species did not differ in size. In this study, we tested four populations from two biogeographic locations that were characterized by different climates and latitudes along the species distribution range. The northern populations, at the range limit, experience cold winters with permanent snow cover, whereas the southern populations of *D. fimbriatus*, from a more central latitude of the range, experience warmer winters with only rarely a snow cover. The northern and southern locations are characterized by temperate and continental climate, respectively (Kottek et al., 2006) and the corresponding range of temperatures might explain the decrease in SCP toward the North. Indeed, temperature influences cold hardiness in arthropods, including spiders (Nentwig, 2012) and a poleward increase in thermal tolerance is observed in many ectotherms (Sunday et al., 2011). An acclimation to warmer temperatures, as for southern spiders, can also reduce the tolerance to cold conditions (Jensen et al., 2019). At the same time, northern *D. fimbriatus* could benefit from their cold acclimation by being more active during cooler periods in summer (Everatt et al., 2013). Indeed, according to the metabolic cold adaptation (MCA) hypothesis, individuals from higher latitude have higher metabolic rate at a given temperature (Clarke, 1991, 1993) by showing clinal latitudinal variation in enzymes associated with cold tolerance (Sinclair, 2002).

The impact of diurnal activity range, together with temperature, is essential cues to determine the cold resistance of ectotherm arthropods (e.g., soil dwelling collembolan *Orchesella cincta* see Jensen et al., 2019, or Paaijmans et al., 2013, Seebacher et al., 2015). These might have impacted spiders differently at the time of our experiments (late summer/ early autumn), as northern *D. fimbriatus* are confronted to earlier and harsher winter. Indeed, the supercooling varies at the individual scale during the season, mainly due to

TABLE 4 Parameter estimates of the most accurate model explaining the SCP values between the two species in continental climate (modSp, see Appendix S2)

	Estimate	CI low	CI high	pd	ROPE (%)	Rhat
(Intercept)	−10.19	−14.50	−5.90	1.00	0.00	1.00
Diff	−0.11	−0.32	0.10	0.83	74.44	1.00
D. plantarius	5.10	−1.14	10.90	0.95	1.15	1.00
Body size	6.57	−1.84	14.10	0.94	1.25	1.00
D. plantarius:Body size	−8.62	−20.33	3.80	0.92	0.76	1.00

Note: CI, 95% credible intervals; Diff, time difference between date of capture and date of test; *D. plantarius*, species variable (*D. fimbriatus* in the intercept); *D. plantarius*:Body size, interactive effect of species and body size; pd, probability of direction; ROPE, percentage of the full region of practical equivalence.

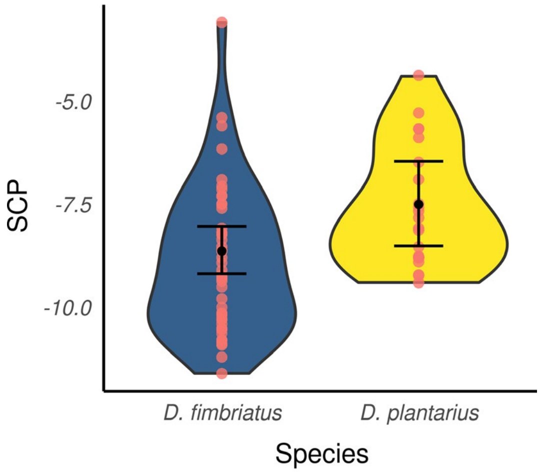

FIGURE 5 Marginal posterior means of SCP (black dot) estimated under modSp for the two different species and its 95% credible interval (black bar). Red dots represent the original data, and the violin distributions represent a density plot

the variation in concentration of cryoprotectants during the year (Sømme, 1982). These two cues have been shown to impact the overwintering of another *Dolomedes* species, from North America (*D. triton*; Spence & Zimmermann, 1998), and might similarly impact the overwintering of *D. fimbriatus*. To our knowledge, *Dolomedes* species are inactive during winter (Aitchison, 1984). Schmidt (1957) noted that *D. fimbriatus* overwinters twice before reaching the adult stage. He also noted that juveniles spend the winter in dry vegetation at high strata, which is probably the overwintering habitat of the southern spiders we tested here. However, the northern *Dolomedes* we tested endure temperatures colder than the SCP measured in this study. For this reason, we hypothesized that, similarly to *Dolomedes triton* in Canada (Spence & Zimmermann, 1998), spiderlings and juveniles overwinter under the snow. Indeed, the temperature in the subnivean layer, which is between the soil surface and the base of the snowpack, is warmer and more stable than the air temperature above the snow, and protect species from temperatures lower than their SCP (Marchand, 1982).

Dolomedes, like other spider species, are not freezing tolerant as none of the spiders tested survived freezing. Cold hardiness of *Dolomedes* is important for winter survival. Based on the cold hardiness classification of Bale (1996, 2002) (see also Appendix S3 for a summarized classification), we hypothesize that both *Dolomedes*, at least from the northern populations, could be either chill-susceptible or freeze-avoidant. The main difference between these two cold hardiness classes is the ability to survive damages caused by cold injuries. Freezing-avoidant species survive until freezing point, while chill-tolerant die at moderately low but not freezing temperatures due to chill injuries. The proximity of the LLT or CTmin (critical thermal minimum) and SCP detected in spiders from a close family (*Pardosa*, Lycosidae) at northern latitudes (Anthony et al., 2019) let us predict that *Dolomedes* are most probably chill-susceptible. Nonetheless, we only tested the SCP and more measurements, such as the lower lethal temperature, would be necessary to define the cold hardiness class more precisely. The cold hardiness class of *Dolomedes* might also vary between the two biogeographic positions as demonstrated for the butterfly *Piries rapae* which is either freeze-tolerant or freezing-avoidant depending on the latitude (Li & Zachariassen, 2007).

Even if *D. fimbriatus* from the two bioclimatic areas did not differ in body size, we found an increase of the SCP with increasing spider body size for the northern populations. Smaller individuals being more cold tolerant than bigger ones is a general trend for ectotherm animals (e.g., for ants see Hahn et al. (2008), for beetles see Johnston and Lee (1990)). This trend is also observed for spiders with smaller instars being more cold tolerant than larger juveniles and adults (Almquist, 1970; Bayram & Luff, 1993).

The converse effect was observed in southern *D. fimbriatus* with a decrease in SCP with increasing body size. This difference in strategy between temperate and colder habitats has been reported in other species from the closely related family of Lycosidae (Ameline et al., 2017). The northern spiders have a shortened breeding season, which can impact life-history traits such as body size (Bowden et al., 2015). The smaller *D. fimbriatus* under continental climate could be advantaged as they can survive colder winters. After the winter, northern fishing spiders could accelerate their development because cold-adapted ectotherms have a higher metabolic rate in an environment with limited energy (Sinclair et al., 2012). Moreover, this pattern might illustrate the clinal variation in life duration. Some *Dolomedes spp*. live one year (see Bonnet, 1930), while others from northern latitudes two years or more (see Duffey, 2012; Spence & Zimmermann, 1998). The northern *D. fimbriatus* would overwinter at a smaller size than southern individuals. The spiders from temperate climate have a longer time window to grow, and they were still growing when we sampled them and this might have resulted in smaller adult body size. Indeed, European spiders from northern latitudes tend to be smaller than spiders from lower latitudes (Hein et al., 2019; Puzin et al., 2014). The absence of difference in body size between latitudes here might be due to a limit in our sampling method, indirectly targeting individuals with similar body size. This might hide an effect of the age (impact of the instar) of spiders on the SCP.

The SCPs measured in this study were close to those measured for phylogenetically close spiders (from the same Lycosoidea superfamily) from northern latitudes (Anthony et al., 2019). These values are considered as medium cold resistance (Nentwig, 2012). Nonetheless, we found slightly higher resistance to cold temperature in *D. fimbriatus* compared to *D. plantarius* (for populations from similar biogeographic areas). Although it seems that *D. fimbriatus* have smaller size, we could not detect a significant difference. Nonetheless, this tendency would confirm the observation that specialist species are larger under harsher conditions because they are more adapted to their environment (Ameline et al., 2018). In turn, the difference between species might explain the wider northward distribution of *D. fimbriatus* compared to that of *D. plantarius*. The former could have benefited from higher cold resistance to expand and increase survival of populations in coldest areas, and this might explain the more limited distribution range of *D. plantarius*, abilities to tolerate cold being an important factor to explain past colonization (Sunday et al., 2011). Nonetheless, a better knowledge of the phylogeny of European fishing spider that is unfortunately still poorly documented (see Macías-Hernández et al., 2020; Piacentini & Ramírez, 2019; Tanikawa & Miyashita, 2008) would allow us to conclude on the difference in species adaptation to climate by using a phylogenetic comparative method (Blomberg & Garland, 2002; Garland & Adolph, 1994).

Climate change impacts spiders in various ways. At northern latitudes, subnivean layer is supposedly a nonfreezing environment with quite stable temperatures (Pruitt, 1957) but snow density and length of the snow season impacts the stability of these conditions (Bale & Hayward, 2010; Pauli et al., 2013). While air temperature increases with climate change, the subnivean layer may become colder (Wipf & Rixen, 2010). This paradox is already negatively affecting invertebrates (Slatyer et al., 2017; Williams et al., 2015). Even though we found that fishing spiders from continental climate tolerated colder temperatures than spiders from temperate climate, the lowest SCP was higher than the lowest air temperature measured historically in Fennoscandia. A weakened subnivean shelter could negatively influence northern populations and even more so for the rare *D. plantarius* which is less cold resistant. Another impact of the increased length of the snow free season could be a second clutch in northern *Dolomedes*, as reported in the arctic Lycosidae *Pardosa glacialis* (Høye et al., 2020).

We found that the cold tolerance of fishing spiders varied among populations, between climates for *Dolomedes fimbriatus*, northern spiders being acclimated to colder climate. Moreover, we found lower SCP for *D. plantarius*, which might be important to consider for the conservation of this red-listed species (Baillie et al., 1996). Indeed, the impact of a smaller snow layer might negatively impact the future distribution of both species in the northern part of their distribution. Moreover, the distribution of understudied invertebrates can be explored and predicted by studying life-history traits like cold resistance (Mammola et al., 2020), especially by explicitly integrating the ecophysiology of species into distribution modeling.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTION

Jérémy Monsimet: Conceptualization (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Writing-original draft (lead); Writing-review & editing (equal). **Hervé Colinet:** Conceptualization (equal); Methodology (lead); Resources (equal); Writing-review & editing (equal). **Olivier Devineau:** Conceptualization (supporting); Formal analysis (equal); Writing-review & editing (equal). **Denis Lafage:** Conceptualization (supporting); Investigation (equal); Writing-review & editing (equal). **Julien Pétillon:** Conceptualization (equal); Investigation (equal); Methodology (lead); Resources (equal); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

All the data and R scripts to analyze them are available on Dataverse (https://doi.org/10.18710/N3P4TH).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Paper IV

Contrasted propensity for waterbone dispersal, lesser for airborne dispersal, between two closely related semi-aquatic spider species

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Abstract

Dispersal abilities are important to support metapopulation survival and to maintain species ranges. Long-distance dispersal is influenced by both context and inherited information, whereas short-distance dispersal is mainly context dependent. This study intended to determine if short- and long-distance dispersal propensity differ between two semi-aquatic spider species of the genus *Dolomedes*. We experimentally tested for airborne and waterborne dispersal using spiderlings and juveniles respectively, which were sampled from populations in south and central Sweden. Long-distance dispersal was more frequent for airborne (ballooning) and waterborne (sailing) spiders of *D. fimbriatus* as compared to *D. plantarius*. The propensity for short-distance dispersal did not differ between species in the air (rappelling). However, we found contrasting results for short-distance dispersal on the water, with rowing being more frequent and running less frequent for *D. plantarius* than for *D. fimbriatus*. The former species is more habitat-specialist and depends more on water bodies than the latter, which might explain the different propensity for dispersal between the two species. The limited propensity for dispersal of the red-listed *D. plantarius* is another argument for conserving an interconnected network of wetlands in Fennoscandia because increased isolation of populations would be detrimental to species maintenance.

Keywords: long-distance dispersal, behaviour, Pisauridae, specialist species, generalist species

Introduction

Dispersal is a crucial process to support gene flow between spatially structured populations (Ronce, 2007). It plays an important role to sustain population genetics and species distributions. There are two types of dispersal, active and passive, which are defined by the three stages of emigration (initiation of the movement to leave an habitat), transfer (movement per se) and immigration (end of the movement, settlement in a novel habitat) (Clobert et al., 2009). In active dispersal, organisms control their own locomotion, whereas in passive dispersal, they depend on external factors (e.g. other animals, wind, water current, etc). Both types of dispersal have a cost (reviewed in Bonte et al., 2012). Habitat quality (Bonte, Lens, et al., 2003) and connectivity (Baguette & Van Dyck, 2007; Van Dyck & Baguette, 2005), as well as intraspecific factors such as sex-ratio (Trochet et al., 2016) all influence the prevalence of dispersal and make it highly context (e.g. taxon and site) dependent. The propensity to disperse also varies across individuals (Clobert et al., 2009; Shaw, 2020) and across personalities (e.g. dispersers vs residents, see Cote et al., 2010). Because it is multi-factorial, dispersal is also influenced by climate changes (Travis et al., 2013).

Few species are plastic enough to cope with their climate change by adapting their physiology or their life-history (Radchuk et al., 2019). Indeed, most species must keep pace with their suitable habitat by expanding or shifting their range (Loarie et al., 2009). Consequently, a northward expansion is expected and observed for species in the northern hemisphere (Parmesan & Yohe, 2003; Sturm et al., 2001). To support this expansion, species require long distance dispersal abilities (Trakhtenbrot et al., 2005). An accumulation of dispersive phenotypes at the northern range limit, the expansion front, is consequently observed for species in expansion (Renault et al., 2018).

Spiders display a broad range of dispersal modes, which can occur by air, water, or on the ground. As such, they make a good model to study dispersal. As in other animal species, dispersal in spiders is context dependent: short-distance dispersal is usually active, whereas long-distance dispersal is usually passive. Negative density-dependence on dispersal behaviour was described for some species (Puzin et al., 2019), whereas some spiders have positive density-dependence on short-distance dispersal (De Meester & Bonte, 2010). Long-distance dispersal in the air via ballooning has variable heritability (Bonte & Lens, 2007). It depends on context and on information accumulated over long time (genetically inherited or not) and larger spatial scales, whereas short-distance dispersal is influenced by shorter time and smaller spatial scale information (Bonte et al., 2009). Ballooning is a passive behaviour that has evolved from an ancestral "suspended ballooning" towards a widely studied pre-dispersal "tiptoe" behaviour (Bell et al., 2005) where spiders take of to travel from some hundred meters to some kilometres throughout the air (Thomas et al., 2003). Ballooning is therefore widely studied as a proxy for dispersal (Bonte, Vandenbroecke, et al., 2003; Frost et al., 2013; Goodacre et al., 2009; Pétillon et al., 2012; Woolley et al., 2007). Because ballooning is passive and uncontrolled, the probability to land in suitable habitats is higher for habitat generalist species than for specialists, the latter having potentially lower propensity for ballooning (Bonte, Vandenbroecke, et al., 2003). This behaviour is also weight-dependent and smaller spiders have higher propensity for ballooning than heavier ones (Bell et al., 2005). Spiders can also travel shorter distances by means of rappelling, when spiders use silk as a bridge between plant stems. Rappelling is mainly present in small spiders like Lyniphidae (Bonte et al., 2009) or younger and smaller spider stages. Moreover, Hayashi et al. (2015) showed that aerial dispersal abilities are usually correlated to abilities on water. Behaviours on water has been well described for one genus, the semi-aquatic spiders *Dolomedes*. This genus is almost the only one with well described behaviours on the water, due to work on *Dolomedes triton* (Suter et al., 1997; Suter, 1999, 2013; Suter & Gruenwald, 2000; Suter & Wildman, 1999). To our knowledge, there is a lack of studies comparing propensity for airborne and waterborne dispersal in spiders. Nonetheless, the ability to move on water is fundamental for spiders that could balloon across the ocean, as reported by Charles Darwin on the Beagle (Darwin, 2005). Furthermore, Suter (1999) hypothesised that sailing, a passive behaviour of spiders raising legs, body or abdomen to catch the wind and travel at low cost, could be considered as ballooning for waterborne dispersal.

In this study, we wanted to compare propensity for airborne and waterborne dispersal of fishing spiders *Dolomedes*. Long distance dispersal on water is illustrated by passive sailing behaviour (Deshefy, 1981; Suter, 1999). Short-distance dispersal can be characterised by three distinct active behaviours, walking, rowing and running (Suter, 2013). Regarding airborne dispersal, most *Dolomedes* spiders normally do tiptoeing followed by ballooning. Frost et al. (2013) described a so-called “spanning” behaviour where *Dolomedes triton* drop themselves from a substrate while producing a silk thread, which can later be used to either balloon or rappel. Consequently, species of the genus have both short- and long-distance airborne behaviours.

In Europe, the *Dolomedes* genus is represented by two species, *Dolomedes fimbriatus* and *Dolomedes plantarius*. We hypothesised that the former, which is more habitat-generalist than the latter (Dickel et al., 2020), has a higher propensity for long-distance dispersal, both in the air and on the water. Based on his observations in the wild, Duffey (2012) hypothesised that *D. fimbriatus* is more likely to show long distance dispersal. We also hypothesised that an edge-core effect would increase the propensity for long-distance dispersal in northern populations to sustain a northward expansion induced by climate change. We hypothesised that *D. plantarius*, due to its higher dependency to water, has a higher propensity for short-distance dispersal on the water than *D. fimbriatus*. Colonisation is indeed more short-distance dispersal dependent for habitat generalist species (Bonte, Lens, et al., 2003).

Material and methods

Study species

Both European fishing spiders species are widespread in Europe. *D. plantarius* has lower population densities, and is red-listed (Baillie et al., 1996). Both species have relatively similar life-cycles. Females lay their eggs into a large silk eggsac, which they carry for about a month before building a nursery in the vegetation. Spiderlings hatch in the nursery and stay there for about a week while the mother stands guard. Spiders usually require about two years to reach maturity, but it varies from one to three or enven more (Duffey, 2012). Nonetheless, *D. fimbriatus* is less restricted by the absence of water, except when females carry their eggsacs which has to be dipped into water to keep the eggs moist. *D. plantarius* is more dependent to the presence of water in the site than *D. fimbriatus* (Dickel et al., 2020; Duffey, 2012).

Spiders sampling

To test the propensity for airbone dispersal of spiders, we sampled spiderlings directly from the nursery web, by gently opening it with tweezers and sucking up about ten spiderlings with an insect aspirator. We used the “sponge-box” technique (Dickel et al., 2020) on the female guarding the nursery to identify the species. We sampled eleven sites in July/August 2019 (Appendix 1). In order to test the difference between species and latitude, we sampled two sites with *D. fimbriatus* (Df1 and Df2), two sites with *D.plantarius* (Dp1 and Dp2) and one site with both species (Bs1) in southern Sweden, and two sites of each species in central Sweden (Df3 and Df4; Dp3 and Dp4; Bs2 and Bs3 respectively).

To test the propensity for waterborne dispersal of spiders, we sampled older juveniles from seven sites (Appendix 1). We used older spiders than for airborne dispersal to be able to see short-distance dispersal on the water, which is more constrained by hydrodynamics in smaller *Dolomedes* (Suter & Wildman, 1999). In order to test the difference between species and latitude, we sampled two sites with *D. fimbriatus* (Df1 and Df2) and one site with *D.plantarius* (Dp2) in southern Sweden and two sites with each species and two sites with both species in central Sweden (Bs3 and Df4; Dp3 and Dp4; Bs2 and Bs3 respectively).

Dispersal experiments

Propensity for airborne dispersal

Before the test, we kept the spiderlings for six days in individual vials with a water-saturated cotton ball, at constant 20°C, 12:12 hours light:dark conditions. They were fed with one fruit fly (*Drosophila melanogaster*) on the day of capture to control for the impact of starvation on ballooning (Bonte et al., 2008).

We tested propensity for airborne dispersal of spiders with a platform (10 X 10cm) with vertical wooden sticks (approximately 20 cm height) arranged in two rows. The platform was surrounded with water to prevent escape. A fan was used to simulate an upward wind at a velocity of 1.0 m/s, which Frost et al. (2013) identified as a favourable speed to observe dispersal behaviours in *Dolomedes triton*. Each spider was tested individually during up to 10 minutes, during which it was put back on the platform after each dispersal events, although a few individuals were lost or died during the first trial. We left spiders moving along silk thread to see if spider dropping from a silk would either use the silk to rappel or balloon. We removed silk from the platform with a brush after each spiderling, to avoid that the presence of another spider's silk affected the frequency of aerial dispersal (see De Meester & Bonte, 2010). After these experiments, we released the spiders back into their site of origin.

We live-recorded the spiderlings' behaviours with software BORIS (Friard & Gamba, 2016). We measured the number of occurrences and duration of ballooning, as a proxy for long-distance dispersal; rappelling, as a proxy for short-distance dispersal; tiptoeing and climbing, which we later excluded from the analysis of dispersal (see Apppendix 2).

Propensity for waterborne dispersal

Before the test, we kept the juveniles for seven days in individual vials with a water-saturated cotton ball, at constant 20°C, 12:12 hours light:dark conditions. They were fed with one fruit fly (*Drosophila melanogaster*) on the day of capture to control for the impact of starvation.

We placed the juvenile spiders on the water in the middle of an aquarium. Behaviours of spiders were observed from the release of the spider to the moment the spider either crossed the "goal line," climbed a wall/window, or reached a platform (see Appendix 3 for details on the experimental design). Spiders were tested for three current speeds (0, 1 and 2 m/s) and three wind speeds (0, 1.5 and 2.5 m/s). Each spider was tested three times at one of the wind/water speed combination. We tested each spider three times to control for potential acclimatisation to the aquarium. Experiments were carried

Table 1: Models with the best fit for each behaviours of interest to discriminate between dispersal and local movement. ID is the individual identifier attributed to each spider tested.

Dispersal	Response	Predictors
airborne	Ballooning	Species + Date sample + (1|Nursery)
	Rappelling	Species + (1|Site) + (1|Nursery)
waterborne	Sailing	Species + Wind water + Weight + Test + Date test + (1|ID)
	Running	Species + Wind water + Test + (1|ID)
	Rowing	Species + Wind water + Test + (1|ID)

out using fresh water at a temperature of 15 ° C. We weighted the spider after the experiment to control for a possible effect of the weight on propensity for waterborne dispersal. After these experiments, we released the spiders back into their site of origin.

Spider behaviours were recorded live with a camera and later analysed with software BORIS (Friard & Gamba, 2016). The different behaviours on the water surface were sailing (with legs, abdomen or by raising the body), considered as a proxy of long-distance dispersal; rowing, walking and running as a proxy of short-distance dispersal; death mimicry, immobility and anchoring were quantified but not considered in the analysis (see Appendix 2).

Statistical Analyses

We fitted generalised linear mixed models in a Bayesian framework to investigate the presence / absence of each behaviour of interest separately. Each behaviour was binarised and analysed separately to account for the spiderlings lost during experiment. For aerial behaviours, i.e. ballooning and rappelling, we considered the species, ecological characteristics of the nursery (distance to water, height in vegetation), and sampling date as predictors. We did a selection on the varying intercept and tried either the nursery, the site or both as varying intercepts.

For behaviours on water, i.e. sailing, rowing and running, we considered the species, wind and water speeds, weight of the spider, and sampling date as predictors. To control for a possible habituation to wind/water speed, we included the trial number as a co-variate in all models for waterborne behaviours. We used the spider ID as a varying intercept to account for repeated trials.

We used the default weakly informative priors of rstanarm, and we fitted the models with four MCMC chains and 2000 to 4000 iterations, and a warmup of 1000 iterations. We used leave-one-out cross-validation values (LOO) to compare the predictive accuracy of fitted models, and to select the most accurate model (Vehtari et al., 2017). We checked the models' convergence and stability visually and by making sure that Rhat values were not larger than 1.01 (Vehtari et al., 2020) and that Effective Sample Sizes (ESS) were higher than 1000.

We represented the median of the posterior distribution and its uncertainty with a credible interval of 95%. To help with the interpretation of the results, we used both the probability of direction (pd), which is the probability that the posterior distribution of a parameter is strictly positive or negative, and the percentage of the full region of practical equivalence (ROPE) (Makowski, Ben-Shachar, & Lüdecke, 2019; Makowski, Ben-Shachar, Chen, et al., 2019). The thresholds beyond which the effect was considered as significant (i.e. non negligible) were pd > 95% and ROPE < 2.5%. All analyses were conducted with packages rstanarm (Goodrich et al., 2020), modelbased (Makowski et al., 2020) and bayestestR (Makowski, Ben-Shachar, & Lüdecke, 2019) in R (R Core Team, 2020).

Results

Propensity for airborne dispersal

For ballooning, the model with the lowest LOO value and therefore the highest predictive power included species and date of sampling with the nursery as varying intercept (Table 1). For rappelling, the best model was a null model with nursery and site ID as varying intercepts. Nonetheless, some models were equivalent according to LOO values and we present the results of the model including species as predictor, nursery and site ID as varying intercepts (Table 1).

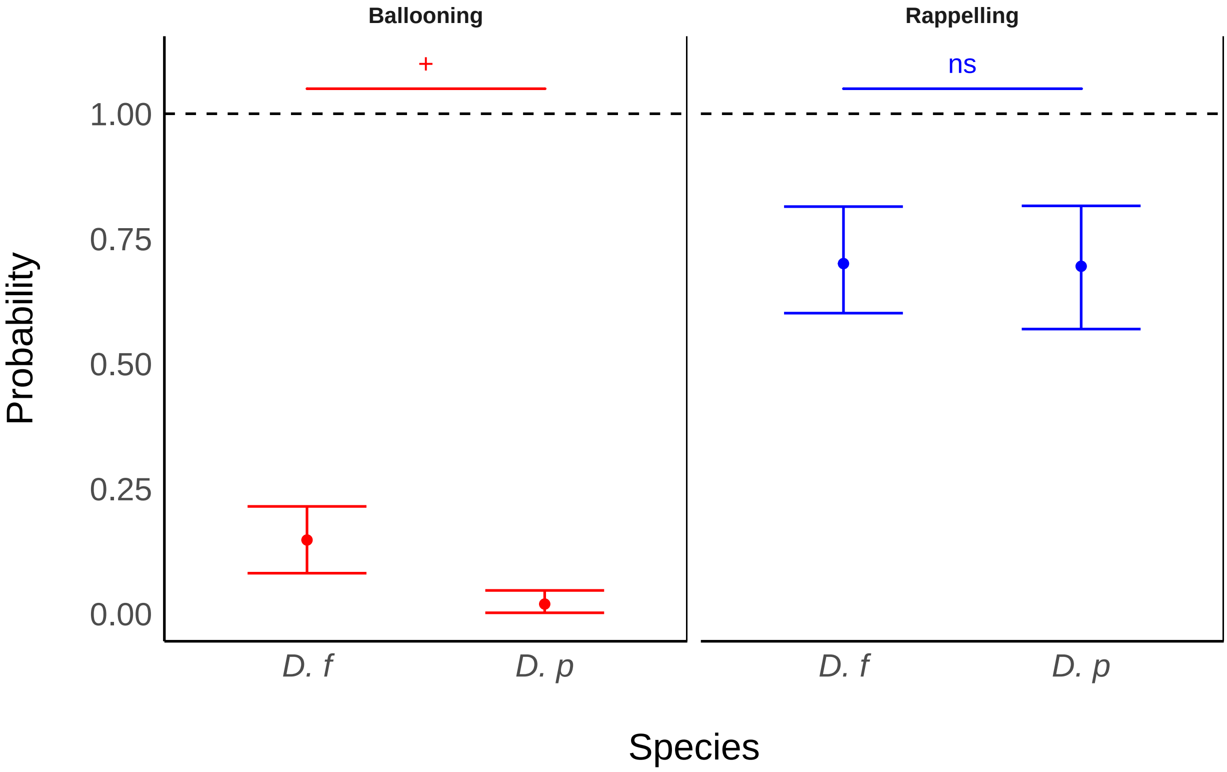

Figure 1: Probability of being ballooners (red dots) and rappellers (blue dots) estimated by the best-fitted model of each behaviour. Errorbars represent the 95% credible interval of the estimated probabilities. D. f: *Dolomedes fimbriatus*; D. p: *Dolomedes plantarius*.

D. fimbriatus had a higher propensity to balloon than *D. plantarius* (Figure 1, estimated contrast = 2.16, credible interval = [0.35, 1.39]), pd=99.95%>95%, ROPE=O%<2.5%) but the two species did not have different propensity to rappel (Figure 1, pd<95%), nor did we find a significant effect of sampling date on ballooning behaviour (ROPE=22.00%>2.5).

Propensity for waterborne dispersal

For sailing, the model with the lowest LOO value included species, wind/water speed, spider weight, trial ID, Date of test, and the interaction between species and weight as predictors, together with sampling date and the spider ID as varying intercepts (Table 1). For both running and rowing behaviours, the best model included species, and wind/water speeds, with trial and spider ID as varying intercepts (Table 1).

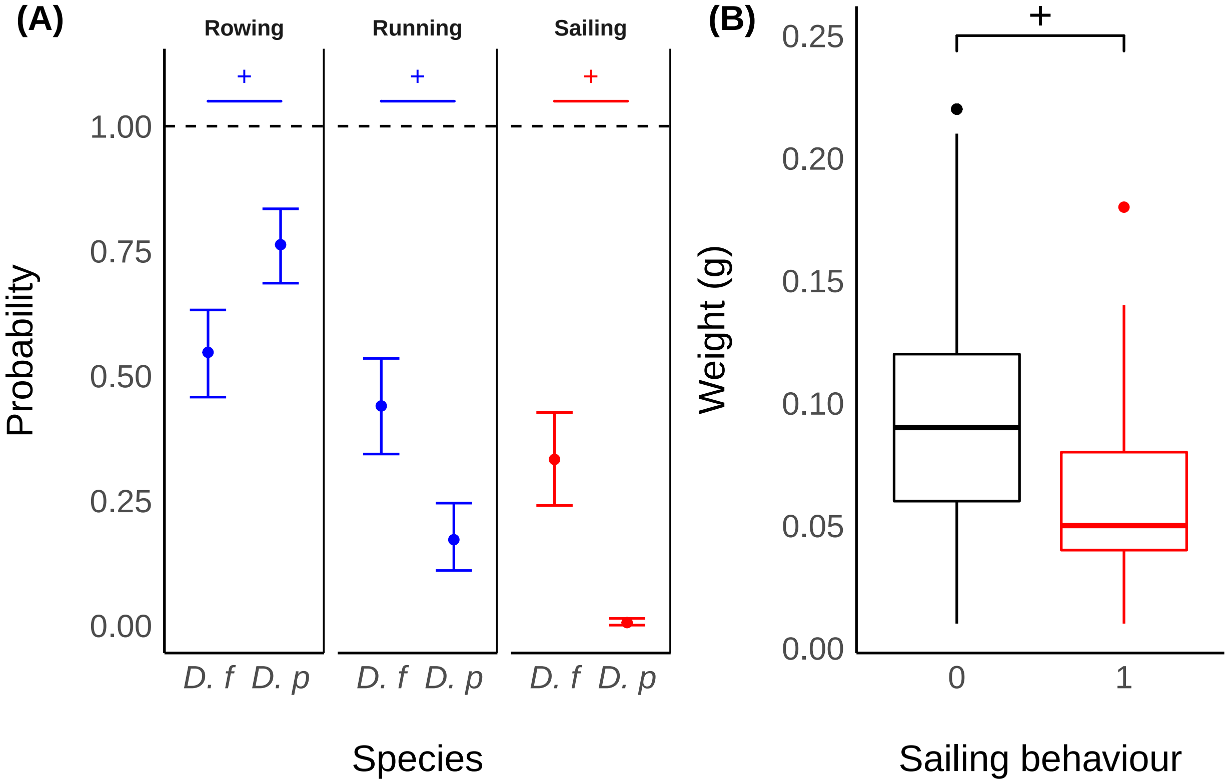

Figure 2: (A) Probability of showing rowing and running behaviours (blue dots) and sailing behaviours (red dots) (B) and influence of the weight on propensity to sail estimated by the best-fitted model of each behaviour. Errorbars represent the 95% credible interval of the estimated probabilities. D. f: *Dolomedes fimbriatus*; D. p: *Dolomedes plantarius*.

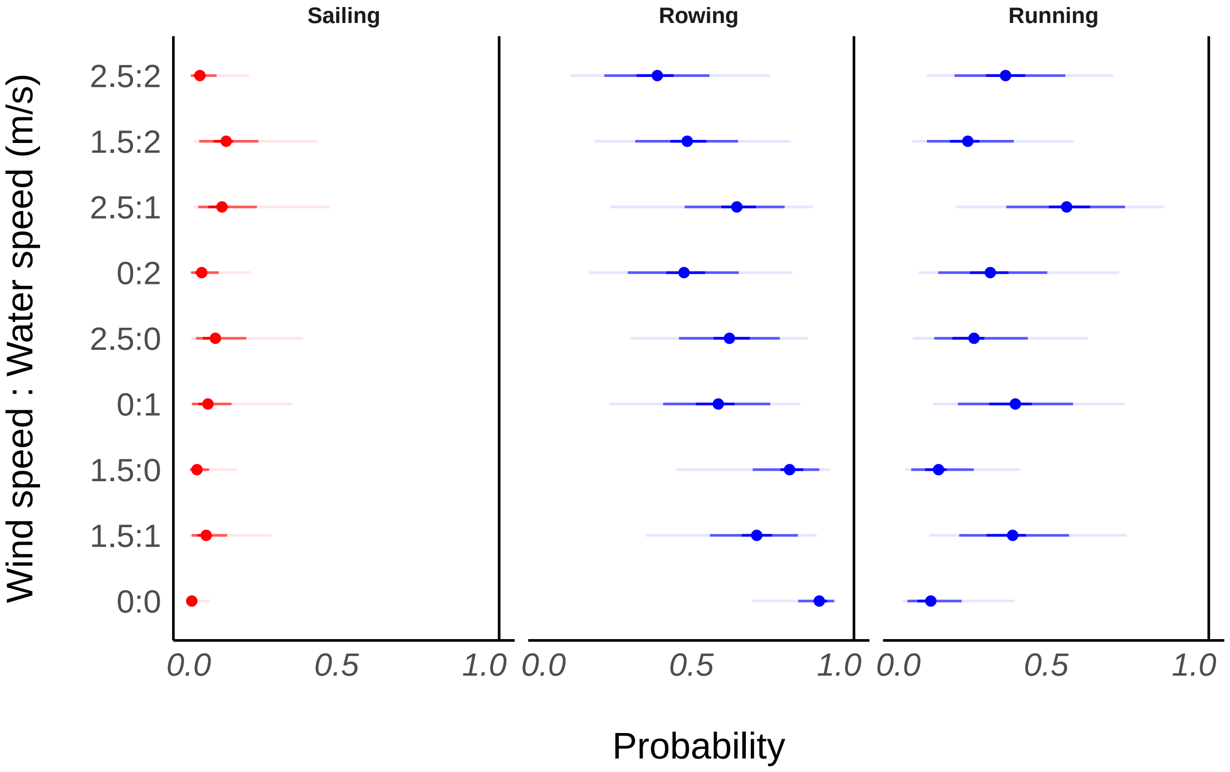

Figure 3: Estimated probability of showing sailing, rowing or running behavirous for different wind and water speed and for sailing, rowing and running models respectively. Dot represents the estimated probability and the 0; 0.5 and 0.95 credible interval from light to dark blue/red respectively.

We found a higher propensity to sail in *D. fimbriatus* than *D. plantarius* (estimated contrast = 4.43 [3.30, 5.68], pd=100%>95%, ROPE=0%<2.5%, see Figure 2A). Moreover, the presence of sailing behaviour decreased with spiders' weight (-0.742 [-1.257, -0.275], pd>95%, ROPE<2.5%, Figure 2B), consequently heavier spiders sailed less than lighter once. The presence of sailing behaviours was also influenced by wind and water speeds with a significantly lower propensity for sailing for the null wind and water current (pd>95%, ROPE<2.5%, Figure 3) except under 1.5:0 m/s wind:water speed condition as well as significantly less sailing behaviours under 1.5:2, 2.5:0 and 2.5:1 conditions (pd>95%, ROPE<2.5%, Figure 3). We found a lowest propensity to sail during the first trial than during the second and third trials (Figure

4, pd>95%, ROPE<2.5%), whereas trials two and three did not significantly differ (Figure 4,pd<95%). We did not find a significant effect of the date of sampling on the propensity to sail (pd<95%).

We found a higher propensity to run in *D. fimbriatus* than *D. plantarius* (estimated contrast = 1.33 [0.70, 1.94], pd>95%, ROPE<2.5%, see Figure 2A). The propensity for running decreased between the first and second trials, and between the second and third trials (Figure 4, pd>95%, ROPE<2.5%). Moreover, the condition of 0:0 wind:water speed presented the lowest propensity for running, followed by conditions 1.5:0 and 2.5:0, which had the lowest number of runners (pd>95%, ROPE<2.5%, Figure 3). Furthermore, we found higher propensity for running under condition 2.5:1 than under any other conditions (Figure 3).

We found a lowest propensity to row in *D. fimbriatus* than *D. plantarius* (estimated contrast = -0.98 [-1.52, -0.44], pd>95%, ROPE<2.5%, see Figure 2A). This behaviour was also used less during the first trial than during the second and third trials (Figure 4, pd>95%, ROPE<2.5%), whereas the trials two and three did not differ significantly (Figure 4, pd<95%). Moreover, a higher propensity to row was found for the wind:water speed conditions 0:0, 1.5:0 and 1.5:1 than the other conditions (pd>95%, ROPE<2.5%, Figure 3).

Discussion

As hypothesised, we demonstrated that *D. fimbriatus* has higher propensity for long-distance dispersal than *D. plantarius*, both airborne and waterborne. We found a lower propensity to sail in heavier spiders when including spiders of both species. However, we could only partially validate the hypothesis that the frequency of waterborne

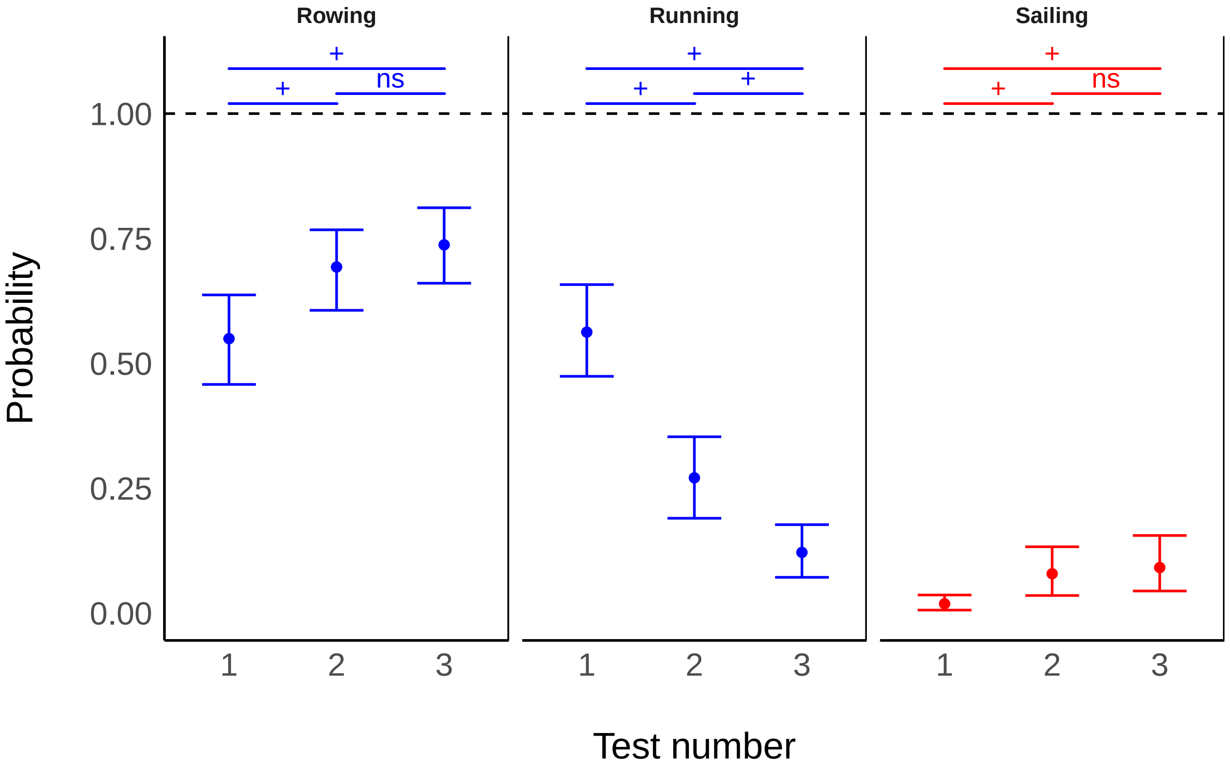

Figure 4: Probability of showing rowing and running behaviours (blue dots) and sailing behaviours (red dots) during the first, second or third trial of each spiders estimated by the best-fitted model of each behaviour. Errorbars represent the 95% credible interval of the estimated probabilities.

short-distance dispersal was higher for *D. plantarius*. Indeed, it was true for the rowing behaviour but we found a higher propensity to run in *D. fimbriatus*. We found no difference between the propensity to short-distance rappel between species, which does not validate our hypothesis. Finally, we were not able to highlight an effect of latitude on propensity for short- and long-distance dispersal, which contradicts our hypothesis on a core-edge populations effect.

Highest propensity for airborne dispersal in *D. fimbriatus*

As expected, *D. fimbriatus* had a higher propensity for long-distance airborne dispersal than *D. plantarius*. This observation is in accordance with observations of specialist spiders having lower propensity to balloon than generalist spiders (Bonte, Vandenbroecke, et al., 2003). Hence the propensity of individuals with a disperser personality (Cote et al., 2010) is higher in *Dolomedes fimbriatus.* Spiders that can balloon tend to have the ability to stand and to move on the water surface, i.e. have water-repellent legs (Hayashi et al., 2015). Accordingly, the same pattern was observed for waterborne spiders with higher sailing propensity for the more generalist spider. Moreover, the absence of this behaviour without wind and water current shows that the behaviour is wind-specific.

The high cost of long-distance dispersal is well known for airborne in spiders. Similar hight cost was expressed in waterborne spiders by the differences in propensity of sailing varying with the trial number. Indeed, spiders were less prone to sail during the first trial in a new, unknown environment that in the last two trials. The effect of the spider weight on the propensity for sailing is similar as for fishing spiders from North America (*Dolomedes triton*, see Suter, 1999), with smaller spiders having higher abilities to raise their body on the water and consequently to use sailing. Studying the propensity to sail for different stages might help to identify at what age the fishing spiders are more prone to disperse on the water. *D. fimbriatus* can occupy a wider variety of more or less wet habitat while *D. plantarius* leaves in site constantly wet, e.g. along streams or on ponds (Dickel et al., 2020; Duffey, 2012; van Helsdingen, 1993). Consequently, the juveniles of *D. fimbriatus*, but not those of *D. plantarius*, could benefit from spring flooding for long-distance dispersal. Lambeets, Hendrickx, et al. (2008) and Lambeets, Vandegehuchte, et al. (2008) found a similar pattern, with flooding facilitating the settlement of generalist spiders in a river bank habitat. Specialist species like *D. plantarius* would preferably recolonise the same habitat after a flood (Lambeets, Vandegehuchte, et al., 2008). We suppose that during a flood, *D.*

plantarius juveniles tend to hide more in the surrounding vegetation than *D. fimbriatus* which could explain their different propensity for short-distance dispersal.

Contrasted propensity for short-distance dispersal

We found two opposite patterns between species for short-distance waterborne dispersal behaviours. Individuals of *D. plantarius* used rowing more often than *D. fimbriatus*, and used running less often. Moreover, running propensity decreased between successive trials, whereas propensity to row increased. Both behaviours might differ in their function and running might be more related to immediate stress (Suter & Wildman, 1999), here in reaction to a new environment during the first trial. The running frequency was indeed the lowest in absence of wind and water current, their presence might consequently represent stressful conditions. Running is for instance used by *D. triton* to escape predators (Hu & Bush, 2010; Suter et al., 1997). The difference in the propensity of rowing behaviour might be explained by the importance of flooding. Moreover, the orientation and movement of generalist spiders on the water is more random than for specialist species (Lambeets & Bonte, 2009). Since *D. plantarius* lives in habitats with constant presence of water and usually exposed to spring flooding, it could use both inherited and direct information from the water environment. On the other hand, *D. fimbriatus* which is less frequently exposed to the water surface environment, could use only direct information from this new environment. This is in line with observations from Lambeets, Van Ranst, et al. (2010), that generalist species use inherited information on water less efficiently. However, we did not find difference in propensity for short-distance (rappelling) dispersal between spiderlings of the two species. Contrary to ballooning, rappelling is based on the direct environment, small spatial scales and not from inherited (genetically or not) information (Bonte et al., 2009). We did not find any difference in rappelling which might be due to our experimental setup where the conditions (context-dependent) were controlled and similar for both species. For this reason, and even though the short-distance dispersal behaviours were considered as “dispersal,” these behaviours might instead characterise movements at the local scale rather than between populations.

Perspectives for future works on poorly documented behaviours

It would be interesting to estimate the abilities of species to settle in new colonised sites. Indeed, we mainly focused in the first two phases of dispersal. Moreover, the actual distance of dispersal (e.g. by sailing) remains largely unknown. Tracking spiderlings ballooning in the field is difficult, but a mark-recapture analysis could be used to track bigger juveniles on the water (e.g., adapting the method used on *D. triton* by Zimmermann & Spence, 1992). Regarding short-distance dispersal on water, it is difficult to differentiate between local-scale movements and actual dispersal behaviours. Rowing and running are sometimes used for short movement on the water and to move back to the edge vegetation or as an escaping behaviour (Suter, 2013). Other behaviours like anchoring or death mimicry could be related to passive and uncontrolled short-distance dispersal. Nonetheless, anchoring is used for hunting or to rest on the surface (Gorb & Barth, 1994) and death mimicry is a stress-related behaviour, which we rarely observed (in less than 5 % of the tests).

No evidence of core-edge effect on propensity for dispersal

We did not find significant variation of propensity for dispersal along a latitudinal, core-margin gradient. A similar observation was recently made in the wasp spider *Argiope bruennichi* (Wolz et al., 2020). New sites with *D. plantarius* were recently found in Europe (in Germany: Harms et al., 2009; in Spain: Bellvert et al., 2013; in Belarus: Ivanov et al., 2017; in Italy: Milano et al., 2018; in Norway: Fjellberg et al., 2018). Nonetheless, this apparent spread is most probably due to an increasing interest in protecting wetlands, as *D. plantarius* is observed when sampling for other species (e.g., see Bellvert et al., 2013), rather than an actual expansion of the species. In addition, the growing interest for *D. plantarius* might also be related to its red-listed status (Baillie et al., 1996; Milano et al., 2021). In a related modelling study involving species distribution models, we found that *D. fimbriatus* might be a better candidate to spread northward (Monsimet et al., 2020). Regardless, it would be interesting to test the fecundity of these species. Indeed, Wolz et al. (2020) observed that the range expansion of *Argiope bruennichi* was (partly) driven by a higher reproductive investment in margin populations rather than by spatial sorting. Resolving the question of *Dolomedes* range expansion should guide decisions for the conservation of the species, especially for the red listed *D. plantarius*.

Consequences for conservation

The presence of interconnected network of wetlands is highly necessary to conserve species (Gibbs, 1993), especially for spiders for which the management of hydrological functioning is fundamental (Lafage & Pétillon, 2016; Lambeets, Vandegehuchte, et al., 2008; Lambeets, Breyne, et al., 2010). It is also important to preserve the already existing habitats of *Dolomedes* because restoration does not necessary permit the relocation of species, even less so for specialist species (Hacala et al., 2020). Moreover, the higher propensity for long-distance dispersal of both waterborne and airborne spiders for *D. fimbriatus* compared to *D. plantarius* can have important consequences for range persistence of the range in a changing climate. Long-distance dispersal seems of primary importance for the sustainability and conservation of threatened species (Trakhtenbrot et al., 2005). Combining dispersal information, mark-recapture and landscape genetic or genomic (reviewed in: Manel et al., 2003; Manel & Holderegger, 2013) on model similar to the one developed by Allgayer et al. (2021) would permit to understand population dynamics of *Dolomedes* along streams. Indeed, gene flow and population dynamic might be threatened by habitat fragmentation and loss of interconnected wetlands due to limited propensity for long-distance dispersal, especially for *D. plantarius*.

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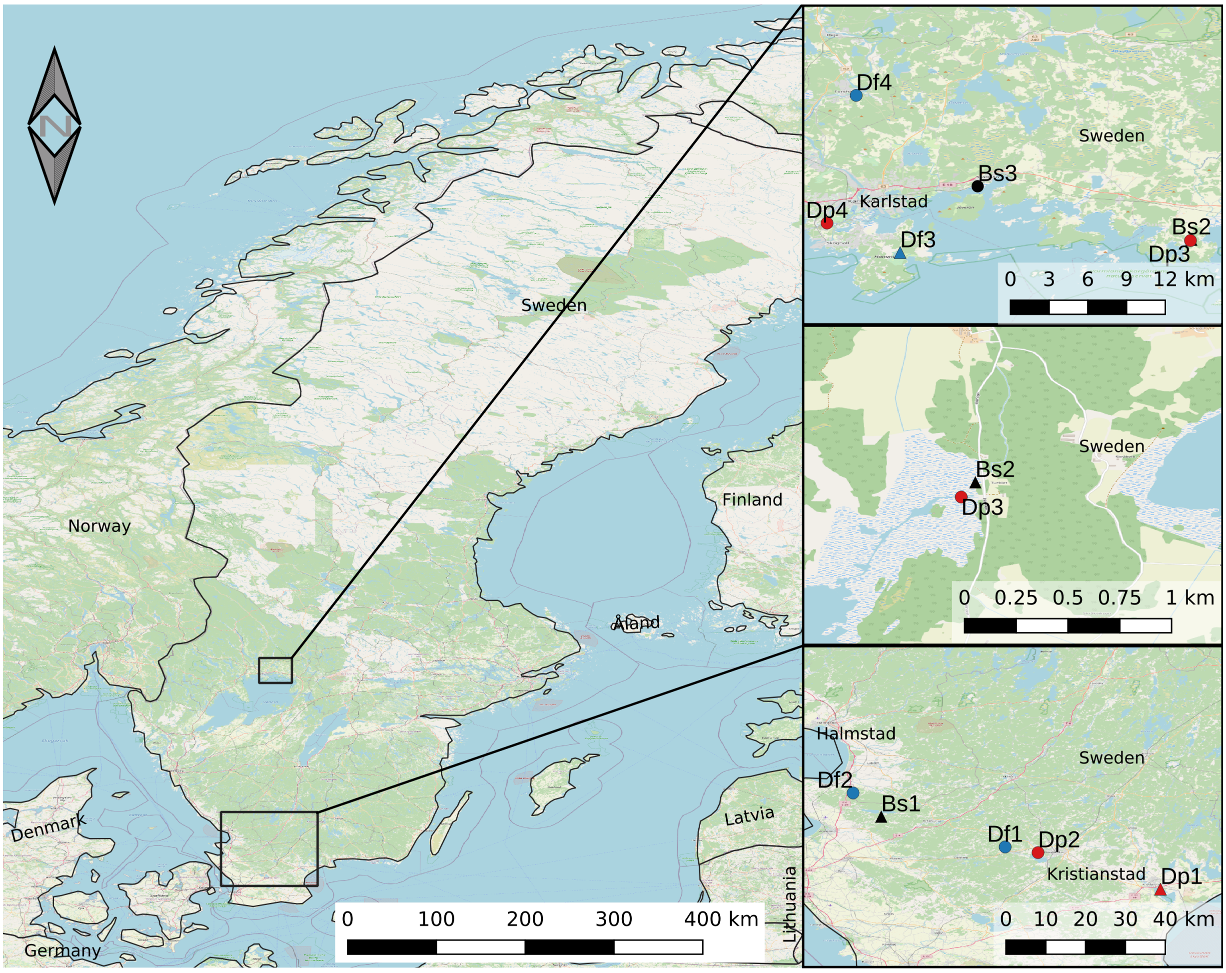
Supplementary material

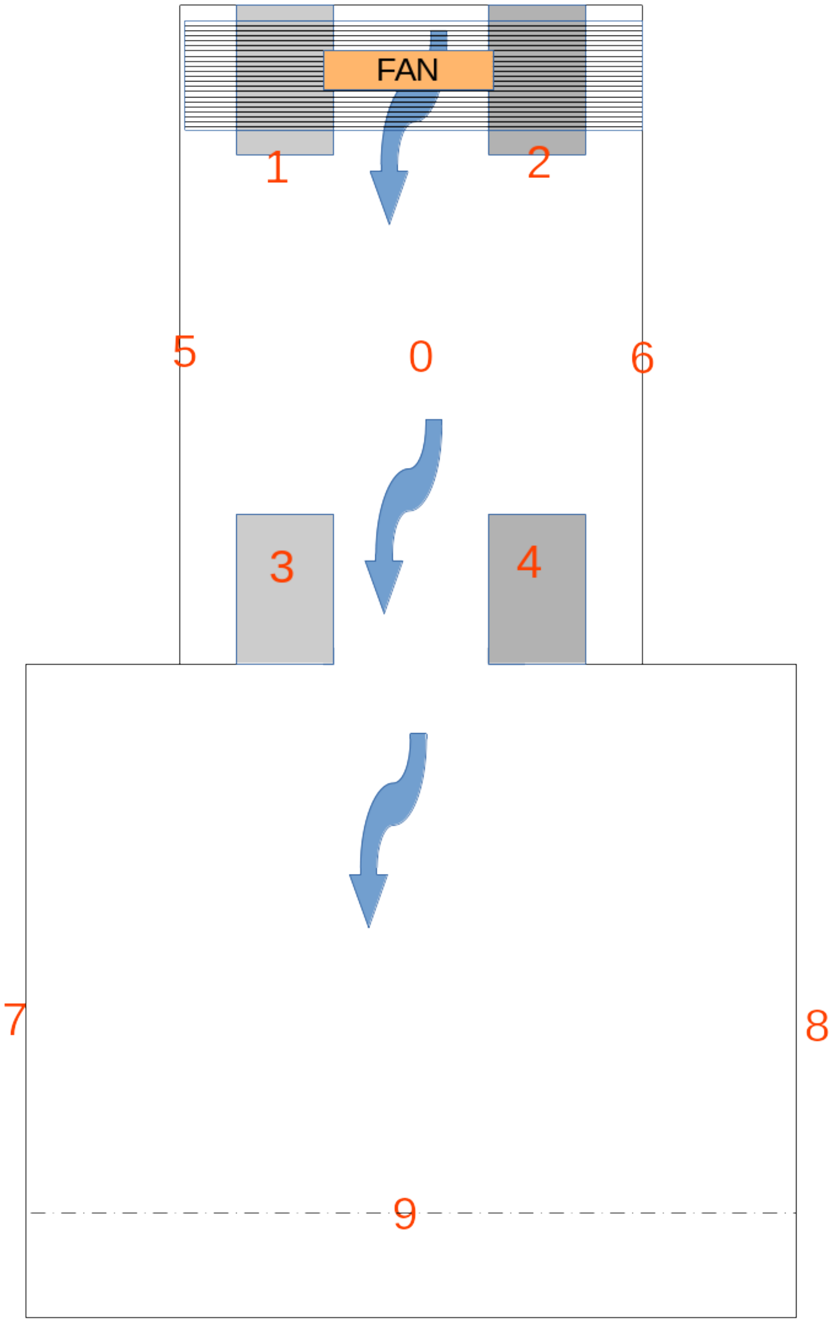
Appendix 1: Location of sampling sites for *Dolomedes fimbriatus* in blue and *Dolomedes plantarius* in red and sites with both species in black in Fennoscandia. Circles represent sites were we sampled spiders for both airborne and waterborne tests while spiders from sites represented with a triangle were only tested for dispersal in the air.



Appendix 2: Summary of propensity for the behaviours experimentally. D. plan: *D. plantarius*, D. fimb: *D. fimbriatus*

Dispersal	Distance	Behaviours	Species	N	Test 1	Test 2	Test 3
Airborne	Long	Ballooning	D. plan	3 (2%)			
			D. fimb	34 (18%)			
	Short	Rappelling	D. plan	86 (70%)			
			D. fimb	125 (68%)			
	Others	Tiptoeing	D. plan	100 (82%)			
			D. fimb	161 (88%)			
		Climbing	D. plan	107 (88%)			
			D. fimb	144 (78%)			
Waterborne	Long	Sailing	D. plan	5 (5%)	35 (5%)	69 (10%)	72 (10%)
			D. fimb	98 (77%)	35 (5%)	69 (10%)	72 (10%)
	Short	Running	D. plan	62 (56%)	130 (18%)	84 (12%)	52 (7%)
			D. fimb	96 (75%)	130 (18%)	84 (12%)	52 (7%)
		Rowing	D. plan	99 (90%)	124 (17%)	148 (21%)	155 (22%)
			D. fimb	100 (78%)	124 (17%)	148 (21%)	155 (22%)
	Others	Anchoring	D. plan	44 (40%)	18 (3%)	37 (5%)	38 (5%)
			D. fimb	32 (25%)	18 (3%)	37 (5%)	38 (5%)
		Immobile	D. plan	19 (17%)	5 (1%)	9 (1%)	14 (2%)
			D. fimb	5 (4%)	5 (1%)	9 (1%)	14 (2%)

Appendix 3: Schematic representation of the aquarium used to test spiders' water-borne abilities. Arrows represent the direction of the simulated wind and current, horizontal lines at the fan represent a wooden platform used to support the fan. 1 to 4 where stone platforms; 5 and 7 represents a wall; 6 and 8 a window; 9 the goal line and 0 is the location where spiders were released.



Paper V

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Explicit integration of dispersal-related metrics improves predictions of SDM in predatory arthropods

Jérémy Monsimet[1]✉, **Olivier Devineau**[1], **Julien Pétillon**[2] & **Denis Lafage**[2,3]

Fishing spiders (*Dolomedes* spp.) make an interesting model to predict the impact of global changes because they are generalist, opportunistic predators, whose distribution is driven mostly by abiotic factors. Yet, the two European species are expected to react differently to forthcoming environmental changes, because of habitat specialization and initial range. We used an original combination of habitat and dispersal data to revisit these predictions under various climatic scenarios. We used the future range of suitable habitat, predicted with habitat variables only, as a base layer to further predict the range or reachable habitat by accounting for both dispersal ability and landscape connectivity. Our results confirm the northward shift in range and indicate that the area of co-occurrences should also increase. However, reachable habitat should expand less than suitable habitat, especially when accounting for landscape connectivity. In addition, the potential range expansion was further limited for the red-listed *D. plantarius*, which is more of a habitat specialist and has a lower ability to disperse. This study highlights the importance of looking beyond habitat variables to produce more accurate predictions for the future of arthropods populations.

Climate change, which is now threatening all ecosystems worldwide[1], is a multi-factor problem that goes beyond raising temperatures only[2,3]. Tackling this complexity requires that ecologists obtain realistic predictions of how species distributions will change in response to global change. A poleward range shift of the distribution is expected in all continents and was observed in different taxa[4–6]. The ability to shift can nonetheless be limited for species with limited dispersal abilities or specialist species[7]. In recent years, species distribution models (SDMs) proved to be an important tool to predict geographic distributions by correlating species occupancy to environmental variables[8]. Applications include conservation planning[9], potential invasion range[10], or forecasting in time[11]. SDMs were successfully applied to a large variety of terrestrial (see Hao et al.[12] for a review) and marine organisms (see Melo-Merino et al.[13] for a review).

The accuracy of predictions produced by SDMs varies from algorithm to algorithm, even when considering that the MaxENT algorithm is most often used[14]. This variation in accuracy can be alleviated with ensemble models, which combine algorithms and produce consensual predictions[15,16]. Of course, input data also influence the predictions[17], and while most SDMs use only climatic variables, including other variables such as land-use might improve predictions[18]. In order to make projections in time, it is fundamental to carefully select the right climatic scenario[17]. Right now, the ones produced and updated by the Intergovernmental Panel on Climate Change[19] are the most widely recognized and used climatic scenarios.

SDMs assume that the species and its environment are at equilibrium[20], so that all suitable locations are occupied. SDMs also assume that the ecological niche is stable, i.e. that the same factors limit the species in space and time[21]. Under these assumptions, SDMs are used to define habitat suitability, which is the range of physical locations where one species can live[22]. However, a properly constructed and calibrated SDM can provide information about the species' realized niche, i.e. a combination of habitat with other biotic and abiotic factors[20,23]. The gold standard of SDMs would be fully mechanistic models which were used, for example to study seed

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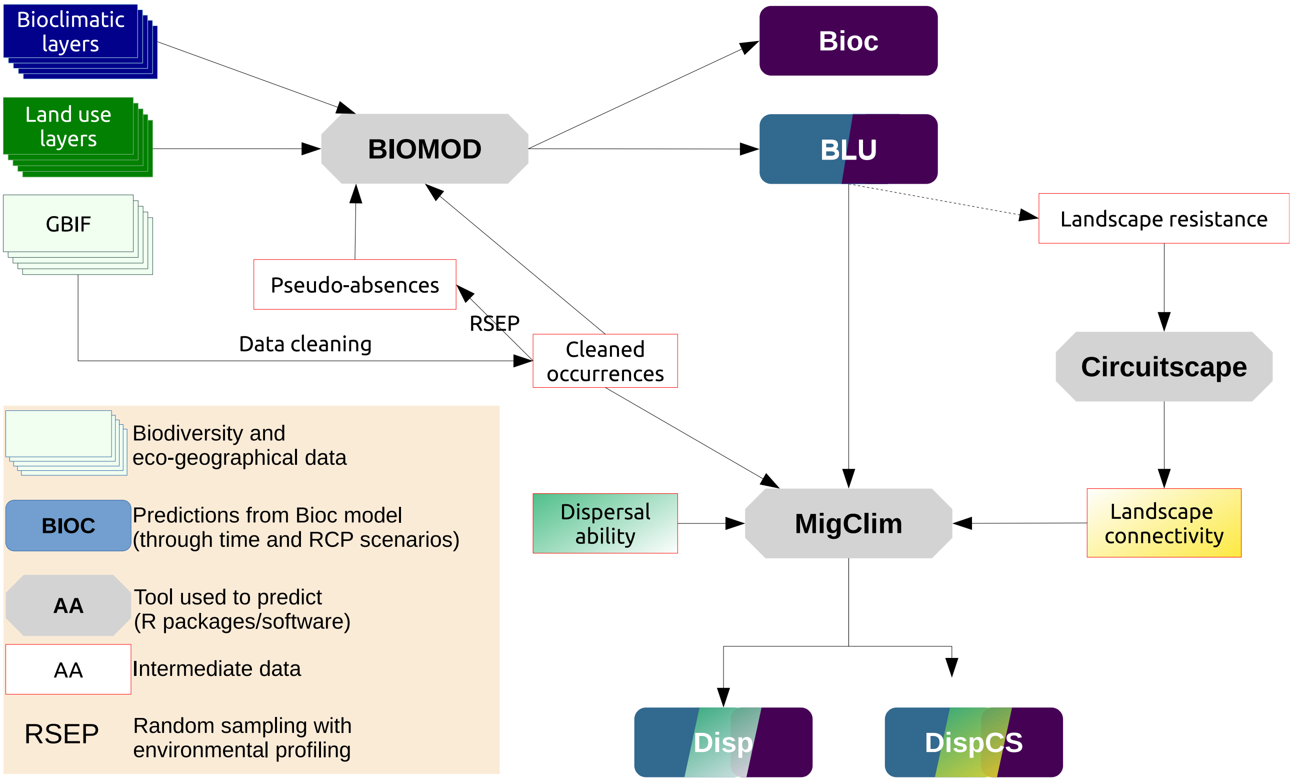

Figure 1. Flowchart of the framework used to study the future distribution of the two European fishing spiders (Bioc: bioclimatic only model, BLU: bioclimatic and land use model, Disp: dispersal model, DispCS: dispersal and landscape connectivity model).

dispersal in birds[24] or population dynamics and evolution of dispersal trait[25]. However, these models are very data-demanding, and simpler hybrid mechanistic-correlative models are often more suitable for less well-studied taxa. In particular these hybrid models allow including active biological processes such as dispersal[26]. Examples include making predictions under full /no dispersal[27] or using a buffer of dispersal around each presence[28].

As generalist predators, spiders are relatively independent of a specific prey community, and their assemblage and distribution are mostly influenced by habitat and land use[29], which makes them good study cases for SDMs. Fennoscandia is a potential climatic refugium for spider populations against the current global warming as their range is expected to expand Northward in Europe[30,31]. Refugia can mitigate the effects of climate change by providing suitable conditions for species persistence through time[32]. *Dolomedes plantarius* could presumably use Fennoscandia as a refugium, but the ability of the species to effectively spread northward has not been accounted for in previous predictions[30,31]. Moreover, fishing spiders are threatened by the decrease of range and quality of their wetland and fenland habitats, which are declining globally[33]. The other European fishing spider, *Dolomedes fimbriatus*, also occurs in Fennoscandia. Co-occurrence of both *Dolomedes*, was considered impossible due to different habitat requirements[34]. *D. fimbriatus* can nonetheless occupy the same habitat type as *D. plantarius* plus marshes, bogs, swampy forests or wet heathland[34]. Syntopy is then possible, as the two species can live close to each other[35], for example around the same lake[36], or in the ecotone habitat between bogs and ponds[37]. *D. fimbriatus* has a larger ecological niche: the species is more drought and shade tolerant[38], e.g. it creates nurseries to lay eggs in the tall grass while *D. plantarius* creates nurseries only above the water surface[34]. *D. frimbriatus* is less sensitive to water quality[35], it is found on mesotrophic or oligotrophic wetlands while *D. plantarius* lives mainly in mesotrophic wetlands[38]. Consequently, *D. fimbriatus* could become a competitor to *D. plantarius* in syntopic sites if global change brings more frequent drought events.

Here, we compare the potential range spread of *D. plantarius* and *D. fimbriatus*, and their ability to use Fennoscandia as a refugium. We aim to provide more conservative predictions for Fennoscandia than previously predicted at the European scale by Leroy et al[30,31]. To do so, we developed hybrid species distribution models including climate and land-use variables, as well as dispersal and landscape connectivity (Fig. 1). We expected that:

1. The distribution of both fishing spiders should expand northward[30,31]. A larger expansion is expected under more intense climate change.
2. Since *D. fimbriatus* is a habitat generalist, the range of habitat it can reach should be larger and occupied faster, than for *D. plantarius*[39].
3. The area of sympatry between the two species should increase with the range expansion of the two species.

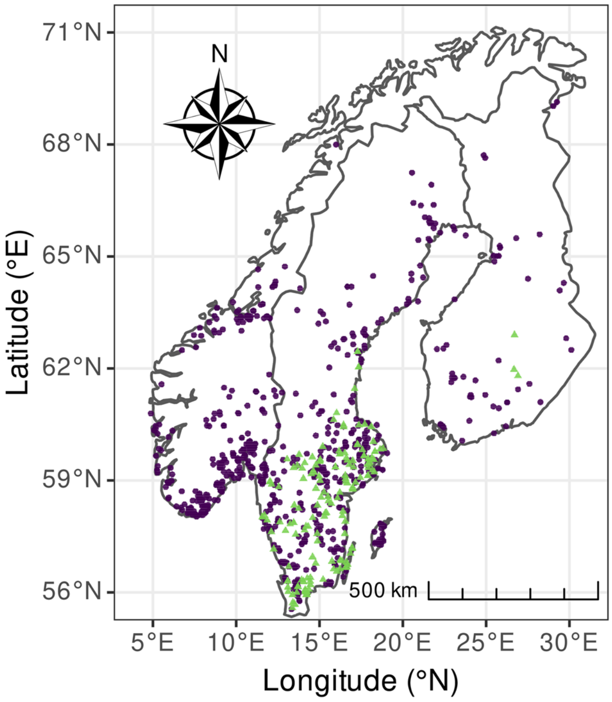

Figure 2. *Dolomedes plantarius* (green triangles) and *Dolomedes fimbriatus* (purple dots) records in Fennoscandia as of October 2019. Data were extracted from the GBIF database and supplemented by field samplings. The figure was created using R v.4.0.2[41] (https://www.R-project.org/) and the R packages ggspatial v.1.1.4[102] (https://CRAN.R-project.org/package=ggspatial), ggplot2 v.3.3.2[103] (https://ggplot2.tidyverse.org) and rnaturalearth v.0.1.0[104] (https://CRAN.R-project.org/package=rnaturalearth).

Material and methods

Occurrence data.

We downloaded records of presence for both spider species from the GBIF[40] via the rgbif package (citations for R packages are provided in Supplementary Material 1) in R[41]. The GBIF database gathers volunteer-based naturalist observations (Supplementary Material 2), which often require a quality check. We used the package CoordinateCleaner (Supplementary Material 1) to remove null or duplicate coordinates, and to flag the records requiring a subjective decision, such as old records or records located in urban areas, or at the centroid of a county. Urban records were not necessarily false presence, and we used aerial photography[42] accessed with packages leaflet and mapedit (Supplementary Material 1) to decide whether to keep these records or not. We visually checked, for instance, if a record was not in a recently modified areas in a city. Some records suggesting co-occurrence of the two species were checked in the field during summer 2018 and 2019 (25 locations, including four actually syntopic locations). We retained 775 records for *Dolomedes fimbriatus* and 181 records for *Dolomedes plantarius* (Fig. 2), reflecting the GBIF data available until October 2019 in Fennoscandia. When several records fell in the same raster cell, we kept only one.

Species distribution modelling.

Predictor variables. For the climatic component of the ecological niche, we included variables which were biologically relevant for spiders, and not too correlated[43]. Using a correlation coefficient threshold of 0.7[44], we selected mean and maximum annual temperature, mean diurnal temperature range, mean temperature of the wettest quarter, and annual precipitation, which we extracted from the WorldClim database[45] at a spatial resolution of 30 arc-seconds (Supplementary Material Table S2).

To predict the future distribution of *Dolomedes* spiders in Fennoscandia, we used IPCC projections for 2050 and 2070, under multi-factors “representative concentration pathways” (RCP) 4.5 and 8.5[46]. RCP4.5 corresponds to medium–low greenhouse gas emissions and air pollution, whereas RCP8.5 considers high greenhouse gas emission, medium air pollution, and an increase in carbon dioxide[46]. We downloaded these climatic projections from Wordclim[47] at a spatial resolution of 30 arc-sec.

For the habitat component of the ecological niche, we integrated information on ground wetness, which is an important community driver for the semi-aquatic fishing spiders[29,48]. We also incorporated forest and grassland density, because the presence of fishing spiders seems to be influenced by the surrounding landscape[49]. We downloaded the corresponding geographic layers from the Copernicus Land Monitoring Service at 100-m resolution[50], and upscaled them to 30 arc-seconds resolution to match the bioclimatic data. The forest layer represents the density of the tree cover (from 0 to 100%) in 2015. The ‘Water and Wetness’ layer represents the occurrence of wet surfaces from 2009 to 2015, using a water and wetness probability index, indicating the degree of physical wetness, independently of the vegetation cover. Finally, the grassland layer represents the percentage of grassland per pixel. We estimated the change in land use between current and future times with a model which harmonises scenarios from different integrated assessment models, namely MESSAGE for RCP8.5 and GCAM for RCP4.5[51].

Calibration area and pseudo-absences. To use presence-absence models with the presence-only GBIF data, we used a random sampling procedure with environmental profiling[52]. Which creates a background of absence records for each algorithm. We generated the pseudo-absences in a different calibration area for each species. *D. plantarius* is a lowland species, so its calibration area was at low altitude < 1000 m. For *D. fimbriatus*, we excluded areas > 1500 m.

Model validation. Although there are many SDMs, none stands out as better than the others[14]. To improve the predictions, we therefore used an ensemble forecast approach, which combines several models weighted by their predictive accuracy[53,54].

Following recommendations in Barbet-Massin et al.[55], we built our ensemble model with 10 runs of gradient boosting models (GBMs), generalized additive models (GAMs) and Maxent. We used 1000 pseudo-absences for the GBMs, and as many pseudo-absences as presences for the GAMs. We used 80% of the data for training the ensemble model and testing the single run of model, and 20% for validation. Each model was cross-validated with a fivefold procedure in package biomod2 (Supplementary Material 1), thus leading to 5 fits for each type of model and each pseudo-absences run. We then evaluated the predictive accuracy of individual models with the true skill statistic (TSS) and the area under the receiving operating curve (AUROC). The TSS metric represents the ratio of hit rate to false alarm rate and varies from − 1 to + 1[56]. We used a threshold of TSS = 0.4 to include models into the ensemble forecast[56]. The AUROC is a measure of "separability", which represents the true positive rates graphically against the true negative rates. Following Fawcett[57], we retained models with AUC > 0.7 for the ensemble model. Finally, we converted the probabilities of presence predicted by the ensemble model into a binary presence/absence, with a cut point based on predictions which maximized the TSS (Supplementary Material 1). In package biomod2, the relative variable contribution is assessed based on the correlation between the prediction of a model including a given variable and the model where this variable was dropped.

We built one model with bioclimatic variables only (model Bioc), and one with bioclimatic and land-use variables (model BLU). We then included dispersal to predict the range of suitable, but unreachable habitat (model Disp). Finally, we accounted for landscape connectivity into model dispCS. The framework is summarized in Fig. 1 (additional details in Supplementary Material Table S3).

Including dispersal into SDM. Although they differ in their general dispersal ability, the two species of fishing spider disperse mostly through ballooning and rappelling, where they catch the wind with a thread of silk, and passively fly. Laboratory tests suggested that few individuals exhibit long-distance dispersal behaviour on the water surface (unpublished data). We recorded this behaviour only in *Dolomedes fimbriatus* through sailing (when spider raised its body and/or abdomen and/or the legs to catch the wind). However, juveniles of *D. fimbriatus* are generally found in the surrounding vegetation rather than on the water[35], which makes aquatic dispersal unlikely.

We modelled dispersal ability via the MigClim package (Supplementary Material 1), based on the predicted map of the BLU model. For each species, the MigClim model evaluates if suitable cells of the raster could become accessible between current time and 2050/2070. The package uses a dispersal kernel, i.e., a vector of probabilities of dispersal, to simulate the dispersal of the species (Supplementary Table S1). We used an imperviousness map50 to locate areas where the species settlement is highly unlikely. Since both fishing spiders are water-dependent, impervious regions where the soil seals, are barrier to settlement. Part of the MigClim modelling process is random[58], so we replicated each model 30 times and model-averaged the estimates.

In experimental settings, aerial dispersal (ballooning) is usually characterized when the spider is observed tiptoeing in response to a controlled wind. However, not all tiptoeing spiders end up ballooning[59,60]. The distance covered by aerial dispersal is less than 5 km on average and is not correlated with the duration of the tiptoeing behaviour[61]. We parametrized the MigClim model with values from the literature on aerial dispersal distance in spiders[61,62]. We weighed these values by the proportion of individuals we observed rappelling in our laboratory experiments (Monsimet et al. in prep), namely, 76.6% of *D. fimbriatus* and 59% *D. plantarius*. For long-distance dispersal, we used the proportion of individuals observed ballooning (*D. fimbriatus*: 14%, *D. plantarius*: 2.9%) for 2019. We considered that the probability of a settlement was similar for both species. Also, we hypothesized that it takes two years for a newly colonized area to produce new propagules, based on the > 2-year lifespan of spiders in Northern Europe[35].

Accounting for landscape connectivity. We used the Circuitscape software[63] to predict the potential dispersal corridors that *Dolomedes* could use to colonize their suitable habitat. Circuit theory estimates multiple pathways based on the resistance and conductance of the landscape[64]. We used the habitat suitability prediction map from our BLU model to define the resistance map used by Circuitscape. We transformed the estimates of habitat suitability according to recommendations in Keeley[65] (see also Supplementary Material 3).

We used a "wall-to-wall" approach[66,67] which estimates the conductivity of the landscape from South to North, and from West to East. A consensus map was produced by multiplying the resistance layers of different directions. This consensus map was an estimation of the landscape connectivity for the two species. The consensus map was binarized by considering conductance higher than mean conductance plus standard deviation as corridors[67]. Areas outside corridors were then considered as a barrier to short-distance dispersal in Migclim. Migclim was parametrized as for the model Disp but accounting for the landscape connectivity barrier to make predictions for model DispCS.

Range expansion and geographic overlap in time. We compared suitable habitat predicted across species, models, and scenarios. To estimate the range expansion or reduction in the future, we used the biomod2

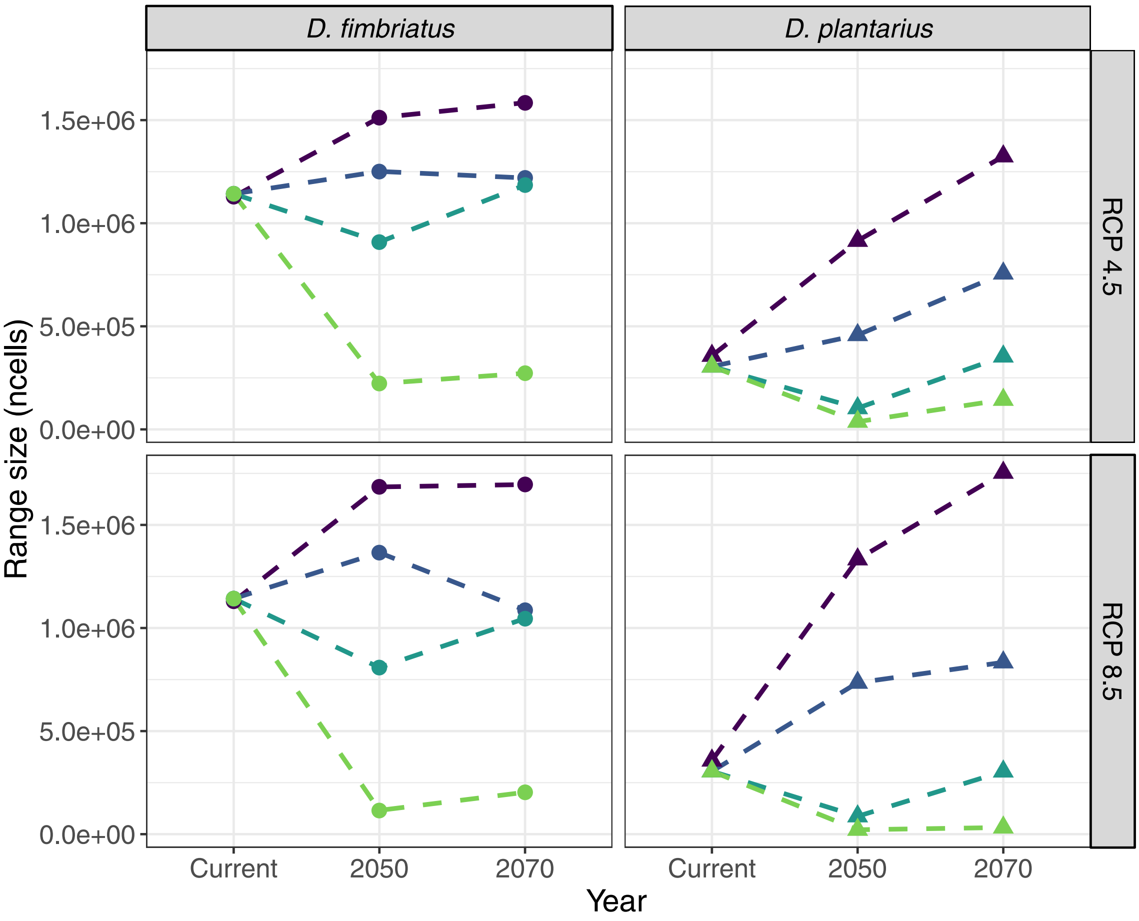

Figure 3. Range size in number of cells of suitable habitat predicted by the different SDMs in time per species and scenarios (dark purple: Bioc model: bioclimatic variables only; dark blue: BLU model, bioclimatic + land use; turquoise: Disp model with dispersal; green: DispCS model: dispersal and landscape connectivity). The figure was created using R v.4.0.2[41] (https://www.R-project.org/) and the R package ggplot2 v.3.3.2[103] (https://ggplot2.tidyverse.org).

package in R. We compared the direction of the shift in suitable habitat by calculating the centre of gravity of the suitable range with the SDMTools package (Supplementary Material 1). To estimate the overlap of suitable habitat range between species for each time/scenario combination, we used the Schoeners' D overlap metric[68], which ranges from 0 for no overlap to 1 for full overlap[69]. We estimated the suitable habitat range overlap and not the full niche overlap here. We calculated D with the ENMtools package (Supplementary Material 1).

Results

Modelling and model validation.

The predictive performance of both Bioc and BLU models was higher than the threshold with either the ROC (>0.7) or the TSS (>0.4) metric (Supplementary Material Table S3). The relative contribution of predictors was the same across models and species, with mean annual temperature the most important variable with a contribution higher than 60%. For Bioc, mean temperature of the warmest month was also important, with a higher contribution for *D. fimbriatus* than for *D. plantarius* (33% and 11%, respectively). Mean temperature of the wettest quarter, annual precipitation and mean diurnal range contributed less than 10% to both models. Forest and ground wetness contributed more than grassland in the BLU models, but their relative contribution was less than 16%.

Range expansion and geographic overlap in time.

The size of the predicted/projected range was similar for both Bioc and BLU models. However, range expansion was predicted to be more restricted when also accounting for land use (BLU) than when considering only climatic variables (Bioc). Indeed, adding land use variables contracted the suitable habitat at the limit of the range. Suitable range was also smaller for RCP4.5 than for RCP8.5, with similar patterns in time, except for *D. fimbriatus* where the range was reduced in 2070 compared to current under model BLU (Fig. 3; Supplementary Material Table S4).

Under RCP4.5 scenario, the suitable range was predicted to increase for both species in 2070 with the BLU model (14% for *D. fimbriatus* and 161% for *D. plantarius*). With model Disp, the range should decrease in 2050 for *D. fimbriatus* (20% decrease) and for *D. plantarius* (66% decrease; Fig. 3). Both species should be able to occupy the suitable range towards 2070, but both should have a limited range expansion of suitable habitat under Disp

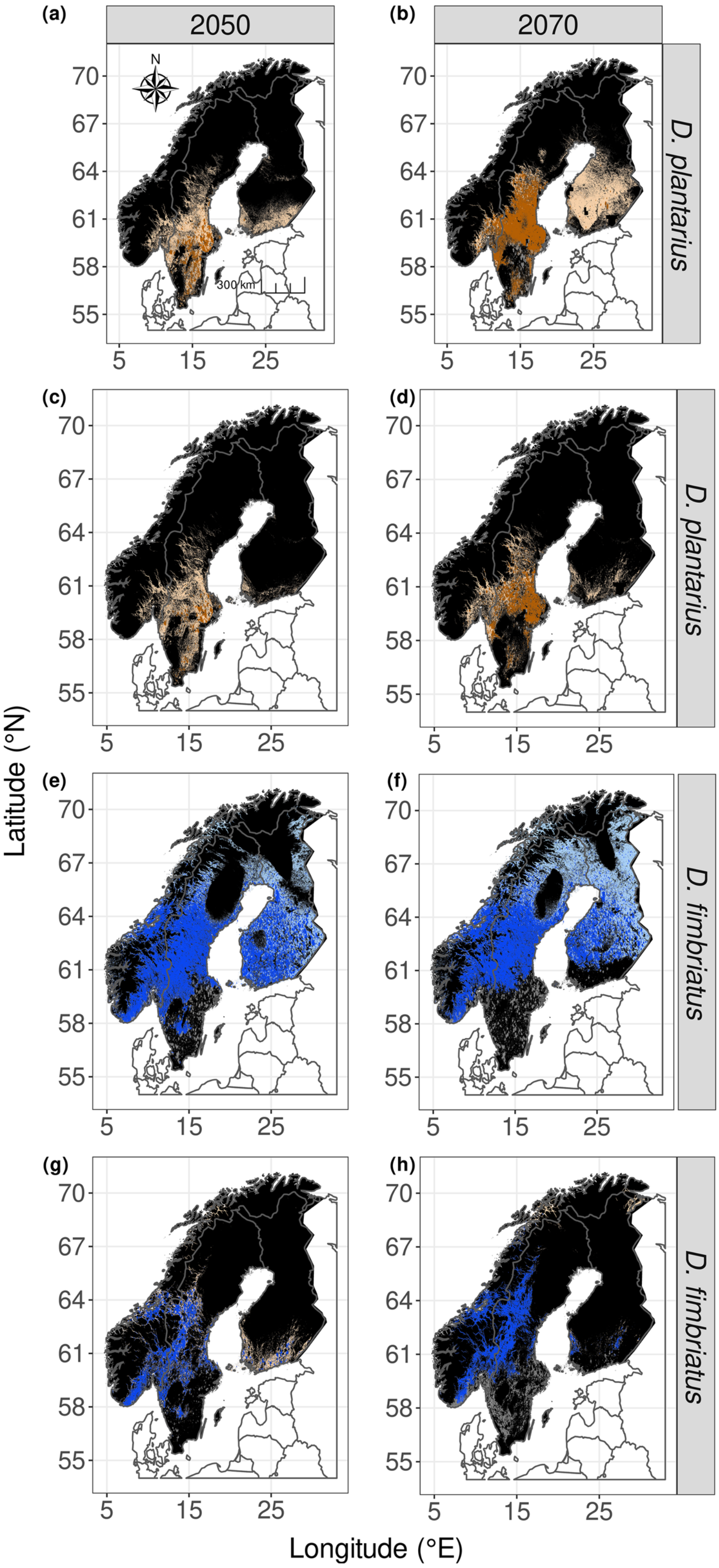

Figure 4. Map of the forecasted suitable habitat with an estimation of the reachable range predicted by the dispersion model (Disp) and reachable area from the connectivity model (DispCS) under the RCP4.5 scenario (RCP: representative concentration pathway; in dark brown the reachable habitat for D. plantarius under Disp (**a** and **b**) and DispCS (**c** and **d**); in dark blue the reachable for D. fimbriatus under Disp (**e** and **f**) and DispCS (**g** and **h**); in black: unsuitable habitat; in grey: previously occupied habitat lost; in light brown and light blue: suitable but non reachable habitat). The figure was created using R v.4.0.2[41] (https://www.R-project.org/) and the R packages ggspatial v.1.1.4[102] (https://CRAN.R-project.org/package=ggspatial), ggplot2 v.3.3.2[103] (https://ggplot2.tidyverse.org), rnaturalearth v.0.1.0[104] (https://CRAN.R-project.org/package=rnaturalearth) and ggpubr v.0.4.0[105] (https://CRAN.R-project.org/package=ggpubr).

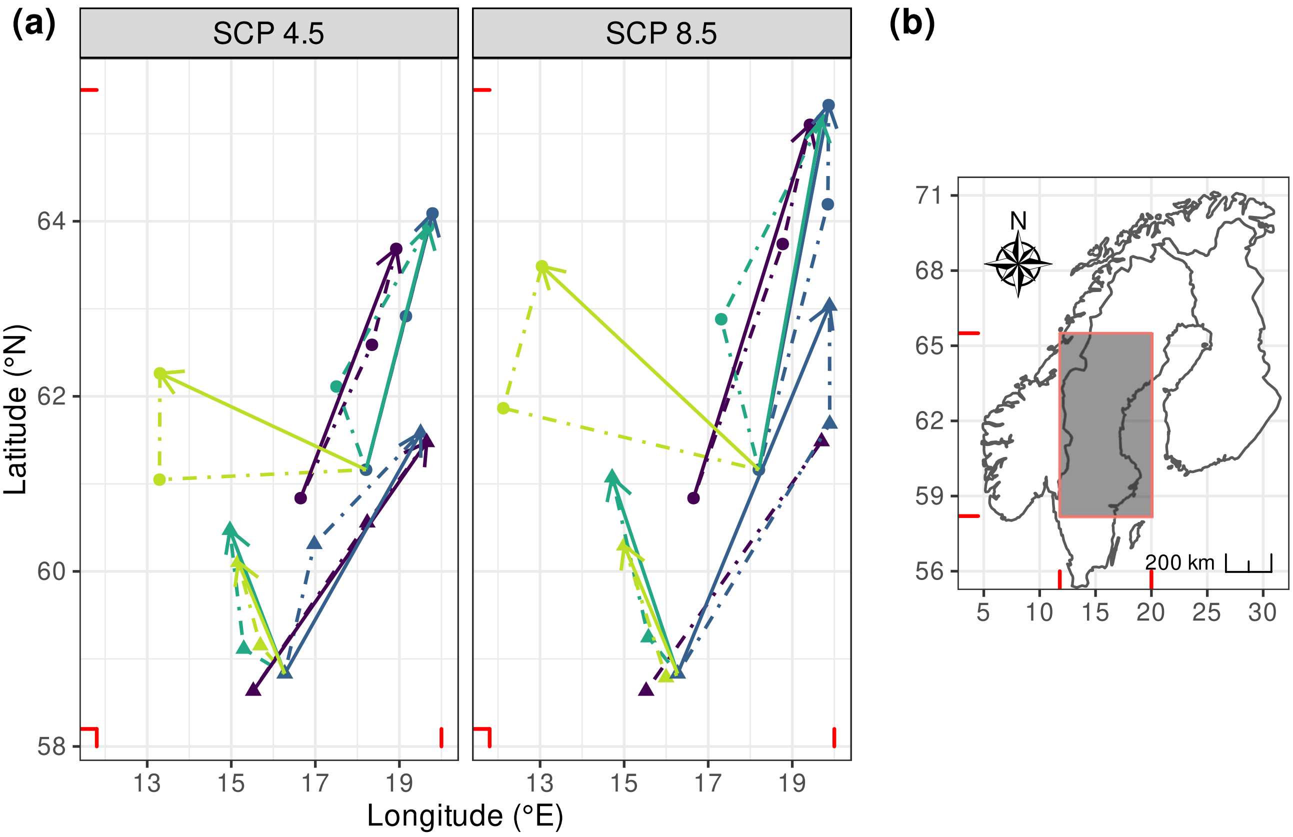

Figure 5. Shift in the centre of gravity of the two species distributions predicted by the four SDMs; solid lines: shift from current to 2070; dashed lines: shift from current time to 2050 and from 2050 to 2070. Dark purple: Bioc model; dark blue: BLU model; turquoise: Disp model; green: DispCS model. The figure was created using R v.4.0.2[41] (https://www.R-project.org/) and the R packages ggspatial v.1.1.4[102] (https://CRAN.R-project.org/package=ggspatial), ggplot2 v.3.3.2[103] (https://ggplot2.tidyverse.org), rnaturalearth v.0.10[104] (https://CRAN.R-project.org/package=rnaturalearth) and ggpubr v.0.4.0[105] (https://CRAN.R-project.org/package=ggpubr).

(Figs. 3 and 4; 14% increase under BLU and 4% under Disp for *D. fimbriatus*; 161% and 16%, respectively, for *D. plantarius*). The range of both species should shrink under DispCS (81% in 2050 and 76% in 2070, compared to current suitable habitat for *D. fimbriatus*; 88% and 53%, respectively, for *D. plantarius*).

The southern part of the suitable range should shrink, especially in Sweden and, to a lesser extent, in Finland. This range should expand in northern Fennoscandia (Fig. 4). According to model dispCS, this shift should occur towards the North-East, with a limited spread in southern Finland (Fig. 3). Similarly, the range of suitable habitat for *D. plantarius* should also increase towards the North-East under model Disp (Fig. 5). The shift of the centre of gravity is at a higher distance for the models which exclude Dispersal (Bioc and BLU) than model including dispersal (Disp and DispCS). The centre of gravity shifts farther without dispersal (models Bioc and BLU) than with dispersal (models Disp and DispCS).

The predicted distribution overlap between species was higher when considering only climatic variables than when accounting for land use at current time (Bioc model). Under the BLU model, the overlap should increase through time and is more important for the scenario SRCRCP8.5 than the 4.5 one (Schoener's D values ranging from 0.55 at current time to 0.62 in 2070 for RCP4.5, it reached 0.68 under 8.5). The overlap should mainly occur at the Southern range of *Dolomedes fimbriatus* distribution (Fig. 6; Supplementary Material Table S5).

Discussion

Using species distribution models (SDMs), we highlighted different range expansions and shifts of two closely related fishing spiders species in Fennoscandia. According to our predictions, the range of suitable habitat should expand for both *D. fimbriatus* and *D. plantarius*. Our climatic and habitat models (Bioc and BLU) confirmed the expansion of *D. plantarius* in Fennoscandia predicted by Leroy et al.[30,31]. In contrast, our hybrid models including dispersal and landscape connectivity (Disp and DispCS) predicted a more limited expansion.

Northward range expansion of both *Dolomedes* species. A northward expansion in Fennoscandia is expected for the two species under both Bioc and BLU models. The range of suitable habitat should increase with the intensity of the climate change for *D. plantarius* and for *D. fimbriatus* in 2050. This northward expansion is also predicted in other taxa, as climate change promote an expansion of the range at the colder margin[4,5]. An increase in annual mean temperature and in temperature of the warmest month, which are the most important

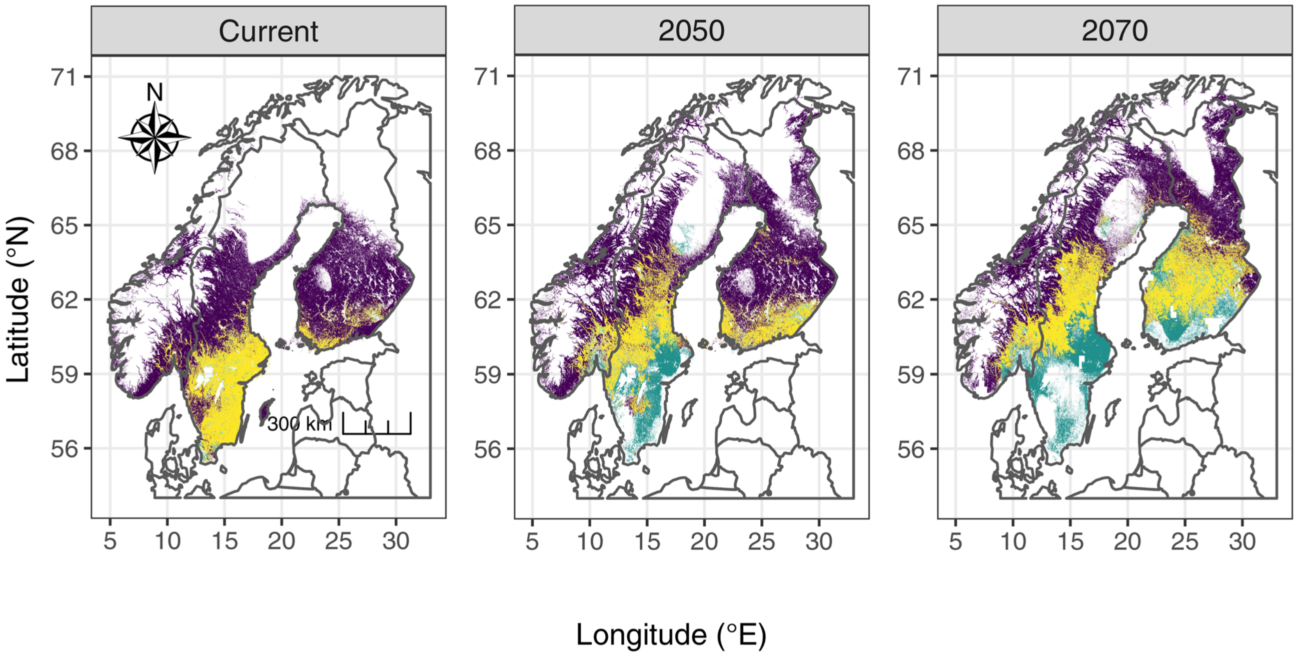

Figure 6. Range overlap predicted by model BLU from current time to 2070 under scenario RCP4.5. In addition to overlap of suitable range, suitable habitat for each species is represented. Dark purple: suitable habitat for *D. fimbriatus*; green: suitable habitat for *D. plantarius*; yellow: suitable habitat overlapping between the 2 species. The figure was created using R v.4.0.2[41] (https://www.R-project.org/) and the R packages ggspatial v.1.1.4[102] (https://CRAN.R-project.org/package=ggspatial), ggplot2 v.3.3.2[103] (https://ggplot2.tidyverse.org), rnaturalearth v.0.10[104] (https://CRAN.R-project.org/package=rnaturalearth) and ggpubr v.0.4.0[105] (https://CRAN.R-project.org/package=ggpubr).

variables for both models, could impact the lifespan of the two spider species, and affect their distribution. Higher temperatures could increase the suitable period to produce juveniles, which could in turn increase the number of juveniles dispersing. The temperature encountered by juveniles also influences the dispersal ability and mode (i.e., long vs short distance dispersal[70]). Moreover, latitude and climate affect the time at which the *Dolomedes* reach maturity[35]. This could increase the frequency of a second brood, which we already observed in September (unpublished data). Such an increase in temperature could, in turn, influence the speed of colonization of new habitats. The inclusion of land use in BLU models shrinks the range of suitable habitat, which confirms results from other, similar studies[71].

Under the Disp model, suitable habitat should be less reachable for *D. plantarius* than for *D. fimbriatus*. The size of the area reached under the Disp model should be smaller than the current area for both species. In 2070, *D. fimbriatus* should have a range slightly equivalent to the suitable habitat estimated under BLU, whereas it should be smaller for *D. plantarius*. The limited expansion of *D. plantarius* is explained mainly by dispersal ability. Indeed, we observe fewer spiderlings of *D. plantarius* showing dispersal behaviours, including long-distance dispersal through ballooning (unpublished data). Differences in predicted suitable habitat and occupied habitat can be explained by either or both past and current limited dispersal, as exemplified by tree species[72]. Some species may be limited in their geographical range and their distributions may have not changed since the last glaciation. Species that either cannot or do not shift range may be responding to climate change in situ whether through microevolution or adaptive phenotypic plasticity[73]. Some species are not yet able to adjust their phenology and physiology to changes induced by climate change. The importance of short-distance dispersal in fishing spiders should nonetheless maintain genetic exchange, or avoid genetic drift, at a smaller scale[74]. A possible prevalence of this behaviour might also reinforce the importance of shorter dispersal as climate change and other factors like the increase of habitat fragmentation decrease long-distance dispersal of spiders[75].

Geographic range overlap and coexistence. The geographic and climatic niche of *D. plantarius* are included in the realised niche of *D. fimbriatus*. The first is a habitat specialist, the last is a more generalist species living in a wider variety of environmental conditions over its range. Climate change increases the chance of overlap between these two sister species. However, we did not make predictions at a meso- or microhabitat scale, which would be too fine for SDMs. Yet, field observations suggest that both *Dolomedes* species also co-occur at finer spatial scales[35]. The discrete nature and propensity to hide and dive of *D. plantarius*[34], together with possible misidentification[36,76] might explain the small number of records and of co-occurrences. In North America, closely related species of *Dolomedes* like *D. trition* and *D. vittatus* were reported to co-occur at small spatial scales[77].

Usually, closely related species co-occur less often than moderately related species[78]. On one hand, an increase in co-occurrence might limit the distribution by segregation at the landscape scale. Indeed, the number of interactions between species in the ecosystem can increase with climate change[79], which may result in a spatial separation between generalist and specialist species[80,81]. Sympatric sister species usually diverge ecologically[82], *Dolomedes* species differ in terms of habitat use[35]. *D. plantarius* needs open habitat with slow-flowing water and water all year, while these factors do not seem to restrict *D. fimbriatus* (unpublished data). On the other hand, spatial segregation might occur at the micro-habitat scale. For instance, a study on *Tetragnatha* spiders showed that one of two co-existing spider species builds nursery webs higher in the vegetation when they co-occur[83]. Finally, an increase in co-occurrence might lead to phenological shift in co-existence sites. Our observation in two Swedish locations of *D. fimbriatus* females with juveniles in the nursery while *D. plantarius* still carried egg sacs could support this. Other closely related wolf spider species (Lycosidae) also show differences in the timing of their breeding season to avoid intraguild predation[84].

Intrinsic limits of hybrid SDMs. Ideally, a mechanistic model should account for all phases of dispersal, ie, emigration, transfer, settlement[85,86]. The SDM accounting for dispersal which we used here it not a mechanistic model but is rather based on assumptions concerning the three stages of passive dispersal. Further studies should consider factors which influence individuals' dispersal such as food availability[87], presence of endosymbionts[88], presence of conspecific in the short-long distance dispersal allocation[89], or genetically inherited propensity for dispersal via ballooning[90]. Since dispersal is not homogeneous within and among species[91], a more realistic model should include information on dispersal and population size for each presence observation. The sampling of all sites is necessary to collect this information. There is a considerable gap between the theory and actual applications of data-demanding mechanistic SDMs[26]. Knowing that the most used habitat is not necessarily the most suitable for the fitness of the species[92], we used a hybrid model based on the lack of sufficient data for a full mechanistic model.

Moreover, accounting for thermal niche information is possible with mechanistic models[93,94]. Including the lower lethal limit of *Dolomedes* could be relevant to estimate their future distributions. Indeed, we used air temperature data to characterize the temperature in our SDMs, but *Dolomedes* spiders overwinter under the snow. Climate change is impacting the snow cover, and thus, the insulation of the subnivean habitat, which is getting colder[95]. However, the current knowledge of eco-physiological responses of fishing spiders to climate change is too scarce to allow fully mechanistic models.

Conservation of fishing spiders. Fennoscandia may become a climatic refugium for *D. plantarius* as its range in continental Europe is expected to decrease[30,31]. The more extreme the climate change is, the more likely Fennoscandia will act as a refugium. The overlap between the two *Dolomedes* species should also increase with the climate change intensity. Arthropod conservation is challenging because of the fine-grain level needed as compared to vertebrates, the low empathy towards invertebrates, and the lowest number of conservation specialists available[96,97]. Nonetheless, spiders have already been used as bio-indicators[98,99]. Our models suggest that the conservation of both species is necessary as the reachable range size should drastically decrease in the future when accounting for dispersal and landscape connectivity. Conservation of preserved sites in a stepping-stones scheme is an alternative for species that are not able to use corridors[100]. Maintaining interconnected suitable sites in the first five kilometres around sites with known presence should help conserve current sites and promote expansion. With respect to fishing spiders, priority should be given to sites in southern Finland and central Sweden, where there is limited connectivity, and the spread of *Dolomedes* species is limited. Since *D. fimbriatus* has higher dispersal abilities, improving the connectivity in the North of the suitable range to make it reachable should improve the future range.

This work, together with other studies on *Dolomedes*, could be used to update the now outdated range assessment of *D. plantarius*[101]. The species' conservation would benefit from such an update.

Data availability

The datasets generated during and/or analyzed during the current study and interactive maps of the predictions of suitable/reachable habitats are available (https://doi.org/10.18710/TYPJXU).

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Author contributions

All authors contributed to the design and implementation of the research. M.J. analysed the data and drafted the manuscript. All authors contributed to writing of the manuscript and approved of the final version.

Competing interests

The authors declare no competing interests.

Additional information

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Given the ability to adapt to climate change varies greatly across species, the goal of this thesis was to evaluate the ability of the two European fishing spiders (*Dolomedes plantarius*, and *Dolomedes fimbriatus*) to shift their range and track their changing habitat. These two semi-aquatic species are widespread in Europe, but *D. plantarius* distribution is scarcer and classified as vulnerable on the IUCN red list. Their habitat -wetlands- is threatened by climate change and human activities.

In this work, I explored the *Dolomedes'* habitat requirements, tolerance to cold, and propensity for long- and short-distance dispersal, with the aim to predict the range of suitable and reachable habitat in Fennoscandia, under plausible climatic scenarios.

The results indicate that *D. plantarius* has narrower habitat requirements than *D. fimbriatus*, which has a better tolerance for lower pH and surrounding coniferous forest, absence of water, and higher altitudes. According to experimental tests with juveniles of *D. fimbriatus*, northern populations (continental climate) were more tolerant to cold than southern populations (temperate climate). In addition, the juveniles of *D. plantarius* were slightly less cold tolerant than those of *D. fimbriatus*, in Fennoscandia. *D. plantarius* also had a higher propensity for long-distance airborne and waterborne dispersal. Results for short-distance dispersal were less clear.

The capacity of the European fishing spiders to track their suitable habitat in its northward shift is constrained by landscape fragmentation, and by the limited dispersal ability of these species. The results of this thesis highlight that it is necessary to update the red-list status of these spider species, and to plan a long-term conservation and management strategy.