

Ecology and evolution of the invasive spider *Mermessus trilobatus* in Europe

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*This research is lovingly dedicated to
my Mom, Lala Narimanova and Brother, Kamran Narimanov,
who have supported me every minute of my life*

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Abstract

Invasive species play increasing roles worldwide. Invasions are considered successful when species establish and spread in their exotic range. Subsequently, dispersal is a major determinant of species' range dynamics. *Mermessus trilobatus*, native to North America, has rapidly spread in Europe via aerial dispersal. Here we investigated the interplay of ecological and evolutionary processes behind its colonisation success.

First, we examined two possible ecological mechanisms. Similar to other invasive invertebrates, the colonisation success of *Mermessus trilobatus* might be related to human-induced habitat disturbance. Opposite to this expectation, our results showed that densities of *Mermessus trilobatus* decreased with soil disturbance in grasslands suggesting that its invasion success was not connected to a ruderal strategy. Further, invasive species often escape the ecological pressures from novel enemies in their exotic ranges. Unexpectedly, invasive *Mermessus trilobatus* was more sensitive to a native predator than native *Erigone dentipalpis* during our predator susceptibility trials. This indicates that the relation between the invasive spider and its native predator is dominated by prey naïveté rather than enemy release.

The remaining three chapters of the thesis investigated the dispersal behaviour of this invasive species. Hitherto, studies of passive aerial dispersal used wind as the primary dispersal-initiating factor despite a recent demonstration of the effects of the atmospheric electric fields on spiders' pre-dispersal behaviour. During our experiments, only the wind facilitated the flight, although electric fields induced pre-dispersal behaviour in spiders. Consequently, studies around passive aerial dispersal should control electric fields but use wind as a stimulating factor.

Rapidly expanding species might be disproportionately distributed in their exotic range, with an accumulation of dispersive genotypes at the leading edge of their range. Such imbalanced spatial segregation is possible when the dispersal behaviour of expanding species is heritable. Our results showed that the dispersal traits of *Mermessus trilobatus* were heritable through both parents and for both sexes with recessive inheritance of high dispersal ability in this species.

Following the heritability experiments, we documented an accelerated spread of *Mermessus trilobatus* in Europe and tested whether dispersal, reproduction or competing ability was at the source of this pattern. Our results showed that the accumulation of more mobile but not reproductive or competitive genotypes at the expansion front of this invasive species gave rise to an accelerated range expansion by more than 1350 km in under 45 years.

Invasive *Mermessus trilobatus* is inferior to native sympatric species with respect to competing ability (Eichenberger et al., 2009), disturbance tolerance and predation pressure. Nevertheless, the species successfully established in its exotic range and spread by accelerating its expansion rate. Rapid reproduction that balances the high ecological pressures might be the other potential mechanism behind its colonisation success in Europe and deserves further investigation.

Chapter 1

General introduction

Nijat Narimanov

Biological invasions

The rates of introduction of non-native species are increasing worldwide (Seebens et al., 2018, 2021). Nonindigenous species become invasive after successful establishment and spread in their exotic range. These species successfully overcome novel ecological and biogeographical barriers, becoming abundant or even dominant in their novel areas (Fig. 1; Blackburn et al., 2011; Elton, 1958; Sakai et al., 2001).

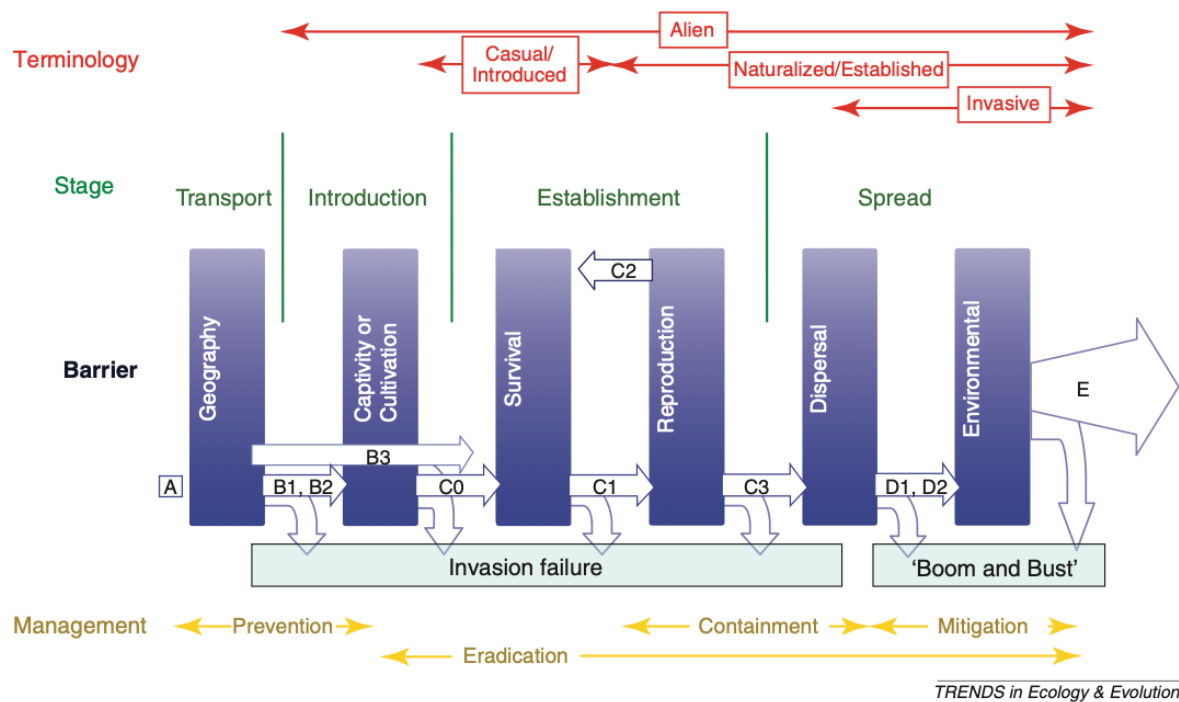


Figure 1: The invasion process comprises different stages (in green). The species are referred to by terms (in red) depending on which stage in the process they have reached after overcoming associated barriers in each stage (after Blackburn et al., 2011).

Successful invaders can play influential roles in native ecosystems (Elton, 1958; Simberloff et al., 2013), causing substantial losses of goods and services (Bradshaw et al., 2016), and hence increasing the economic investments for management strategies (Hoffmann & Broadhurst, 2016). Therefore, this does not come as a surprise that the global costs of invasions to the society of the most invasive species, *Homo sapiens*, was calculated as a total of US\$1.288 trillion between 1970 and 2017 with a mean cost of US\$26.8 billion per year (Diagne et al., 2021). There are many vivid examples of invasive species which cause economic harm in their exotic areas. For instance, the cane toad, *Rhinella marina* in Australia (Phillips et al., 2006, 2010a, 2010b; Shine et al., 2021; Urban et al., 2008), the zebra mussel, *Dreissena polymorpha* in Europe, Russia and North America (Hebert et al., 1989; Karatayev & Padilla, 1997), Asian long-horned beetle, *Anoplophora glabripennis* in Europe and North America (Hu et al., 2009; Nowak et al., 2001) or water hyacinth, *Eichhornia crassipes*, spreading in Africa, Asia, Australia, New Zealand and North America (Patel, 2012; Villamagna & Murphy, 2010). Nevertheless, the negative effects of invasive species are often unknown and hard to distinguish from other anthropogenic impacts such as human-induced habitat degradation. Thus, a growing number of studies criticise and doubt the negative impact of all biological invasions while

scientific facts are not even disputed (Munro et al., 2019; but see Sagoff, 2020, and Cuthbert et al., 2020 as a response to the previous). Such discrepancy might also arise due to the positive impact of some invasive species on their invaded ecosystems. For example, the positive effects of the invasive red macroalga, *Gracilaria vermiculophylla*, on most invertebrates in their exotic range was demonstrated (Thomsen, 2010). However, it is important to note that apart from the positive impact, the negative influence of *G. vermiculophylla* on the native ecosystem has also been identified (e.g., changing the light intensity and water movement; for a more extensive review, see Hu & Juan, 2014). Subsequently, not all invasive species negatively impact native ecosystems in their exotic range unless the effects are not identified yet, or even in some cases, the impact might have a positive character. Thus, studies investigating mechanisms behind successful invasions are needed to fully understand the complex impact of invasive species on native ecosystems.

Spiders play a central role in natural and agricultural ecosystems (Hogg et al., 2010; Michalko et al., 2019; Nyffeler & Birkhofer, 2017; Pétillon et al., 2020). Still, in contrast to insects, invasions by spiders have long been understudied (e.g., Campbell et al., 2020; Chuang & Riechert, 2021, 2022; Mowery et al., 2021; Nentwig, 2015). This is possible due to the lack of evidence for economic damage by invasive spiders and their predominantly synanthropic lifestyle (Kobelt & Nentwig, 2008; Nentwig & Kobelt, 2010). However, up to 1.3% of all spider species alone in Europe are non-native, and one new species per year is projected (Nentwig & Kobelt, 2010). *Mermessus trilobatus* (Emerton 1882), originating from North America (Millidge, 1987), is a dwarf spider from the family of Linyphiidae (Chapter 5: Fig. 1) and was first recorded in Europe in 1978 (Dumpert & Platen, 1985). Since then, the species has undergone rapid range expansion via aerial dispersal and has been registered in more than 15 European countries (Feng et al., 2021; Grbić et al., 2021; Hirna, 2017). Despite the lower competing ability with native sympatric species (Eichenberger et al., 2009), *M. trilobatus* often reaches high local abundances and is considered one of the most frequently occurring spiders in its invaded range (Nentwig & Kobelt, 2010; Schmidt et al., 2008). The mechanisms behind its invasion success in Europe are still unknown. This knowledge has implications for the invasions by non-native arthropods worldwide.

Invasion hypotheses

Up to 39 hypotheses have been developed to explain the mechanisms behind biological invasions (Table 1; Enders et al., 2020). For example, the disturbance hypothesis posits that the invasion success of non-native species is higher in areas with high disturbance levels than in those with relatively low disturbance (Elton, 1958). Thus, invasive species might benefit from reduced competition and/or high resource availability after disturbance events in ecosystems (Lear et al., 2020). Unlike other invasive spiders, *M. trilobatus* has mostly been found in open habitats within agricultural landscapes (Schmidt et al., 2008), where it could benefit from reduced competition with native species (Elton, 1958). Hence, the invasion of *M. trilobatus* in Europe might be disturbance-mediated.

Furthermore, the enemy release hypothesis speculates that non-native species transported to the new and exotic ranges leave their long-established enemies (predators, parasites, or parasitoids) in their native areas. Hence, in their exotic range, the species are released from the ecological pressures and not recognised as prey or host by local enemies due to the absence of co-evolutionary history (Elton, 1958; Keane &

Crawley, 2002). Missing co-evolution with local enemies in the invaded range and subsequent release from their ecological pressures could be another key mechanism of *M. trilobatus*' invasion success in Europe. However, note that the high reproductive ability might also drive the establishment success and rapid spread of invasive species. Consequently, *M. trilobatus* might spread in Europe despite being under high pressure by ecological and bio-geographical factors, balancing it out by possibly high reproductive investments.

Table 1: List of common invasion hypotheses and their descriptions (after Enders et al., 2020).

Hypothesis	Description	References
1. Adaptation	The invasion success of non-native species depends on the adaptation to the conditions in the exotic range before and/or after the introduction. Non-native species that are related to native species are more successful in this adaptation	Duncan & Williams (2002)
2. Biotic acceptance	Ecosystems tend to accommodate the establishment and coexistence of non-native species despite the presence and abundance of native species	Stohlgren et al. (2006)
3. Biotic indirect effects	Non-native species benefit from different indirect effects triggered by native species	Callaway et al. (2004)
4. Biotic resistance	An ecosystem with high biodiversity is more resistant against non-native species than an ecosystem with lower biodiversity	Elton (1958); Levine & D'Antonio (1999)
5. Colonisation pressure	Colonisation pressure is defined as the number of species introduced to a given location. As colonisation pressure increases, the number of established or invasive non-native species in that location is predicted to increase	Lockwood et al. (2009)
6. Dynamic equilibrium model	The establishment of a non-native species depends on natural fluctuations of the ecosystem, which influence the level of competition from local species	Huston (1979)

7. Darwin's naturalisation	The invasion success of non-native species is higher in areas that are poor in closely related species than in areas that are rich in closely related species	Daehler (2001); Darwin (1859)
8. Disturbance	The invasion success of non-native species is higher in highly disturbed than in relatively undisturbed ecosystems	Elton (1958); Hobbs & Huenneke (1992)
9. Ecological imbalance	Invasion patterns are a function of the evolutionary characteristics of both the recipient region and potential donor regions. Species from regions with highly diverse evolutionary lineages are more likely to become successful invaders in less diverse regions	Fridley & Sax (2014)
10. Ecological/ Evolutionary/ Eco-evolutionary naivety	The impact of a non-native species on biodiversity is influenced by the evolutionary experience of the invaded community. Thus, the largest impacts are caused by species (e.g., predators, herbivores, pathogens) invading systems where no phylogenetically or functionally similar species exist	Diamond & Case (1986); Ricciardi & Atkinson (2004)
11. Enemy of my enemy	Introduced enemies of a non-native species are less harmful to the non-native than to the native species	Eppinga et al. (2006)
12. Enemy inversion	Introduced enemies of non-native species are less harmful for them in the exotic than the native range, due to altered biotic and abiotic conditions	Colautti et al. (2004)
13. Evolution of increased competitive ability	After having been released from natural enemies, non-native species will allocate more energy in growth and/or reproduction (this re-allocation is due to genetic changes), which makes them more competitive	Blossey & Nötzold (1995)

14. Empty niche	The invasion success of non-native species increases with the availability of empty niches in the exotic range	MacArthur (1970)
15. Enemy release	The absence of enemies in the exotic range is a cause of invasion success	Keane & Crawley (2002)
16. Enemy reduction	The partial release of enemies in the exotic range is a cause of invasion success	Colautti et al. (2004)
17. Environmental heterogeneity	The invasion success of non-native species is high if the exotic range has a highly heterogeneous environment	Melbourne et al. (2007)
18. Global competition	A large number of different non-native species is more successful than a small number	Colautti et al. (2006)
19. Human commensalism	Species that live in close proximity to humans are more successful in invading new areas than other species	Jeschke & Strayer (2006)
20. Habitat filtering	The invasion success of non-native species in the new area is high if they are pre-adapted to this area	Weiher & Keddy (1995)
21. Invasional meltdown	The presence of non-native species in an ecosystem facilitates invasion by additional species, increasing their likelihood of survival or ecological impact	Simberloff & Holle (1999)
22. Increased resource availability	The invasion success of non-native species increases with the availability of resources	Sher & Hyatt (1999)
23. Increased susceptibility	If a non-native species has a lower genetic diversity than the native species, there will be a low probability that the non-native species establishes itself	Colautti et al. (2004)
24. Island susceptibility hypothesis	Non-native species are more likely to become established and have	Jeschke (2008)

	major ecological impacts on islands than on continents	
25. Ideal weed	The invasion success of a non-native species depends on its specific traits (e.g., life-history traits)	Baker (1965); Rejmánek & Richardson (1996)
26. Limiting similarity	The invasion success of non-native species is high if they strongly differ from native species, and low if they are similar to native species	MacArthur & Levins (1967)
27. Missed mutualisms	In their exotic range, non-native species suffer from missing mutualists	Mitchell et al. (2006)
28. New associations	New relationships between non-native and native species can positively or negatively influence the establishment of the non-native species	Colautti et al. (2006)
29. Novel weapons	In the exotic range, non-native species can have a competitive advantage against native species because they possess a novel weapon, that is, a trait that is new to the resident community of native species and, therefore, affects them negatively	Callaway & Ridenour (2004)
30. Opportunity windows	The invasion success of non-native species increases with the availability of empty niches in the exotic range, and the availability of these niches fluctuates spatio-temporally	Johnstone (1986)
31. Plasticity hypothesis	Invasive species are more phenotypically plastic than non-invasive or native ones	Richards et al. (2006)
32. Polyploidy hypothesis	Polyploid organisms, particularly plants, are predicted to have an increased invasion success, since polyploidy can lead to higher fitness during the establishment phase	Te Beest et al. (2012)

	and/or increased potential for subsequent adaptation	
33. Propagule pressure	A high propagule pressure (a composite measure consisting of the number of individuals introduced per introduction event and the frequency of introduction events) is a cause of invasion success	Lockwood, Cassey, & Blackburn (2005)
34. Resource-enemy release	The non-native species is released from its natural enemies and can spend more energy in its reproduction, and invasion success increases with the availability of resources	Blumenthal (2006)
35. Reckless invader	A population of a non-native species that is highly successful shortly after its introduction can decline or disappear over time due to different reasons (such as competition with other introduced species or adaptation by native species)	Simberloff & Gibbons (2004)
36. Shifting defence hypothesis	After having been released from natural specialist enemies, non-native species will allocate more energy to cheap (energy-inexpensive) defences against generalist enemies and less energy to expensive defences against specialist enemies (this re-allocation is due to genetic changes); the energy gained in this way will be invested in growth and/or reproduction, which makes the non-native species more competitive	Doorduyn & Vrieling (2011)
37. Specialist-generalist	Non-native species are more successful in a new region if the local predators are specialists and local mutualists are generalists	Callaway et al. (2004)
38. Sampling	A large number of different non-native species is more likely to become invasive than a small number due to interspecific	Crawley et al. (1999)

competition. Also, the species identity of the locals is more important than the richness in terms of the invasion of an area

39. Tens rule	Approximately 10% of species successfully take consecutive steps of the invasion process	Williamson & Brown (1986)
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Dispersal and rapid spread

Dispersal is a crucial feature of species' distributions and range dynamics (Bonte & Dahiriel, 2017; Chuang & Peterson, 2016). Since invasive species are characterised by rapid range expansion, dispersal plays a central role in successful invasions (Blackburn et al., 2011). Spiders, and especially linyphiids, engage in passive aerial dispersal (Blandenier, 2009; Simonneau et al., 2016) by actively performing a pre-dispersal behaviour (Reynolds & Reynolds, 2009). Spiders' dispersal can be influenced by external factors, namely meteorological factors before and during the flight (Bell et al., 2005; Cho, 2021; Sheldon et al., 2017), environmental conditions during development (Bonte, Lukáč, et al., 2008; Bonte, Travis, et al., 2008; De Meester & Bonte, 2010; Mestre & Bonte, 2012), habitat quality (Entling et al., 2011), and individuals' internal states (e.g., behaviour, physiology, morphology, genetic predisposition; Bonte et al., 2018; Clobert et al., 2009; Renault et al., 2018; Saastamoinen et al., 2018). Thus, the effects of atmospheric forces in spiders' dispersal are well studied. Although, the role of atmospheric electric fields in spiders' dispersal was long hypothesised (Loudon et al., 1830), it was only recently demonstrated for linyphiids' pre-dispersal behaviour (Morley & Robert, 2018). Yet, the comparisons of the role of electric fields relative to the wind in spiders' dispersal behaviour (successful takeoff) are missing. This knowledge has implications for the studies around passive aerial dispersal since fluctuating strengths of electric fields in the air during dispersal experiments can create an unexplained variation in the dispersal behaviour of the aeronauts.

Successful invaders rapidly expand in their exotic ranges. Expanding ranges of invasive species include the core of invasion where the species were first introduced and were present long enough to reach the balanced state of population dynamics and the highly dynamic leading range edge with the most recent spread (Chuang & Peterson, 2016). Individuals at the vanguard of the expansion are often under higher environmental pressures due to the unique selective pressures (Chuang & Peterson, 2016; Phillips et al., 2010a). Consequently, species spreading rapidly into unoccupied territories are often spatially sorted across their expansion with selection for dispersal-mediating traits at the leading edge of their expanding range (Fig. 2; Bonte et al., 2018; Chuang & Peterson, 2016; Phillips et al., 2010a). *Mermessus trilobatus* has undergone largely concentric range expansion in Europe, rapidly spreading for more than 1000 km in under 50 years (Feng et al., 2021; Grbić et al., 2021; Hirna, 2017). Hence, if the dispersal behaviour is heritable for *M. trilobatus* through generations, this species might be spatially sorted across its invaded range in Europe with an accumulation of mobile genotypes at the leading edge of the expansion.

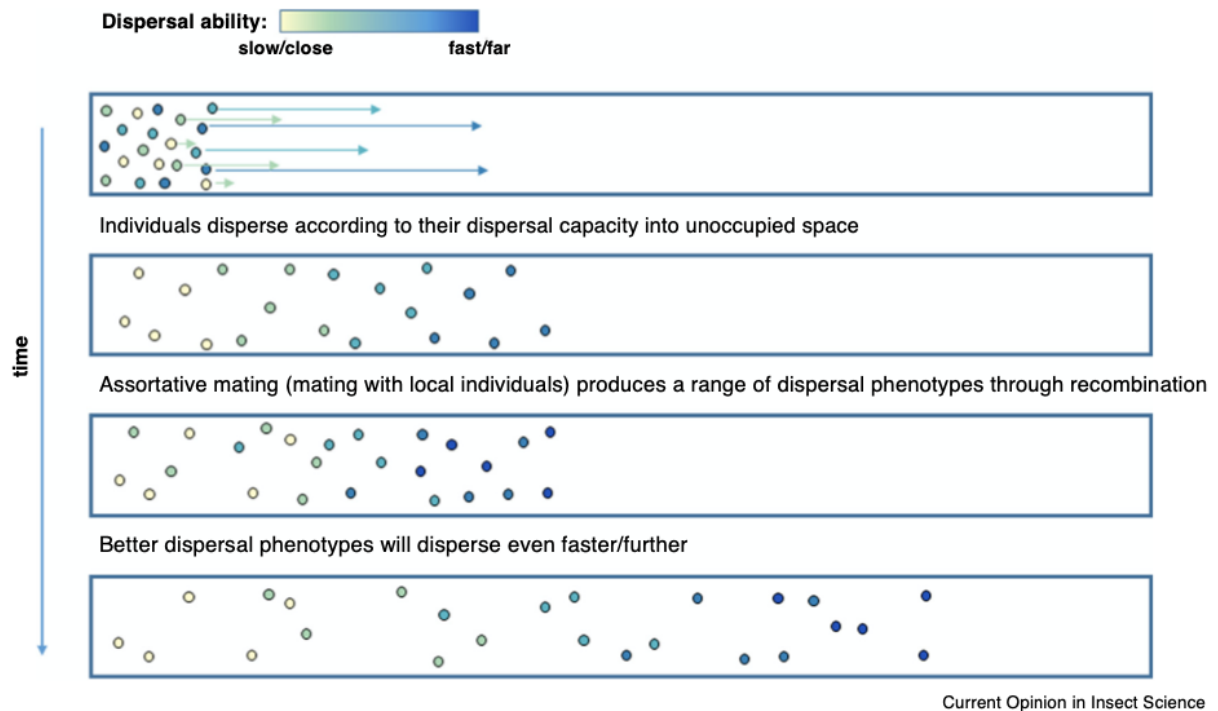


Figure 2: Diagram of the spatial sorting of the expanding species across their range based on dispersal ability. High dispersers will travel fast and far, resulting in the accumulation of high dispersers at the leading range edge. Assortative mating of high dispersers at the range edge potentially produces even better dispersers that will travel faster and further and, hence, accelerate the spread (after Bonte et al., 2018).

Research questions

Successful establishment, rapid spread, and colonisation success of *Mermessus trilobatus* in Europe make the species a suitable candidate to study ecological and evolutionary processes that determine the invasions of arthropod species worldwide. Consequently, the following questions were addressed in this research: (1) Is the invasion success of *M. trilobatus* in Europe facilitated by habitat disturbance (ruderal strategy)? (2) Is *M. trilobatus* released from a native general predator in its exotic range (enemy release)? (3) What are the roles of atmospheric electric fields in spiders' dispersal behaviour? (4) Is the dispersal behaviour of *M. trilobatus* heritable through its dam and/or sire? (5) Is the spread of *M. trilobatus* accelerated throughout its invasion history in Europe? If the spread is accelerated, (6) is *M. trilobatus* spatially sorted in Europe and which life-history traits (dispersal, reproduction or competing ability) are the driving forces of such a pattern?

(1) *Is the invasion success of M. trilobatus in Europe facilitated by habitat disturbance (ruderal strategy)?*

Mermessus trilobatus is the most abundant spider in open habitats within agricultural landscapes in parts of Europe (Schmidt et al., 2008). Its high abundance in agricultural fields and lower competing ability with sympatric species (Eichenberger et al., 2009) suggest that this invasive spider might be associated with habitats with a high level of disturbance, where it benefits from the reduced competition with native species

(Eichenberger et al., 2009; Elton, 1958). Thus, we studied the densities of *M. trilobatus* and seven native linyphiids in grasslands with and without artificial soil disturbance (see Chapter 2).

(2) *Is M. trilobatus released from a native general predator in its exotic range (enemy release)?*

Our invasive spider might not be recognised as prey in Europe due to the missing co-evolution with native predators. Thus, the enemy release hypothesis could explain the invasion success of *M. trilobatus* in Europe. To investigate that, we compared the susceptibility of *M. trilobatus* and one native linyphiid species to a shared native predator with which both linyphiid species often co-occur in European grasslands (see Chapter 3).

(3) *What are the roles of atmospheric electric fields in spiders' dispersal behaviour?*

Although the effects of atmospheric electric fields on spiders' dispersal were hypothesised already in the 1800s (Loudon et al., 1830), the role of electric fields in spider' pre-dispersal behaviour was only recently experimentally demonstrated (Morley & Robert, 2018). However, the effects of electric fields on the dispersal behaviour per se have never been investigated. To minimise the unexplained variation in individual dispersal behaviour during our experiments, we sought to disentangle the roles of electric fields and wind, as well as the combination of both in the dispersal behaviour of spiders (see Chapter 4).

(4) *Is the dispersal behaviour of M. trilobatus heritable through its dam and/or sire?*

Rapidly expanding species might be spatially sorted in their exotic range (Bonte et al., 2018; Chuang & Peterson, 2016; Phillips et al., 2010a; Shine et al., 2011). One of the main conditions of such a pattern is the genetic determination of dispersal behaviour (Bonte et al., 2018; Chuang & Peterson, 2016; Shine et al., 2011). Hence, we investigated the heritability of dispersal traits in *M. trilobatus* across two generations (see Chapter 5).

(5) *Is the spread of M. trilobatus accelerated throughout its invasion history in Europe?*

Mermessus trilobatus has spread in Europe for more than 1000 km in under 50 years (Hirna, 2017). This indicates that this invasive species has accelerated the expansion rate in its invaded range. In order to illustrate the accelerated speed of range expansion, we collected both published and unpublished data on the records of *M. trilobatus* in Europe and plotted their distribution against time (see Chapter 6).

If the spread is accelerated, (6) is M. trilobatus spatially sorted in Europe and which life-history traits (dispersal, reproduction or competing ability) are the driving forces of such a pattern?

Due to unique environmental conditions, individuals at the leading range edge of the expanding species are often under higher ecological pressures and selected for survival-facilitating traits (Bonte et al., 2018; Chuang & Peterson, 2016; Phillips et al., 2010a; Shine et al., 2011). Thus, we investigated the dispersal behaviour, reproductive output and competing ability of invasive spiders derived from two populations close to the presumed

centre of invasion (less than 50 km) and two distant populations (~600 and 780 km from the presumed centre of invasion; Dumpert & Platen, 1985; see Chapter 6).

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Chapter 2

Unexpected sensitivity of the highly invasive spider *Mermessus trilobatus*
to soil disturbance in grasslands

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Abstract The dwarf spider *Mermessus trilobatus* (Araneae: Linyphiidae), native to North America, has expanded its range over large parts of Europe within less than fifty years. It is notable for occurring in a wide range of mostly agricultural habitats, while most other invasive spiders in Europe are associated with human buildings. As in other invasive invertebrates and plants, the tremendous colonisation success of *Mermessus trilobatus* might be related to anthropogenic habitat disturbance. Here we aim to test if the

invasion success of *Mermessus trilobatus* in Europe is associated with high tolerance towards soil disturbance. We sampled spiders from eight grasslands experimentally disturbed with superficial soil tillage and eight undisturbed grasslands without tillage. Opposite to our expectation, *Mermessus trilobatus* densities decrease sharply with soil disturbance. This is in contrast to several native species such as *Oedothorax apicatus*, which becomes more abundant in the fields after superficial soil tillage. Our study suggests that invasion success of *Mermessus trilobatus* is not connected to a ruderal strategy. The ecological and evolutionary processes behind

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colonisation success of *Mermessus trilobatus* need to be further investigated.

Keywords Araneae · Disturbance · Habitat preference · Invasibility · Linyphiidae · *Oedothorax apicatus*

Introduction

Despite their essential role in ecosystems (Michalko et al. 2019; Nyffeler and Birkhofer 2017), invasions by spiders have only recently started to receive scientific attention (Nentwig 2015). One of the most widespread alien spider species in Europe is the North American dwarf spider *Mermessus trilobatus* (Araneae: Linyphiidae), formerly known as *Eperigone trilobata* (Milledge 1987; Nentwig 2015; Nentwig and Kobelt 2010; Schmidt et al. 2008). It was first detected in Europe in the late 1970s in the Upper Rhine valley near Karlsruhe in South-West Germany (Dumpert and Platen 1985). The species has undergone a largely concentric range expansion and has been recorded in numerous other countries since 1990, such as Austria, Belgium, Croatia, Czech Republic, France, Great Britain, Hungary, Italy, the Netherlands, Poland, Slovakia, Slovenia, Switzerland, and Ukraine (Hirna 2017). To our knowledge, this rapid spread makes *M. trilobatus* currently the most invasive (sensu Richardson et al. 2000) spider in Europe.

Mermessus trilobatus has mostly been collected in open habitats within agricultural landscapes and can be among the most abundant spider species there (Schmidt et al. 2008). Its occurrence in agricultural lands suggests that the invasion success of *M. trilobatus* could be based on a ruderal strategy, whereby it would benefit from reduced competition with native species in disturbed habitats (Elton 1958). Lab experiments confirm that *M. trilobatus* is a poor competitor due to its slightly smaller body size compared to native spiders living in the same habitats (Eichenberger et al. 2009). Furthermore, *M. trilobatus* might benefit from post-disturbance resource influxes to the habitat (e.g. from decomposing plant material), or from altered structure and habitat opening (Lear et al. 2020).

Here we aim to test if *Mermessus trilobatus* benefits from soil disturbance in one of its preferred habitats, perennial hay meadows. We compare its abundance to

native linyphiid spiders in replicated experimentally disturbed and control grassland sites, expecting that *M. trilobatus* abundances increase after disturbance.

Methods

Field characteristics and sampling

The experiment was conducted in 16 permanent hay meadows in the Canton of Bern, Switzerland, in 2008 (Table S2 in supplementary material). All grassland sites belonged to the same community type and were situated 0.5–50 km from each other. The treatments were randomly assigned to the 16 grassland sites. In each grassland, one plot of 240 m² was used. Eight plots were superficially tilled with a rotary tiller (Figure S1 and Figure S2 in supplementary material) in the first half of April, creating soil and ground surface disturbance (disturbed fields). The vegetation was left to decay. The other eight grasslands served as a control and were mown instead of tilled also in the first half of April, and the mown grass was left to decay (undisturbed fields in the following). Disturbance with the rotary tiller had profound effects, killing part of the vegetation and loosening the soil surface, but still leaving sufficient perennial plants alive for continuous vegetation cover. By contrast, mowing only shortened the vegetation at an early growing stage, which is common practice in this grassland type and was required for a plant introduction experiment reported elsewhere (Kempel et al. 2013), but did not affect the ground surface. The sites received the same set of plant species with variable propagule pressure at the beginning of May for the plant introduction experiment. Most adults of *M. trilobatus* are found in summer (Arachnologische Gesellschaft 2020). Thus, the spiders were sampled in late June to early July, 1–2 months after the disturbance event, which meant that the immediate impact was over, but that the vegetation was still different between disturbed and undisturbed sites. The sown plants were hardly visible at the time of sampling and were therefore unlikely to have affected the spiders in the field. We sampled spiders with a vacuum sampler with an 11 cm diameter nozzle (modified STIHL SH85 blower; Stihl, Waiblingen, Germany). It was lowered 150 times per meadow, each time over a different location, resulting in a sampled area of 1.4 m² per meadow, except for

two undisturbed plots with 200 times each, or 1.9 m² (Table S2 in supplementary material). Densities per square metre were analysed to account for this difference in sampling effort. By lowering the nozzle until just above the ground, both the vegetation and ground surface was sampled (Sanders and Entling 2011). All samples were transferred in ethanol (70%) for further identification in the lab.

Study species

All spiders were identified to species level with the aid of a stereomicroscope (Table S1 in supplementary material). Linyphiid species were identified using “The Spiders of Great Britain and Ireland” by Roberts (1987) and “Spiders of Europe” online key (Nentwig et al. 2020). The non-linyphiid spiders were identified with “Collins Field Guide: Spiders of Great Britain and Northern Europe” by Roberts (1995), names following the World Spider Catalog (Nentwig et al. 2020). To reduce the effects of rare species, we used only species present in at least half of the plots in each treatment group (at least 4). We ended up with eight linyphiids: the invasive species *Mermessus trilobatus* and seven native species, namely, *Agyneia rurestris*, *Erigone atra*, *Erigone dentipalpis*, *Oedothorax apicatus*, *Oedothorax fuscus*, *Pelecopsis parallela* and *Tenuiphantes tenuis*. These are all small (< 3 mm) spider species that live among vegetation close to the ground surface. They represent a gradient in hunting strategies, with *A. rurestris*, *M. trilobatus* and *T. tenuis* being obligatory builders of horizontal sheet webs; *E. atra*, *E. dentipalpis* and *P. parallela* capturing prey both within and outside webs; and *O. apicatus* and *O. fuscus* being free hunters (ME, personal observation; Cordoso et al. 2011).

Statistical analysis

We calculated the number of individuals per square meter in each field. We modelled the number of individuals per spider species fitting a multivariate generalized linear model (MvGLM) from mvabund package in R 3.6.1 (R Core Team 2019; Wang et al. 2012). We used a negative binomial distribution as the most flexible and appropriate for count data (O’Hara and Kotze 2010). We analysed soil disturbance (disturbed, undisturbed) as a fixed predictor with the “anova.manyglm” function with correction for

multiple tests using the “p.uni” function (test = “LR”) with 100,000 permutations.

Results

Mermessus trilobatus individuals were found in half of the disturbed and in 7 out of 8 undisturbed sites. Community composition of spiders was significantly affected by soil disturbance (Dev = 22.71; $P = 0.02$). Opposite to our expectations, *M. trilobatus* densities were reduced almost 90% after disturbance (Dev = 9.451; $P = 0.003$), and none of the native species showed a comparable decline (Fig. 1). In undisturbed grasslands, *M. trilobatus* was the most abundant spider together with *Erigone dentipalpis*. Densities of *O. apicatus* were approx. 13-fold higher in disturbed than in undisturbed meadows (Dev = 5.099; $P = 0.03$). The other six native linyphiids showed no significant response to the disturbance treatment (Fig. 1).

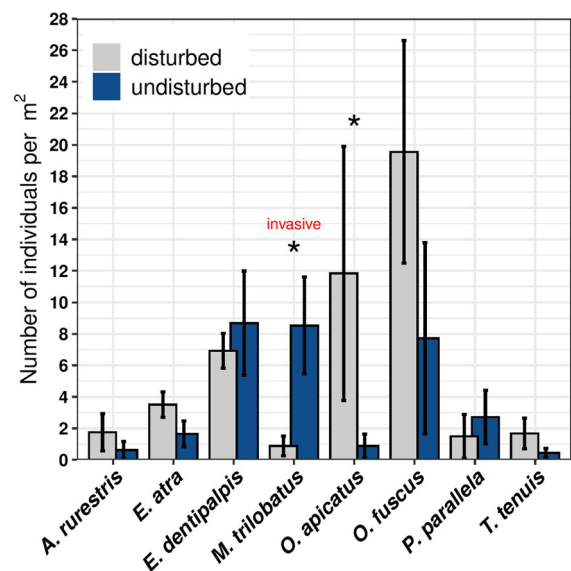


Fig. 1 Response of spiders to soil disturbance. The number of individuals per 1 m² for all 8 spider species are illustrated. Spiders were sampled from 8 meadows after soil tillage (disturbed) and 8 meadows without tillage (undisturbed). Mean ± SE are presented, with significant differences marked with asterisk. Invasive species: *Mermessus trilobatus* (Dev = 9.451; $P = 0.003$); Native species: *Agyneia rurestris* (Dev = 0.968; $P = 0.39$), *Erigone atra* (Dev = 2.909; $P = 0.12$), *Erigone dentipalpis* (Dev = 0.283; $P = 0.61$), *Oedothorax apicatus* (Dev = 5.099; $P = 0.03$), *Oedothorax fuscus* (Dev = 1.127; $P = 0.21$), *Pelecopsis parallela* (Dev = 0.194; $P = 0.64$), and *Tenuiphantes tenuis* (Dev = 2.681; $P = 0.22$)

Discussion

Opposite to our expectations, our results suggest that the highly invasive spider *M. trilobatus* is more sensitive to soil disturbance than sympatric native European species. One of the native species, *O. apicatus*, even increases in abundance in the disturbed grassland sites. The increase of *O. apicatus* in disturbed grassland does not come as a surprise since they are adapted to live and even overwinter in annual crop fields with little vegetation cover (Mestre et al. 2018; Schmidt and Tscharrntke 2005). Furthermore, since mainly cursorial spiders show avoidance behaviour towards intraguild predators like ants (Mestre et al. 2020), *O. apicatus* may benefit from soil disturbance which destroys ant nests. By contrast, the webs of *M. trilobatus* can protect them against predators (Blackledge et al. 2003). *Mermessus trilobatus* uses webs for prey capture (ME, personal observation). The destruction of these webs during disturbance represents a disadvantage. However, native obligatory web builders like *A. rurestris* and *T. tenuis* (ME, personal observation; Cardoso et al. Cardoso et al. 2011) are not sensitive to disturbance, so the hunting mode cannot fully explain the decline of *M. trilobatus*. Thus, other factors such as microclimate, prey availability, or competition with the better disturbance-adapted native species (Eichenberger et al. 2009) are potential mechanisms behind the sensitivity of *M. trilobatus* to disturbance but require further study. From an evolutionary perspective, the reduced adaptation of *M. trilobatus* to soil disturbance compared to European species may be related to the much more recent spread of annual cropping systems in its native North American range, and thus reduced time to co-evolve with intensive land-use.

Irrespective of the mechanisms, the decline of *M. trilobatus* after disturbance raises the question of how it can nevertheless be so successful in European agricultural landscapes. Importantly, the short-term decline of *M. trilobatus* observed here should not be mistaken for a general avoidance of disturbed habitats. Most (86%) of the specimens in Germany have been recorded from grasslands, which depend on regular disturbance of the vegetation layer, i.e. mowing or grazing, in this climatic region. *Mermessus trilobatus* is rarely found both in completely undisturbed habitats such as forests (2.4% of individuals), but also in highly disturbed annual crops (1.3% of individuals)

(Arachnologische Gesellschaft 2020). This avoidance of habitats with cultivated soil is in line with the results found in the current experiment.

Possible ecological mechanisms for the success of this species in Europe include the enemy release hypothesis (Roy et al. 2011). Reduced pressure by native predators, parasitoids and pathogens enhances the survival of alien relative to native species. Such potential advantages could be straightforwardly tested experimentally using important enemies of linyphiid spiders such as ants (Hymenoptera: Formicidae) or wolf spiders (Araneae: Lycosidae; Nyffeler 1999). Lastly, it is possible that *M. trilobatus* can spread in its invasive range without being limited by ecological interactions with native species, just as high numbers of native linyphiid spiders are able to coexist in the same habitat.

In summary, our study shows that in contrast to the theory of disturbance-mediated invasion success, *M. trilobatus* does not benefit from soil disturbance. Thus, other potential mechanisms behind its colonisation success remain to be studied, notably its potentially higher reproduction or reduced sensitivity to predators, parasitoids, or pathogens. Given the increasing dominance of invasive spiders in many agricultural (e.g. Hogg et al. 2010) and natural habitats (e.g. Pétiillon et al. 2020) across the globe, further studies on their ecology are strongly encouraged.

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Authors' contributions AK, ME and MvK conceived the idea; AK and MvK designed and performed the disturbance experiment; ME collected the data; NN analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Availability of data and material The dataset generated during and/or analysed during the current study is available in the Figshare repository, [<https://doi.org/10.6084/m9.figshare.12726998.v1>]

Compliance with ethical standard

Conflicts of interest The authors declare no competing interests.

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Supplementary material

Table S1

List of spider species found in 16 experimental fields. We identified all adult spiders sampled from 8 disturbed and 6 undisturbed grasslands with 150 sampling pulses and 2 undisturbed fields with 200 sampling pulses per site. Linyphiid species were identified using “The Spiders of Great Britain and Ireland” by Roberts (1987) and “Spiders of Europe” online key (Nentwig et al. 2020). The non-linyphiid spiders were identified with “Collins Field Guide: Spiders of Great Britain and Northern Europe” by Roberts (1995), names following the World Spider Catalog (Nentwig et al. 2020).

Family	Species	Total number of individuals	
		Disturbed grasslands	Undisturbed grasslands
Araneidae	<i>Araniella cucurbitina</i> (Clerck 1757)	2	0
	<i>Mangora acalypha</i> (Walckenaer 1802)	0	3
Gnaphosidae	<i>Drassyllus praeficus</i> (L. Koch 1866)	0	2
Linyphiidae	<i>Agyneta rurestris</i> (C. L. Koch 1836)	20	7
	<i>Agyneta</i> spp. 1	0	2
	<i>Agyneta</i> spp. 2	0	1
	<i>Araeoncus humilis</i> (Blackwall 1841)	7	0
	<i>Bathyphantes gracilis</i> (Blackwall 1841)	4	0
	<i>Cnephalocotes obscurus</i> (Blackwall 1834)	0	1
	<i>Dicymbium nigrum</i> (Blackwall 1834)	3	15
	<i>Diplostyla concolor</i> (Wider 1834)	1	0
	<i>Erigone atra</i> (Blackwall 1833)	40	19
	<i>Erigone dentipalpis</i> (Wider 1834)	79	109
	<i>Erigonella hiemalis</i> (Blackwall 1841)	0	1
	<i>Mermessus trilobatus</i> (Emerton 1882)	10	104
	<i>Micrargus subaequalis</i> (Westring 1851)	0	2
	<i>Microlinyphia pusilla</i> (Sundevall 1830)	1	0
	<i>Oedothorax apicatus</i> (Blackwall 1850)	135	10
	<i>Oedothorax fuscus</i> (Blackwall 1834)	223	88
	<i>Pelecopsis parallela</i> (Wider 1834)	17	31
	<i>Tenuiphantes tenuis</i> (Blackwall 1852)	19	5
	<i>Tiso vagans</i> (Blackwall 1834)	4	17
Lycosidae	<i>Alopecosa pulverulenta</i> (Clerck 1757)	0	4
	<i>Arctosa leopardus</i> (Sundevall 1833)	7	0
	<i>Pardosa agrestis</i> (Westring 1861)	2	6
	<i>Pardosa amentata</i> (Clerck 1757)	2	0
	<i>Pardosa lugubris</i> (Walckenaer 1802)	0	2
	<i>Pardosa palustris</i> (Linnaeus 1758)	27	20
	<i>Pardosa pullata</i> (Clerck 1757)	1	6
Phrurolithidae	<i>Piratula latitans</i> (Blackwall 1841)	0	19
	<i>Trochosa ruricola</i> (De Geer 1778)	1	0
Phrurolithidae	<i>Phrurolithus minimus</i> (C. L. Koch 1839)	0	1
Salticidae	<i>Heliophanus cupreus</i> (Blackwall 1841)	0	1
	<i>Heliophanus flavipes</i> (Hahn 1832)	1	4
Tetragnathidae	<i>Pachygnatha clercki</i> (Sundevall 1823)	14	3

	<i>Pachygnatha degeeri</i> (Sundevall 1830)	22	48
	<i>Pachygnatha listeri</i> (Sundevall 1830)	1	0
	<i>Tetragnatha extensa</i> (Linnaeus 1758)	2	0
	<i>Tetragnatha pinicola</i> (L. Koch 1870)	1	5
	<i>Cryptachaea riparia</i> (Blackwall 1834)	0	1
	<i>Enoplognatha latimana</i> (Hippa & Oksala 1982)	0	1
Theridiidae	<i>Enoplognatha ovata</i> (Clerck 1757)	0	1
	<i>Neottiura bimaculata</i> (Linnaeus 1767)	0	2
	<i>Phylloneta impressa</i> (L. Koch 1881)	12	1
	<i>Robertus lividus</i> (Blackwall 1836)	0	1
Thomisidae	<i>Xysticus cristatus</i> (Clerck 1757)	0	2
	<i>Xysticus kochi</i> (Thorell 1872)	1	2

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Table S2

Experimental grasslands characteristics, locations (Kempel et al. 2013) and sampling effort (number of sampling pulses per site).

Site name	Soil disturbance	Latitude	Longitude	Sampling effort
Heimiswil	disturbed	N47° 03' 58"	E7° 39' 58"	150
Signau	undisturbed	N46° 56' 28"	E7° 45' 35"	200
Rüderswil	disturbed	N46° 59' 31.81"	E7° 42' 49.31"	150
Rüderswil	undisturbed	N46° 59' 02.51"	E7° 42' 59.73"	200
Kräiligen	undisturbed	N47° 08' 30"	E7° 31' 20"	150
Bätterkinden	disturbed	N47° 07' 34"	E7° 32' 17"	150
Büren a. d. Aare	disturbed	N47° 08' 35"	E7° 23' 22"	150
Mülchi	undisturbed	N47° 06' 03"	E7° 28' 13"	150
Hindelbank	disturbed	N47° 02' 25"	E7° 33' 25"	150
Bützberg	disturbed	N47° 12' 19"	E7° 43' 24.41"	150
Bützberg	undisturbed	N47° 12' 44.15"	E7° 45' 33.31"	150
Walliswil	undisturbed	N47° 14' 51"	E7° 49' 30"	150
Worblaufen	undisturbed	N46° 59' 33.86"	E7° 28' 43.73"	150
Wiedlisbach	disturbed	N47° 14' 48"	E7° 39' 34"	150
Albligen	disturbed	N46° 51' 16.58"	E7° 19' 14.28"	150
Heimiswil	undisturbed	N47° 03' 38"	E7° 38' 43"	150

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Figure S1

Soil and ground surface disturbance created by superficial tillage with the aid of a rotary tiller (on the photo: Anne Kempel).



Figure S2.

View on a randomly assigned experimental plot of 240 m². The soil and ground surface disturbance was created with a rotary tiller (on the photo: Mark van Kleunen).



Chapter 3

Prey naïveté rather than enemy release dominates the relation of an
invasive spider towards a native predator

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Prey naïveté rather than enemy release dominates the relation of an invasive spider toward a native predator

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Abstract

Ecosystems may suffer from the impact of invasive species. Thus, understanding the mechanisms contributing to successful invasions is fundamental for limiting the effects of invasive species. Most intuitive, the enemy release hypothesis predicts that invasive species might be more successful in the exotic range than resident sympatric species owing to the absence of coevolution with native enemies. Here, we test the enemy release hypothesis for the invasion of Europe by the North American spider *Mermessus trilobatus*. We compare the susceptibility of invasive *Mermessus trilobatus* and a native species with similar life history to a shared predator with which both species commonly co-occur in Europe. Contrary to our expectations, invasive *Mermessus trilobatus* were consumed three times more frequently by native predators than their native counterparts. Our study shows that invasive *Mermessus trilobatus* is more sensitive to a dominant native predator than local sympatric species. This suggests that the relation between the invasive spider and its native predator is dominated by prey naïveté rather than enemy release. Further studies investigating evolutionary and ecological processes behind the invasion success of *Mermessus trilobatus*, including testing natural parasites and rapid reproduction, are needed to explain its invasion success in Europe.

KEYWORDS

Araneae, biological invasions, enemy release hypothesis, invasion biology, Linyphiidae, *Mermessus trilobatus*

1 | INTRODUCTION

Nonindigenous species can play influential roles in their exotic range once becoming invasive. Invasions are considered successful when alien species establish and rapidly expand their ranges in novel environments by overcoming biogeographical barriers and ecological pressures (Sakai et al., 2001). The impact of invasive species on native ecosystems has been described since the middle of the 20th

century (Elton, 1958). However, the mechanisms behind the often striking success of invasive species are still uncertain (Schultheis et al., 2015). Up to 39 hypotheses were developed to better describe the processes behind successful invasions (Enders et al., 2019). As one of the most predominant and intuitive, the enemy release hypothesis posits that nonindigenous species are released from the pressure of predators and parasites once introduced to their exotic ranges (Elton, 1958; Keane & Crawley, 2002). Introduced species

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might have advantages over resident species against native enemies by, for example, not being recognized as prey or hosts for parasites in the exotic range (e.g., Cottrell & Shapiro-Ilan, 2003; Gozzi et al., 2020; Montes et al., 2020; Tierney et al., 2020). However, Elton (1958) mentions that species leaving coevolved predators and parasites from the native areas immediately meet novel potential enemies once introduced in the exotic range. Hence, due to the lack of the coevolutionary history with novel predators, parasitoids, and pathogens, introduced species might be naïve toward novel enemies' archetypes under comparable or even higher enemy pressure in their exotic range (Cox & Lima, 2006).

Despite the popularity of the enemy release hypothesis (Hierro et al., 2005), the growing literature provides only mixed support (Heger & Jeschke, 2014; Schultheis et al., 2015). Such a discrepancy might come from the studies' different approaches based on the scale of the analysis. Biogeographical studies investigate enemy release comparing invasive animals from native and exotic populations. In contrast, community studies examine native and invasive species from the same community in the exotic range (Colautti et al., 2004). While studies at the biogeographical scale largely support the enemy release hypothesis, the results from community studies are equivocal (Colautti et al., 2004). Such differences between biogeographical and community scale studies might arise due to, for example, failure to distinguish two types of enemy release, namely compensatory, when the limited resources utilized for defense are repositioned elsewhere, and regulatory, when the loss of enemies leads directly to increase in demographic parameters (Colautti et al., 2004). This may lead to inaccurate conclusions about the net effect of enemy release at biogeographical scales. Further, studies investigating enemy release comparing the number of enemy species between natural and exotic ranges at the biogeographical scale might be ambiguous since invasive species and their enemies are often better studied in their native rather than exotic range. Hence, more enemies would be expected in native populations due to sampling efforts (Colautti et al., 2004). Additionally, only a portion of the population is being relocated to exotic regions during the transport of invasive species. Therefore, introduced populations are often genetically less diverse compared with native populations. Hence, such invasion bottlenecks could also lead to nonvalid comparisons of the populations on the biogeographical scale (for a more extensive review, see Colautti et al., 2004). Consequently, all introduced species lose enemies at the biogeographical level, irrespective of their release from enemies in their introduced range at the community level (Colautti et al., 2004).

An increasing number of studies indicate a changing role of enemy release through the different invasion phases, namely introduction, establishment, and spread (first: Drake, 2003; reviewed in Roy et al., 2011). Accordingly, release from enemies might play different roles during the introduction, establishment, or spread of invasive species in their exotic range. For instance, the parasitism of invasive mosquito *Aedes albopictus* (Diptera: Culicidae) by a native enemy is low in the introduced area only for at least two years following the colonization (Aliabadi & Juliano, 2002). Still, many invasive species fail to establish in the exotic regions after introduction.

One of the most plausible contributing mechanisms of establishment failure of invasive species may be an increased pressure by novel enemies in the introduced range (Cox & Lima, 2006; Elton, 1958). Therefore, the enemy release hypothesis as a driving force behind successful invasions should be tested for already established invasive species that are in their spreading phase (i.e., abundant or dominant) in the exotic range. Furthermore, studies investigating the role of enemy release as a causal mechanism of invasiveness are mainly based on invasive plant and vertebrate species (e.g., Carpenter & Cappuccino, 2005; Gozzi et al., 2020; Hawkes, 2007; Hierro et al., 2005; van Kleunen et al., 2010; Lankau et al., 2004; Liu & Stiling, 2006; Meijer et al., 2016; Montes et al., 2020; Schultheis et al., 2015; Tierney et al., 2020), whereas only a limited number is focused on arthropods (e.g., Aliabadi & Juliano, 2002; Juliano et al., 2010; Paula et al., 2021; Zuharah & Lester, 2010).

Spiders play essential roles in ecosystems (Birkhofer et al., 2017; Michalko et al., 2019) and can consume up to 800 million tons of prey annually (Nyffeler & Birkhofer, 2017). Despite the growing dominance both in agricultural (e.g., Hogg & Daane, 2010) and natural habitats (e.g., Pétilion et al., 2020), invasive spiders have only recently started to attract scientific attention (Campbell et al., 2020; Narimanov et al., 2021; Nentwig, 2015). The role of enemy release behind successful spider invasions, to our knowledge, has never been tested.

The North American dwarf spider *Mermessus trilobatus* (Araneae: Linyphiidae; formerly known as *Eperigone trilobata*; Millidge, 1987) was first recorded in Europe in the late 1970s near Karlsruhe in South-West Germany (Dumpert & Platen, 1985). The species has undergone a concentric range expansion in Europe, spreading by > 1,000 km in less than 50 years (Hirna, 2017) and often reaching high local abundances (Narimanov et al., 2021; Schmidt et al., 2008). The invasion success of *M. trilobatus* seems to be neither based on high competitiveness toward native linyphiids (Eichenberger et al., 2009) nor a ruderal strategy, as they do not benefit from soil disturbance (Narimanov et al., 2021). Therefore, reduced susceptibility to native predators might explain the invasion success of *M. trilobatus* in Europe.

Here, we investigate, at the community level, whether the invasion success of *M. trilobatus* in Europe is explained by the release from the pressure of native predators. Thus, we compare the invasive *M. trilobatus* and a native sympatric species' susceptibility to a shared native predator with which they frequently co-occur. We expect that in contrast to the shared coevolutionary history of the native prey and predator, invasive *M. trilobatus* would benefit from reduced predation by native predators, which could explain their invasion success in Europe.

2 | MATERIAL AND METHODS

2.1 | Study species

We chose *Erigone dentipalpis* (Araneae: Linyphiidae) as native prey because of their similar size (Table 1) and hunting mode to

M. trilobatus and because the two species often dominate in the same habitats (Narimanov et al., 2021). Spiders are exposed to various natural enemies, including other spiders as perhaps the most important predators (Foelix, 2011). Therefore, we chose *Pachygnatha degeeri* (Araneae: Tetragnathidae; body length = 3–4.2 mm), the most abundant linyphiid-eating spiders, as predators for the experiments. *Pachygnatha degeeri* are free hunters living close to the ground of the grasslands where both *M. trilobatus* and *E. dentipalpis* are found and can easily climb and invade linyphiid webs. Moreover, these generalist predators are not found in North America and, thus, are ideal candidates as native European predators (Nentwig et al., 2021). We sampled all spiders from perennial hay meadows as the preferred habitat of *M. trilobatus* (Narimanov et al., 2021). The meadows were situated next to the river Queich, close to Landau in Germany (see Table 2 for coordinates). Spiders were sampled between July and September 2020 using a vacuum sampler (modified STIHL SH86 blower; Stihl, Waiblingen, Germany). We sampled 14 *M. trilobatus* and 16 *E. dentipalpis* females and 85 adult *P. degeeri* individuals. All linyphiids were transferred individually into glass jars (405 ml) with a 1 cm layer of moist plaster of Paris to ensure high humidity inside the glasses. We kept all spiders in climate cabinets under standard conditions (25°C, RH = ~65%, L:D = 16:8). We fed all linyphiids *ad libitum* with springtails (*Sinella curviseta*) to obtain a high number of egg sacs. We transferred all offspring singly into 30-ml glass jars with a layer of humid plaster on the bottom and fed *ad libitum* until adulthood. We also kept all *P. degeeri* individuals in 100-ml glass jars with a layer of humid plaster on the bottom and fed *ad libitum* with drosophila flies (*Drosophila hydei*).

2.2 | Experimental design

Experiments were performed in 405-ml glass jars with approximately 1 cm layer of moistened plaster on the bottom and five vertical sticks to facilitate web building. We used only adult linyphiids reared in the laboratory. Prior to experiments, we measured all spiders' prosoma widths (see Table 1 for means) as an estimate of body size that is independent of the current feeding condition (Moya-Laraño et al., 2008). We assigned a randomly chosen pair of prey (invasive *M. trilobatus* and native *E. dentipalpis*) to the same predator (*P. degeeri*). Then, each linyphiid pair was tested with the same predator during two trials in random order. We calculated the difference in prosoma width by

subtracting the respective value of the predator minus the prey. We let linyphiids build webs in the glasses without food for two days before experiments. All linyphiids, irrespective of sex and species, built a web. Simultaneously, we starved predators also for two days prior to each trial for standardization. From previous observations, we expected that *E. dentipalpis* builds the web slightly closer to the surface than *M. trilobatus*. As spiders in low webs may be more exposed to ground-hunting predators such as *P. degeeri*, we sprayed the webs with water and measured their lowest and the highest position to the plaster in each glass after two days of web building. We placed predators on the surface of the plaster, avoiding any damage to webs, and gave the trials three days. We checked spiders every 24 hr. In total, we had 202 trials and tested 101 *M. trilobatus* and 101 *E. dentipalpis*.

2.3 | Statistical analysis

We modeled the consumption rate (consumed, not consumed) by fitting a generalized linear mixed-effect model (GLMM) for a binomial response from the lme4 package (Bates et al., 2015) in R 4.0.3 (R Core Team, 2020). We then applied ANOVA chi-square test (the car package in R; Fox & Weisberg, 2019) to the GLMM model to analyze the effects of prey species (*M. trilobatus*, *E. dentipalpis*), prey and predator sex, the difference in prosoma width of the predator and prey, and web minimum and maximum positions to the surface on the consumption rate. We included predator ID as a random factor since each predator was used at least twice during experiments. Additionally, we modeled the linyphiids' web positions to the surface (minimum and maximum) by fitting linear models (lm) from the R package stats (R Core Team, 2020) and included linyphiid species as fixed predictors. We then applied ANOVA *F* test to the lm models to investigate the web-building strategies of two species (*M. trilobatus* and *E. dentipalpis*). We validated the lm model results using permutation tests (PermTest function from pgirmess package in R; Giraudoux, 2021).

3 | RESULTS

Opposite to our expectation, the invasive *M. trilobatus* was consumed almost three times more often compared with native *E. dentipalpis* (Table 3, Figure 1). Furthermore, smaller prey (compared

TABLE 1 Mean values of prosoma widths (in mm), sample sizes, and the status for Europe of all spider species used for the experiments

Species	Family	Status	Prosoma widths (mm)					
			Females		Males		Combined	
			Mean	N	Mean	N	Mean	N
<i>Erigone dentipalpis</i>	Linyphiidae	Native	0.75	55	0.84	46	0.795	101
<i>Mermessus trilobatus</i>	Linyphiidae	Invasive	0.68	55	0.73	46	0.701	101
<i>Pachygnatha degeeri</i>	Tetragnathidae	Native	1.21	38	1.09	47	1.144	85

Note: Spider names follow the World Spider Catalog (Nentwig et al., 2021).

TABLE 2 Geographical coordinates of six grassland sites where all spider species (invasive *Mermessus trilobatus* and native *Erigone dentipalpis* and *Pachygnatha degeeri*) were collected

Site	Latitude	Longitude	Location
1	N49°12'03.0"	E8°08'49.2"	Landau
2	N49°12'10.7"	E8°09'24.8"	Landau
3	N49°12'16.2"	E8°06'22.3"	Landau
4	N49°12'02.7"	E8°08'57.6"	Landau
5	N49°12'05.8"	E8°10'11.4"	Offenbach an der Queich
6	N49°11'59.7"	E8°09'18.3"	Landau

TABLE 3 Outputs for logistic regression model predicting the consumption rate of prey by their species, the difference in prosoma widths between predators and prey (calculated by subtracting the respective value of the predators minus prey), spiders' sex (predators and prey), and the distance of the web to the surface (web minimum and maximum)

	χ^2	<i>p</i>
Prey species	12.49	.0004
Difference in prosoma widths	5.57	.018
Sex of prey	0.41	.52
Sex of predators	0.27	.603
Web minimum	0.16	.693
Web maximum	0.09	.761

Note: Significant correlations are shown in bold.

with predators) were consumed with slightly a higher rate than larger ones (Table 3, Figure 2). There were no effects of spiders' sex (predators and prey) and linyphiids' web positions (minimum and maximum) on their susceptibility to predation (Table 3). However, on average, native *E. dentipalpis* built their webs around 2.5 times closer to the surface (plaster) than invasive *M. trilobatus* (web minimum; $F_{1,200} = 9.843$, $p = .002$; Figure 3). There was no difference in linyphiids' web maximum positions to the surface (web maximum; $F_{1,200} = 2.472$, $p = .118$). In total, 95 out of 202 linyphiids were consumed. The highest number of *M. trilobatus* was consumed during the first two days (35 and 24, respectively), followed by the last day (11). Similarly, the highest number of *E. dentipalpis* (15) was consumed the first day, leaving the following two days with an equal number of individuals consumed (5 each). A higher number of females of *E. dentipalpis* compared with males were consumed (20 and 5, respectively), whereas similar numbers of *M. trilobatus* females and males were consumed during experiments (39 and 31, respectively).

4 | DISCUSSION

To our knowledge, this is the first empirical study testing the enemy release hypothesis on a spider. Contrary to our expectations, invasive *M. trilobatus* was more susceptible to native European predators than a sympatric native species. Our results support that the consumption rate is dependent on the predator–prey size difference (e.g., Binz et al., 2014; Preisser & Orrock, 2012). With increasing size

differences, prey were consumed more frequently. Moreover, as expected, *E. dentipalpis* built the webs closer to the ground surface than invasive *M. trilobatus*. Nevertheless, web positions (minimum and maximum) had no significant effects on linyphiids' consumption rate by predators during our trials.

During our experiments, native predators consumed seventy individuals of invasive *M. trilobatus* compared with only 25 native *E. dentipalpis*, indicating possible invasive prey naïveté toward local predators. The prey naïveté hypothesis predicts that native prey often fail to recognize and/or avoid an introduced predator due to a lack of the coevolutionary history (Cox & Lima, 2006; Sih et al., 2010). Similarly, but in a different scenario where introduced species are prey for local predators, lack of native predator recognition by invasive prey can result in increased predation on the introduced species (e.g., Barrio et al., 2010; Carthey & Banks, 2018; Ruland & Jeschke, 2020). We observed that *M. trilobatus* frequently abandoned their webs after the predators' intrusion, and once outside their webs were easily subdued by *Pachygnatha*. In contrast, native *E. dentipalpis* usually remained sheltered in their webs during our experiments. *Pachygnatha degeeri* were unable to reach *E. dentipalpis* hiding in the densest parts of their webs (KH and NN, personal observations). Thus, native linyphiids might have a better surviving strategy against these local predators through hiding rather than fleeing. Suppose such behavior is an adaptation to the situation in Europe. In that case, this could be directly tested using spiders from North America, where *E. dentipalpis* is invasive in the native range of *M. trilobatus* and confronted with North American generalist predators, which are not found in Europe (e.g., *Pachygnatha autumnalis* or *P. brevis*; World Spider Catalog, 2021).

Our results show that the invasive *M. trilobatus* is sensitive toward local European predators. *Mermessus trilobatus* has undergone rapid concentric range expansion in Europe. Spiders used in our experiments were derived from the populations less than 50 km of the presumed core of the invasion range (Dumpert & Platen, 1985). Individuals in these areas were present for at least 45 years, during which local predators might have adapted to these novel prey. Indeed, a meta-analysis by Hawkes (2007) found that invasive plant species may accumulate novel enemies over time. Additionally, another meta-analysis by Chun et al. (2010) showed that invasive plant species suffered relatively less damage than native species studied in the fields compared with greenhouses. Hence, some invasive species may dominate in the fields where natural enemies do not recognize them as a suitable food source,

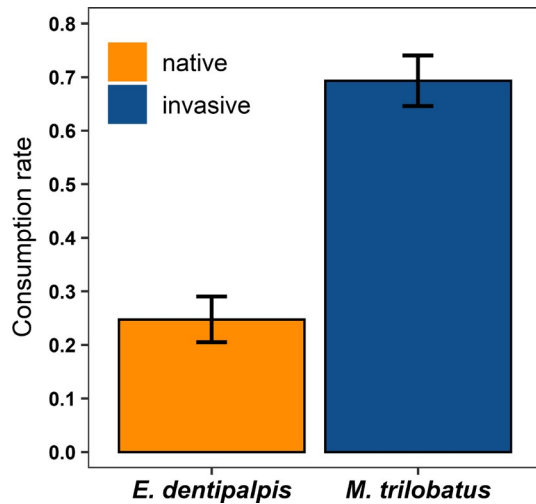


FIGURE 1 Effects of prey susceptibility to predators based on prey species (invasive: *Mermessus trilobatus*; native: *Erigone dentipalpis*). Means \pm SE are presented

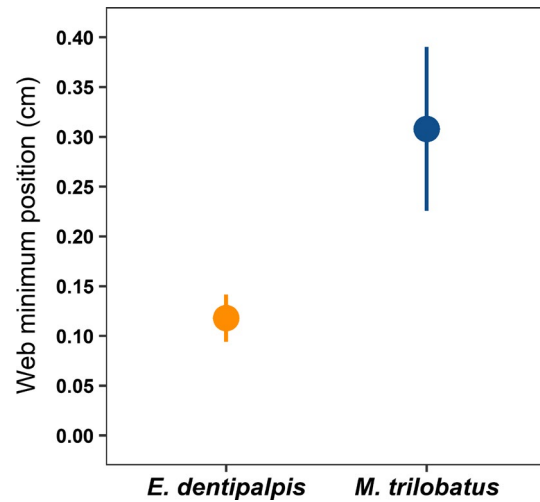


FIGURE 3 Effects of linyphiids' web minimum positions (distance to the surface in cm) based on species (native *Erigone dentipalpis* and invasive *Mermessus trilobatus*). Means \pm SE are presented

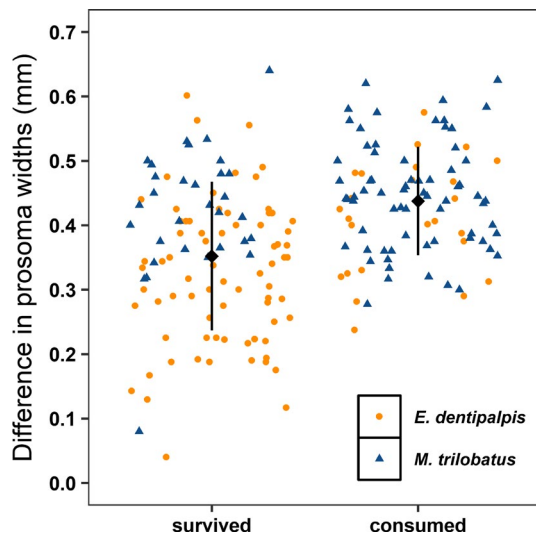


FIGURE 2 Effects of the difference in prosoma width between predator and prey on prey survival. Invasive and native prey species are shown with different shape and color (blue triangles for invasive *Mermessus trilobatus* and orange dots for native *Erigone dentipalpis*). Means \pm SE are presented

but these enemies would feed on them in enclosed conditions (e.g., Siemann & Rogers, 2003; Lankau et al., 2004; Siemann et al., 2006; but see Carpenter & Cappuccino, 2005). Consequently, ecological and evolutionary processes that drive invasions might change over time (Hawkes, 2007) and different phases of the invasion process (Drake, 2003; Roy et al., 2011), whereby local predators may increasingly recognize invasive species as potential prey over time. However, most studies on the enemy release hypothesis are focused on invasive plants and vertebrates and only a limited number on arthropods. Therefore, studies investigating enemy release as a causal effect of successful arthropod invasion and the loss of enemy pressure over time are needed to bridge this research gap.

Investigations comparing susceptibility of *M. trilobatus* to *P. degeeri* derived from the populations where *M. trilobatus* have never been found (e.g., Ireland, Russia) could test for a possible loss of enemy release and/or adaptation of *P. degeeri* to *M. trilobatus* as novel prey over time.

The invasive *M. trilobatus* tested here are sensitive toward native predators, indicating possible high top-down controlled systems. Indeed, a recent meta-analysis showed that spiders' total biomass across 54 North American grasslands failed to increase with total invertebrate biomass (Welti et al., 2020), indicating the potential control by their own predators (Sanders & Platner, 2007). Nevertheless, *M. trilobatus* was successful in colonizing a major part of Europe in a relatively short time. Higher reproductive ability of *M. trilobatus* compared with native sympatric species, balancing their high sensitivity to local predators, might still explain their rapid colonization success in Europe.

The invasion success of *M. trilobatus* is not explained by the ruderal strategy (Narimanov et al., 2021), and laboratory experiments showed that *M. trilobatus* are less competitive than native linyphiids (Eichenberger et al., 2009). Additionally, our results suggest that invasive *M. trilobatus* is more susceptible to local predators, namely *P. degeeri*, compared with a native linyphiid species. Yet, it is possible that release from parasitoids and pathogens may play a role in the colonization success of *M. trilobatus* in Europe. This deserves further investigation. Further, *M. trilobatus* might spread in their invasion range without being pressured by interspecific interactions, coexisting with natural species in the same habitats (Narimanov et al., 2021).

In conclusion, our study finds no evidence for the enemy release from a generalist native predator of the invasive *Mermessus trilobatus* in Europe. On the contrary, the invasive spiders were consumed at higher rates than native sympatric species, likely due to their naïveté toward resident predators. Previous studies investigating mechanisms behind the colonization success of *M. trilobatus* in Europe

also found no evidence for the role of soil disturbance (Narimanov et al., 2021) or higher competitive ability toward local sympatric species (Eichenberger et al., 2009). Therefore, other potential mechanisms behind their rapid spread and successful establishment, notably their high reproduction, remain to be investigated.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

Nijat Narimanov: Conceptualization (supporting); data curation (equal); formal analysis (lead); investigation (supporting); methodology (equal); visualization (lead); writing—original draft (lead); writing—review and editing (lead). **Kamal Hatamli:** Data curation (supporting); investigation (lead); methodology (supporting); writing—original draft (supporting); writing—review and editing (supporting). **Martin H. Entling:** Conceptualization (lead); Data curation (equal); formal analysis (supporting); funding acquisition (lead); investigation (supporting); methodology (equal); supervision (lead), visualization (supporting); writing—original draft (supporting); writing—review and editing (supporting).

DATA AVAILABILITY STATEMENT

The dataset generated and analyzed during this study is available in the Figshare repository [<https://doi.org/10.6084/m9.figshare.14500239.v1>].

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Chapter 4

Disentangling the roles of electric fields and wind in spider dispersal
experiments

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SHORT COMMUNICATION

Disentangling the roles of electric fields and wind in spider dispersal experiments

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Abstract. Observations of spiders' pre-dispersal behavior can be used to answer various ecological and evolutionary questions. So far, dispersal experiments have often used air currents as a stimulating factor. Effects of electric fields on the pre-dispersal behavior of spiders have recently been discovered. Electric fields may lead to unexplained variation in results and limit comparability between previous studies. Here we aim to disentangle the roles of wind and electric fields on the passive aerial dispersal of three linyphiid spider species. Our results confirm that strong electric fields in the air elicit pre-dispersal behavior, and in combination with a light wind, facilitate dispersal (take-off). Nevertheless, even the strong electric fields employed here played a rather supplementary role in spiders' dispersal with wind remaining the most influential factor. We recommend that studies of passive aerial dispersal should control for electric field strength but otherwise use wind as the primary stimulating factor.

Keywords: Araneae, atmospheric electricity, ballooning, Linyphiidae, tiptoe behavior

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Dispersal is a widespread feature of animal life (Sheldon et al. 2017). Numerous species from at least 29 spider families disperse passively as aerial plankton (Bell et al. 2005). Such airborne migrants are largely dependent on atmospheric forces and have very little ability to control their flight. However, the take-off is mostly initiated by the organism, and individuals usually enter the airstream actively by performing pre-dispersal behavior (Reynolds & Reynolds 2009).

In spiders, dispersal over a long distance is called “ballooning”, where individuals become airborne by emitting threads of silk in the air. Spiders also disperse over short distances by “rappelling”, when the thread attaches to nearby substrate and is then used by the spider as a bridge to climb along. Prior to ballooning and rappelling, a spider performs a pre-dispersal behavior called “tiptoeing”. It shows a motivation to disperse by climbing to an elevated position, straightening its legs, lifting its abdomen and releasing silk threads into the air. Apart from dispersal behavior, tiptoeing is important for ecological and evolutionary studies since it indicates spiders' willingness to disperse (Weyman 1993; but see Lubin & Suter 2013).

Multiple environmental conditions can influence spider ballooning behavior, including temperature, humidity and wind speed (Bonte et al. 2007; Simonneau et al. 2016; Postiglioni et al. 2017). Hitherto, most experiments addressing evolutionary and ecological questions around spider ballooning have used air currents (< 3 m/s) as stimulating factors and driving forces for aerial dispersal (e.g., Greenstone 1982; Weyman 1995; Bonte et al. 2007; Entling et al. 2011; Mestre et al. 2014; Wolz et al. 2020). However, a role of atmospheric electric fields in passive aerial dispersal was hypothesized and discussed already in the 19th century (Loudon et al. 1830). It was recently demonstrated that electric fields (e-fields) in the air elicit pre-dispersal behavior in linyphiid spiders and that spiders can sense e-fields with their trichobothria (Morley & Robert 2018). Consequently, the lack of control on the presence of e-fields during earlier ballooning experiments could lead to unexplained variation in the results and limit comparability between studies.

Here we aim to disentangle the roles of wind and e-fields for passive aerial dispersal using three spider species from the family Linyphiidae, which are frequent aeronauts (Blandenier 2009). We study the single and combined effects of e-fields and wind on tiptoe behavior and aerial dispersal (take-off).

We collected three spider species from the family Linyphiidae, namely *Agyneta rurestris* (C. L. Koch, 1836), *Erigone dentipalpis* (Wilder, 1834) and *Mermessus trilobatus* (Emerton, 1882) from hay meadows in southwest Germany and northeast France between June and August 2019 using a vacuum sampler (modified STIHL SH86 blower; Stihl, Waiblingen, Germany). *Agyneta rurestris* and *E. dentipalpis* were selected because they were most abundant in the sampled grasslands. *Mermessus trilobatus*, which is native to North America, was included because we were planning a more detailed study on the evolution of its dispersal during its invasion process in Europe (Narimanov et al. 2021). We transferred all individuals into glass jars (100 ml) with a 1 cm layer of plaster of Paris to create a humid environment for housing and kept them inside climate cabinets under standard conditions (25°C, RH = ~100%, L:D =16:8). We fed all spiders *ad libitum* with springtails (*Sinella curviseta*).

We adapted our experimental setup from the experiments of Morley & Robert (2018). The setup was comprised of a wooden frame holding two horizontal 0.8 × 0.8 m² metal electrodes, 0.8 m above each another. We used a high voltage power supply (PHYWE Systeme GmbH und Co. KG; Göttingen, Germany; Product number: 13671-93) to create an electric field in the area between the electrodes. To match natural conditions, where the lower electrode acts as the negatively charged grounded earth surface and the area above as the atmospheric potential gradient, we charged the upper electrode positively relative to the grounded lower electrode. We used the field strength of 6.25 kV/m by applying 5 kV over the distance of 0.8 m between the electrodes. The value is quite high and represents the e-fields in the atmosphere during disturbed weather. The value was chosen because it revealed clear responses in a previous study (Morley & Robert 2018). We placed the dispersal platforms in the middle of the lower electrode. To provide an elevated point, the dispersal platform consisted of a 7-cm tall

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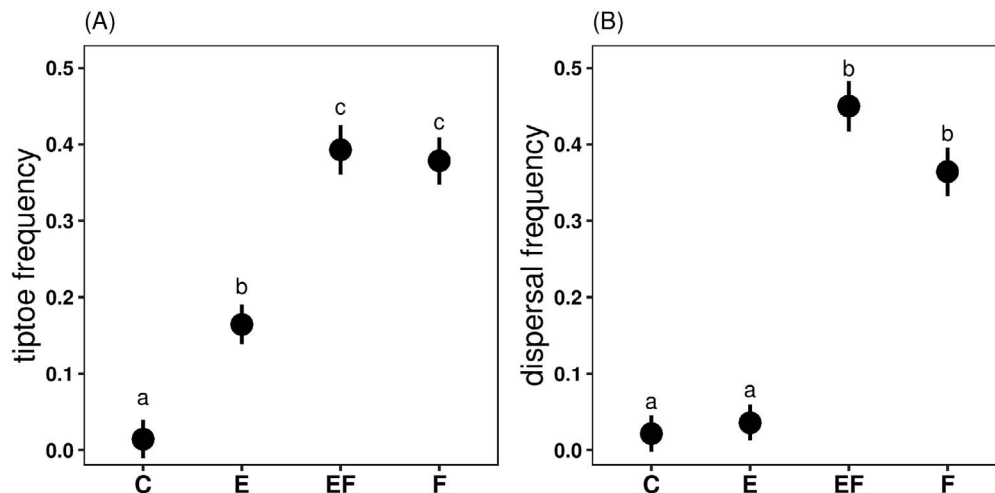


Figure 1.—Effect of treatments (C = control; E = e-fields; EF = e-fields and fan; F = fan) on tiptoe (A; presence/absence) and dispersal behavior (B; presence/absence). Means \pm SE are presented. Differences between the treatment groups are illustrated with letters based on the results from the Tukey contrast test.

wooden stick pointed vertically upwards in a 2.5 cm diameter disk made of plaster of Paris. We prevented spiders from escaping by placing the platforms in the middle of a 7-cm petri dish filled with water. The plaster was saturated with water, and a wire grounded it to the lower electrode. We placed a table fan (diam. = 23 cm, 30 W) approx. 1 m beside the arena at the level of the lower electrode to provide a suitable wind with a range of 1.3 m/s – 2.3 m/s (Simonneau et al. 2016). Before the experiments, we measured the wind velocity at the position of the arena, in the middle of the bottom electrode, using a cup anemometer (PCE – A420). For control and wind treatments, no voltage was applied, and the interconnected electrodes were electrically grounded in order to shield the arena against possible e-fields existing in the room. We used a vertically oriented textile mesh at a horizontal distance of 1.5 – 2 m downwind from the arena to capture dispersing individuals.

We had four treatments, namely control (C), e-fields (E), fan (F), and the combination of e-fields and fan (EF) to test the roles of the wind and e-fields, as well as a combination of both on dispersal behavior. We subjected each spider to all treatments in a randomized order during consecutive days; one treatment a day. In each trial, we placed a spider on the dispersal platform and observed it for up to 10 minutes. We stopped experiments after 10 minutes or once the spider dispersed. We washed and wiped the dispersal platforms between the trials to remove silk and possible chemical cues left by the previous spider. All individuals were offered no food for at least three days before the experiment to standardize starvation levels and to increase the likelihood of dispersal (Weyman et al. 1994). We used 140 adult individuals in total (40 *A. rurestris*; 36 *E. dentipalpis*; 64 *M. trilobatus*) for dispersal assays. We recorded the presence of tiptoe behavior and dispersal events (take-off) during the 10 minutes of observation.

We modelled tiptoe and dispersal behavior (presence/absence) by fitting generalized linear mixed-effects models (GLMM) for a binomial response from the lme4 package (Bates et al. 2015) in R 3.6.1 (R Core Team 2019). We analysed the explanatory variables, namely treatment (C, E, EF, F), species (*A. rurestris*, *E. dentipalpis*, *M. trilobatus*) and also the interaction (treatment \times species) as fixed predictors by ANOVA χ^2 -test from the R package car (Fox & Weisberg 2019) on logistic regression (glmer). We used a Tukey contrast test to illustrate the difference between the treatments by using the glht function from the multcomp package in R (Hothorn et

al. 2008). We included individual ID as a random factor for the within-subject design. Data are available from Figshare, online at: <https://doi.org/10.6084/m9.figshare.13116509.v1>

Both tiptoe ($\chi^2 = 38.21$, d.f. = 3, $P < 0.0001$) and dispersal behavior ($\chi^2 = 49.78$, d.f. = 3, $P < 0.0001$) were strongly influenced by the experimental treatments. E-fields alone significantly increased the spiders' tiptoe behavior, but the effect of wind was more than twice as strong (Fig. 1A). By contrast, spiders' dispersal did not increase under the e-fields but was dependent exclusively on the presence of wind (Fig. 1B). Highest rates of tiptoe behavior and dispersal were observed when the e-fields and wind were combined, but the difference from wind alone was not significant (Fig. 1). There were also significant differences in behavior among species, both in tiptoe ($\chi^2 = 47.8$, d.f. = 2, $P < 0.0001$) and dispersal ($\chi^2 = 32.76$, d.f. = 2, $P < 0.0001$) (Fig. S1 in supplementary material, online at: <http://doi.org/10.1636/JoA-S-20-063.s1>). The highest number of tiptoe events were performed by *E. dentipalpis* (60%), followed by *A. rurestris* (23%) and *M. trilobatus* (17%). Also, dispersal frequencies were higher in *A. rurestris* (47%) and *E. dentipalpis* (42%) than in *M. trilobatus* (11%). The interaction of treatment and species was not significant (tiptoe: $\chi^2 = 6.95$, d.f. = 6, $P > 0.05$; dispersal: $\chi^2 = 10.13$, d.f. = 6, $P > 0.05$), indicating a similar response to the treatments among the tested species.

To our knowledge, this is the first empirical study testing the single and combined effects of e-fields and wind on passive aerial dispersal. Our study confirms that e-fields motivate linyphiid spiders' dispersal by eliciting a higher frequency of tiptoe behavior. However, linyphiids become airborne more frequently in the presence of wind. There was only a single case among the trials where the e-field alone was sufficient to lift the spider in the absence of wind. Interestingly, 80% (4 out of 5) of all dispersal events with the e-field treatment was performed by rappelling. Thus, the forces provided by e-fields in isolation were sufficient to drag and lift a negatively charged thread (Hawthorn & Opell 2002) but not to bring the spider aloft within our experimental setup. However, as the upper electrode limited the vertical room of our setup to 0.8 m, investigations in setups that provide more vertical space or even field studies would be needed to appropriately test if spiders can get airborne with electric fields alone. As e-fields were not required to motivate high tiptoe or dispersal events in our study, future experiments could work with air currents only. Still, the setups should be shielding experimental arenas from

the ambient e-fields to avoid any uncontrolled variation that these may cause in spider behavior. Alternatively, e-fields could be measured and statistically controlled for. However, as the measurement of static e-fields requires specialized equipment, shielding the experiment from the ambient field will usually be the more pragmatic solution.

The values of e-fields used here are relatively high, typical for exposed positions such as tree crowns in so-called disturbed weather (Bennett & Harrison 2007). By contrast, spider ballooning has widely been reported in fair weather conditions when the values of e-fields are much lower (Vugts & Van Wingerden 1976). Moreover, the studied linyphiid species are grassland spiders that prevalently balloon from the tip of grass or any other elevated position in open habitats. The strengths of e-fields in open habitats can vary between +0.05 and +0.3 kV/m (Bennett & Harrison 2007) with simulated values at the tip of grass blade reaching up to 1 kV/m (Morley & Gorham 2020). In contrast to the 6.25 kV/m applied here, e-fields of 1.25 kV/m had no significant effect on the tiptoe behavior of *Erigone* spp. in Morley & Robert (2018). Hence, the effects of even weaker e-fields appear unlikely. Still, to explore the roles of e-fields in less extreme situations, experiments implementing a wider range of e-fields strengths are needed. For example, the e-fields equivalent to the strength often found in grassland with the inclusion of a combination of different wind speeds.

The present study confirms that strong electric fields in the air motivate linyphiid spiders to disperse by eliciting higher tiptoe behavior, and in combination with a light wind, facilitate dispersal (take-off). Nevertheless, even the strong e-fields employed here played a rather supplementary role in linyphiid spiders' dispersal with air current remaining the most influential factor. Thus, e-fields could function as initial cues to initiate movement, but their potential roles for take-off requires study in more realistic situations. Considering also the higher technical effort to create electric fields compared to airflow, we recommend that ecological and evolutionary studies of passive aerial dispersal should control for electric fields strength but should otherwise use wind as a primary stimulating factor.

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SUPPLEMENTAL MATERIAL

Figure S1, available online at <http://doi.org/10.1636/JoA-S-20-063.s1>

Data are available from Figshare, online at: <https://doi.org/10.6084/m9.figshare.13116509.v1>

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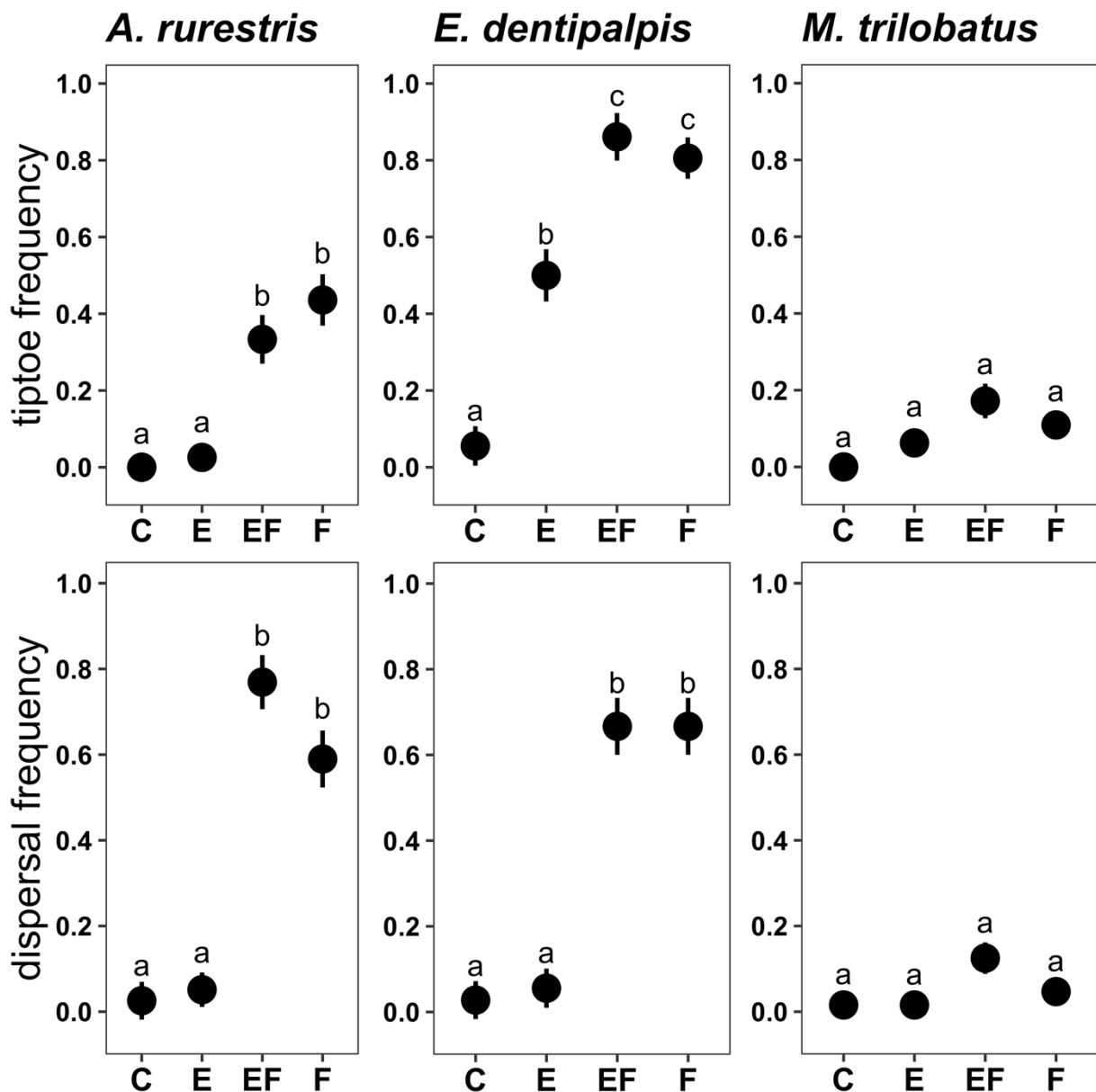
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Supplementary material

Figure S1

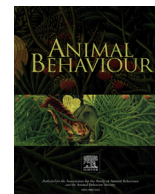
Effect of treatments (C = control; E = electric fields; EF = electric fields and fan; F = fan) on tiptoe (presence/absence) and dispersal behaviour (presence/absence) for all three species, namely *Agyneta rurestris* (N = 40; tiptoe: $\chi^2 = 10.39$, d.f. = 3, P = 0.015; dispersal: $\chi^2 = 27.28$, d.f. = 3, P < 0.0001), *Erigone dentipalpis* (N = 36; tiptoe: $\chi^2 = 25.12$, d.f. = 3, P < 0.0001; dispersal: $\chi^2 = 21.43$, d.f. = 3, P < 0.0001) and *Mermessus trilobatus* (N = 64; tiptoe: $\chi^2 = 3.60$, d.f. = 3, P = 0.308; dispersal: $\chi^2 = 8.19$, d.f. = 3, P = 0.042). Means \pm SE are presented. Differences between the treatment groups are illustrated with letters based on the results from the Tukey contrast test.



Chapter 5

Heritability of dispersal in a rapidly spreading invasive spider

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Heritability of dispersal in a rapidly spreading invasive spider

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Dispersal is an inseparable feature of animal life and a major determinant of species distributions and range dynamics. However, the role of the genetic architecture of dispersal behaviour, and hence the potential for its evolution in range-expanding species, is poorly understood. Here, we aimed to determine the heritability of dispersal behaviour for an invasive dwarf spider, *Mermessus trilobatus*, which has undergone rapid range expansion in Europe in the last few decades. Our results showed that spider dispersal traits were repeatable for the parental generation and heritable through both dam and sire. Behaviours were similarly heritable for female and male offspring. Interestingly, offspring of highly dispersive dams and sires exhibited almost three times higher dispersal propensity than offspring of at least one low-dispersive parent. The substantially high dispersal behaviour of the offspring of strictly highly vagile dams and sires indicates its recessive inheritance in this species. Recessive inheritance could favour invasiveness by facilitating high dispersal in inbred founder populations at the invasion front and returning to nonexaggerated mobility soon after an increase in genetic diversity.

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Dispersal is essential for adaptation and survival in new or changing environments (Hansson & Åkesson, 2014; Sheldon et al., 2017). It comprises all types of movements of animals and their propagules that result in increased gene flow across space (Ronce, 2007; Saastamoinen et al., 2018). Despite associated costs and risks (Bonte et al., 2012), dispersal can be favourable for species through lowering the density of kin, decreasing the rates of inbreeding and the probability of lineage extinction, and escaping pressures from natural enemies and conspecifics (Chuang & Peterson, 2016; Gandon, 1999; Lambin et al., 2001). Individual variation in dispersal can be explained by external factors (e.g. density dependence, habitat quality, inbreeding and outbreeding risks, kin competition, temperature during development) and internal state (e.g. behaviour, morphology, physiology; Bonte et al., 2008; Clobert et al., 2009; De Meester & Bonte, 2010). However, most studies focus on external factors as the main driving forces behind variation in individual dispersal behaviour. In contrast, the genetic background of dispersal behaviour and its role behind

species distributions and range expansions are largely understudied (Bonte et al., 2018; Renault et al., 2018). Moreover, the available evidence is biased towards birds, insects and plants (Saastamoinen et al., 2018).

Range expansions could lead to spatial sorting whereby better dispersers accumulate in the areas close to the edge of the expanding range. At these low-density sites, highly vagile individuals often mate with each other resulting in dispersal-mediated spatial selection (Bonte et al., 2018; Shine et al., 2011). Owing to the variation in the offspring's dispersal ability, the process could repeat by creating positive feedback loops manifesting in a continually expanding range (Bonte et al., 2018; Chuang & Peterson, 2016; Phillips et al., 2010a). One of the most intuitive causal mechanisms behind this accumulation of dispersive genotypes at the invasion front is the possible heritability of the dispersal traits across generations (Chuang & Peterson, 2016; Shine et al., 2011). Thus, if any dispersal component is heritable, then highly vagile parents will also produce highly dispersive offspring, leading to the 'Olympic Village effect' (Phillips et al., 2010a; Shine et al., 2011). A meta-analysis across 71 species by Dochtermann et al. (2019) showed that migratory/dispersal behaviours, defined as a single or repeated movement between areas during an organism's life, are more heritable than other behavioural and life

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history traits and physiological responses. Although the analysis showed no difference in heritability estimates between vertebrates and invertebrates, the data set was taxonomically biased (83% from vertebrates; [Dochtermann et al., 2019](#)), indicating a lack of research in invertebrate trait heritability.

Evolutionary drivers of behaviour can differ between the sexes, often leading to behavioural differences between males and females (reviewed in [Schuett et al., 2010](#)). Correspondingly, the heritability of behavioural traits can also be sex specific (e.g. [Han & Dingemanse, 2017](#); [Kralj-Fišer et al., 2019](#); [Li & Kokko, 2019](#); [Saastamoinen, 2008](#); [Yip et al., 2021](#)). Sex-specific heritability of dispersal might play an important role in the dynamics of range expansion ([Trochet et al., 2016](#)). For example, inheritance of the often higher dispersal in males than females would contribute little to range expansions and could even reduce expansion velocity at the range fronts ([Miller & Inouye, 2013](#)). By contrast, high female dispersal could accelerate the spread, particularly if fertilized females are capable of long-distance dispersal ([Van Wingerden, 1980](#); [Weyman et al., 2002](#)). This is the case in dwarf spiders (Araneae: Linyphiidae; [Weyman et al., 2002](#)), which are the numerically dominant spider family in temperate to cold climates ([Coddington & Levi, 1991](#)).

Biological invasions play an increasing role in global biodiversity patterns ([Simberloff et al., 2013](#)). Non-native species are considered invasive when they successfully establish and rapidly spread in their exotic range by overcoming novel ecological pressures ([Blackburn et al., 2011](#); [Sakai et al., 2001](#)). Since the role of dispersal is central in range expansions, the phenotypic variation in individual dispersal ability may accelerate or limit biological invasions ([Renault et al., 2018](#)). Therefore, dispersal behaviour and hence the heritability of high dispersal, including sex-specific inheritance, could play an essential role in invasion success.

Despite the growing impact of invasive species on ecosystems and human welfare ([Mooney, 2005](#); [Pimentel et al., 2005](#)), invasions by spiders have only recently started to attract scientific attention ([Campbell et al., 2020](#); [Chuang & Riechert, 2021](#); [Mowery et al., 2021](#); [Narimanov, Kempel et al., 2021](#); [Nentwig, 2015](#)). *Mermessus trilobatus* (Araneae: Linyphiidae; formerly known as *Eperigone trilobata*) is a North American dwarf spider ([Millidge, 1987](#)) that was first recorded in Europe in the late 1970s in southwest Germany ([Dumpert & Platen, 1985](#)). The species has undergone a rapid spread in Europe ([Hirna, 2017](#)), expanding its range by more than 1000 km in 50 years. These small spiders (1.6–2.1 mm) live among vegetation close to the ground surface ([Nentwig et al., 2021](#)) and frequently engage in aerial dispersal ([Blandenier, 2009](#)).

Spiders disperse over long distances via ‘ballooning’, where individuals release threads of silk in the air from their spinnerets and become airborne with the aid of meteorological forces ([Bell et al., 2005](#); [Weyman, 1993](#)). Dispersal over a short distance is called ‘rappelling’ when the thread attaches to a nearby object and is then used by the spider to walk along ([Bonte et al., 2009](#)). Before ballooning or rappelling, spiders show motivation to disperse by performing predispersal behaviour. *Mermessus trilobatus* often performs two types of predispersal behaviour. First, when spiders tiptoe, they release strands of silk in the air by straightening their legs and lifting their abdomens ([Eberhard, 1987](#)). Second, spiders perform ‘rafting’ when they attach the silk threads to elevated positions and slide down on these threads. They use the silken lines as platforms to take off once the meteorological factors are strong enough to lift the spiders ([Bell et al., 2005](#); [Tolbert, 1977](#)). Predispersal behaviour is important for ecological and evolutionary studies since it indicates spiders’ willingness to disperse ([Weyman, 1993](#); but see [Lubin & Suter, 2013](#)).

The invasion success of *M. trilobatus* in Europe is not explained by a ruderal strategy ([Narimanov, Kempel et al., 2021](#)), competition

with native sympatric species ([Eichenberger et al., 2009](#)) or release from a generalist predator ([Narimanov, Hatamli et al., 2021](#)). Nevertheless, *M. trilobatus* often reach high local abundances in grasslands ([Narimanov, Kempel et al., 2021](#); [Schmidt et al., 2008](#)) and have colonized a major part of Europe in a relatively short time ([Hirna, 2017](#)). Therefore, the heritability of dispersal might play an essential role in their spread and colonization success in Europe in less than 50 years. Although several empirical studies report the heritability of dispersal in spiders (e.g. [Bonte & Lens, 2007](#); [Yip et al., 2021](#)), it has, to our knowledge, never been studied in an invasion context.

In this study, we investigated the heritability of dispersal traits, namely tiptoe, rafting and take-off, for *M. trilobatus*. With the aid of repeated dispersal experiments across two generations, we sought to determine: (1) whether the dispersal traits are inherited through the dam and/or sire; and (2) if heritable, whether dispersal traits of offspring are inherited sex specifically.

METHODS

Study Species and Generations

We sampled spiders from two distant locations to capture high genetic variability: around Vienna in Austria and Landau in Germany, approximately 600 and 50 km from the presumed core ([Dumpert & Platen, 1985](#)) and 560 and 1200 km from the current front ([Hirna, 2017](#)) of the invaded range, respectively. Offspring from Vienna showed a similar dispersal propensity to their counterparts from Landau (negative binomial generalized linear models: $P > 0.3$). Sampling was done in June and July in 2020 using a vacuum sampler (modified STIHL SH86 blower; Stihl, Waiblingen, Germany). In total, we sampled 26 females in Vienna and 28 in Landau from six different hay meadows in each location. Only mated females (F_0) were sampled and identified by the presence of a mating plug ([Fig. 1](#)). The plug is developed after the first mating and covers the epigyne ([Fig. 1a and b](#)) to secure paternity ([Uhl et al., 2010](#)). Thus, while males of *M. trilobatus* ([Fig. 1c](#)) can mate several times in their lives, females are monandrous. We treated perennial hay meadows as the preferred type of habitat of *M. trilobatus* in Europe ([Narimanov, Kempel, et al., 2021](#)). All spiders were transferred individually into glass jars (405 ml) with a 1 cm layer of plaster of Paris to ensure high humidity inside the glasses. We kept all individuals in climate cabinets under standard conditions (25 °C, relative humidity = ca. 65%, 16:8 h light:dark) to obtain a high number of egg sacs. Each female produced multiple egg sacs, and we were able to obtain at least 500 offspring. To minimize stress during development and thus ensure basic dispersal levels when adult ([De Meester and Bonte, 2010](#); [Mestre & Bonte, 2012](#)), we fed all spiders ad libitum with springtails, *Sinella curviseta*, and separated the new generation of spiderlings (F_1). We transferred all F_1 offspring individually into 30 ml glass jars with a layer of humid plaster on the bottom and fed them ad libitum until adulthood. The second generation of spiders (F_2) was reared in a similar manner.

Ethical Note

We kept spiders under the conditions described above to ensure the welfare of these animals. The spiders were separated from siblings at the early stage of development and kept individually in glass jars with enough space for web building, which resulted in a high survival rate (> 90%). Almost all spiders successfully mated and produced offspring. After experiments, spiders sampled in Landau and their offspring were released to fields around Landau when possible. Spiders originating from Vienna were euthanized at – 20 °C.



Figure 1. (a) A virgin female, (b) a mated female with a plug and (c) a male of *Mermessus trilobatus*. The photos were taken with a LEICA S9i stereo microscope with an integrated 10 MP CMOS-camera.

Dispersal Experiment

The spiders' propensity for aerial dispersal was tested in an arena (shown in [Appendix Fig. A1a](#)). To provide a suitable airflow of 1 m/s (± 0.1) for dispersal ([Entling et al., 2011](#)), we placed a table fan (diameter = 10 cm, 2.5 W) approximately 0.8 m beside the arena. We measured wind velocity at the position of the arena using a hot-wire anemometer (VOLTcraft PL-135). The experimental arena was shielded from ambient electric fields to reduce the potential influence of atmospheric electric fields on spiders' dispersal behaviour ([Narimanov, Bonte, et al., 2021](#)). We used an experimental frame consisting of two metal electrodes ($0.8 \times 0.8 \text{ m}^2$) held parallel to each other and 0.8 m apart. The interconnected electrodes were electrically grounded. A dispersal platform was placed in the middle of the lower electrode ([Appendix Fig. A1a](#)). This consisted of a disk of plaster of Paris with a 2.5 cm diameter and a 7 cm tall wooden stick in the middle to provide an elevated position for take-off ([Appendix Fig. A1b](#)). We prevented spiders from walking out of the arena by placing the platforms in the middle of petri dishes filled with water. We used a vertically oriented textile mesh 1.5–2 m downwind from the arena to capture dispersing spiders.

We tested each spider three times on consecutive days (one trial a day). In each trial, we placed a spider on the dispersal platform and observed its behaviour. The trial was ended after 10 min or once the spider took off. We washed and wiped the platforms with water between the trials to remove the silk and possible chemical cues left by the previous spider. To increase the likelihood of dispersal ([Weyman et al., 1994](#)), we starved all individuals for 3 days before the experiment. We recorded the frequency of tiptoe, rafting and take-off. The behaviour was analysed blind to spiders' previous performance, their IDs and groups. We tested 425 adult F_1 individuals in total (212 females and 213 males).

Breeding Design

We assigned 26 F_1 spiders (15 females and 11 males) with the highest predispersal propensity (at least one tiptoe or rafting event in each of three trials) to a high-dispersive group and 30 F_1 individuals (19 females and 11 males) with no predispersal behaviour to a low-dispersive group to establish groups for high and low dispersal, respectively. We mated high- and low-dispersive individuals randomly (also including crossed pairs originating from Vienna and Landau), avoiding direct inbreeding and resulting in a set of 34 F_1 female broods: seven high-high (HH); eight high-low

(HL); 11 low-high (LH); eight low-low (LL; the first letters stand for dams' and the second letters for sires' dispersive groups). We kept individuals under standard conditions (25 °C, relative humidity = ca. 65%, 16:8 h light:dark) and fed them ad libitum to obtain the F_2 generation. We reared 477 F_2 offspring in total (for sample sizes, see [Appendix Table A1](#)). To demonstrate the heritability of dispersal propensity and to determine the role of dam and sire heritability, we carried out the dispersal experiment three times with each F_2 individual during 3 consecutive days as described above.

Statistical Analysis

All analyses were performed in R 4.0.3 ([R Core Team, 2021](#)).

Repeatability

The portion of the variation in behaviour that is due to between-individual differences is expressed as the repeatability of this trait. Thus, behaviour is considered repeatable when between-individual variance is higher than within-individual variance and consistent through time ([Bell et al., 2009](#); [Hayes & Jenkins, 1997](#)). Consequently, high repeatability of behaviour indicates that the individuals differ from each other in their behaviours. Therefore, we estimated the repeatability of tiptoe, rafting and take-off behaviours for the parental generation (F_1) by using the rpt function with binomial distribution from the rptR package ([Stoffel et al., 2017](#)) with 1000 permutations. We included F_1 spiders' sex as a fixed predictor and calculated adjusted repeatability (R_{adj}) with 95% confidence intervals as the appropriate parameter for the models including fixed effects ([Nakagawa & Schielzeth, 2010](#)). We used only repeatable traits as a proxy for dispersal ability.

Heritability

To investigate the role of dam and sire heritability in dispersal behaviour of the offspring generation (F_2), we modelled the frequency of tiptoe, rafting and take-off by fitting negative binomial generalized linear models (glm.nb) from the MASS package ([Venables & Ripley, 2002](#)). We included F_1 dam and sire dispersive groups (factor of two: High and Low), offspring sex and all interaction terms (dam*sire; dam*sex; sire*sex; dam*sire*sex) as fixed predictors. We determined the role of the dam and/or sire and the possible sex-specific heritability using the Anova function (chi-square test) from the R package car ([Fox & Weisberg, 2019](#)). To determine the portion of the variation in behaviour explained by dam and sire components, we calculated the variance of dam and

sire dispersive groups using negative binomial generalized linear mixed-effects models (glmer.nb) from the lme4 package (Bates et al., 2015). We used a negative binomial distribution as the most flexible and appropriate for the count data (O'Hara & Kotze, 2010). We also used the Games–Howell post hoc test to illustrate the difference between the breeding groups' performance (HH, HL, LH, LL) by using the games-howell-test function from the rstatix package (Kassambara, 2020).

RESULTS

Repeatability

Tiptoe, rafting and take-off behaviours of spiders from the parental generation (F_1) were repeatable at the individual level (Fig. 2, Appendix Table A2). Calculated 95% confidence intervals for all measured behaviours did not overlap with 0 (Fig. 2). These repeatability scores are in line with the values found in the literature (average repeatability in behaviours of 98 species across eight taxa: 0.37; Bell et al., 2009) and can be considered moderate. Consequently, we used all three traits in subsequent analyses.

Heritability

Spiders' tiptoe, rafting and take-off behaviours were largely heritable through dam and sire. Interestingly, on average, offspring of only high-dispersive dams and sires (group HH) showed an approximately three times higher frequency for tiptoe, rafting and take-off than offspring of at least one low-dispersive parent (groups HL, LH and LL; Table 1, Fig. 3). Offspring of a vagile dam or sire showed at least twice as much tiptoe, rafting and take-off propensity as offspring of the respective low-dispersive parent (Fig. 4). The additive genetic components (dam + sire) explained 33, 41 and 38% of the variation in tiptoe, rafting and take-off behaviour of the offspring generation, respectively (Fig. 5, Table 2). The sire components explained twice as much variation in tiptoe as dam components, whereas the difference was only slightly biased towards sire components in the offspring's take-off behaviour. In rafting, the dam and sire components similarly explained the variation in behaviour (Fig. 5, Table 2). We found no evidence for sex-specific heritability of any trait (Table 1). Overall, males showed higher

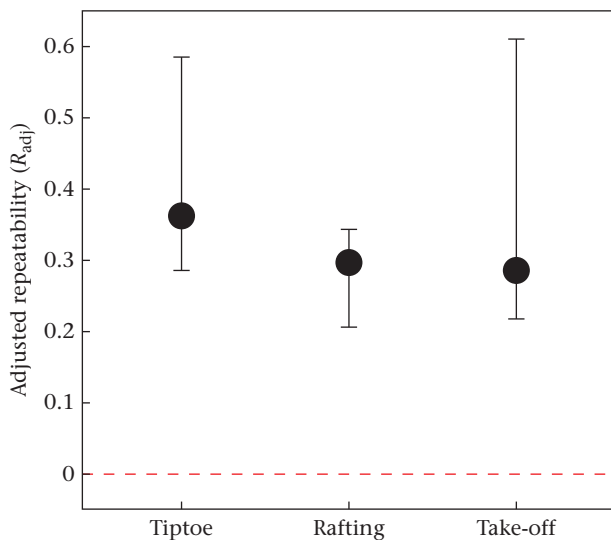


Figure 2. Adjusted repeatability (R_{adj}) and 95% confident intervals of tiptoe, rafting and take-off frequencies of spiders from the parental generation (F_1). The dashed line represents 0. See Appendix Table A2 for P values.

Table 1

Outputs for logistic regression models predicting the frequency of tiptoe, rafting and take-off behaviour of the offspring generation (F_2)

	Tiptoe		Rafting		Take-off	
	χ^2_1	P	χ^2_1	P	χ^2_1	P
Dam	18.89	< 0.0001	50.70	< 0.0001	22.24	< 0.0001
Sire	39.37	< 0.0001	53.28	< 0.0001	32.94	< 0.0001
Dam*Sire	5.40	0.02	8.95	0.003	6.58	0.01
Sex	1.77	0.183	9.20	0.002	8.09	0.005
Dam*Sex	0.08	0.776	0.01	0.913	0.08	0.783
Sire*Sex	0.99	0.321	0.73	0.392	2.15	0.143
Dam*Sire*Sex	0.38	0.540	0.13	0.721	0.05	0.825

The models predict frequency of behaviours considering the dispersive groups of dam and sire (High; Low), offspring sex and all interaction terms (dam*sire; dam*sex; sire*sex; dam*sire*sex). Significant correlations are shown in bold.

frequencies of rafting and take-off than females but a similar frequency of tiptoe behaviour (Table 1).

DISCUSSION

External factors and individual internal states, including the genetic prerequisites, are drivers of individual variation in dispersal. Although numerous studies have investigated external factors as the main forces behind individual dispersal behaviour, little is known about the role of the genetic background of dispersal and its heritability in species' range dynamics (Bonte et al., 2018; Renault et al., 2018). Here, we found high heritability of dispersal behaviour of a highly invasive spider, *M. trilobatus*. The dispersal behaviour of *M. trilobatus* was heritable through both dam and sire and similarly heritable for both female and male offspring.

The additive genetic components (dam + sire) explained on average 37% of the variation in offspring dispersal behaviour. The values calculated here are in line with values found in the literature (Dochtermann et al., 2019). Dispersal (distance moved) has been proven heritable for invasive cane toads, *Rhinella marina*, which have rapidly expanded their range in Australia (Phillips et al., 2010b). However, in contrast to *M. trilobatus*, the toads were introduced en masse (Lever, 2001), and hence high genetic variability was expected. Further, our results showed that on average 63% of the variance in behaviours was unexplained by additive genetic components. We assume that this unexplained variation was largely random since all spiders were kept under standard conditions and separated from siblings at an early stage of development.

Besides genetic background, external factors, such as temperature during development (Bonte et al., 2008) or density dependence of dispersal (De Meester & Bonte, 2010), might also affect the dynamics of range expansions. Consequently, a high dispersal and/or plasticity in dispersal behaviour based on individual development (e.g. temperature, population density) could make species equally prone to accelerated range expansions without the genetic predisposition of dispersal. Furthermore, the variability in dispersal behaviour can also be explained by the interplay of genetic and external factors (e.g. wind*sire components in dispersal motivation of the lycosid spider *Pardosa purbeckensis*; Bonte & Lens, 2007).

Interestingly, only offspring of both high-dispersive dams and sires (HH group) had substantially higher tiptoe, rafting and take-off propensity than the offspring with at least one low-dispersive parent (HL, LH and LL groups). The pattern was similar for both sexes. This indicates that high dispersal is inherited recessively and present in offspring in which strictly both parents were highly dispersive. We expect high dispersal, if inherited recessively, to be suppressed in dense, stable populations. In contrast, at low-density

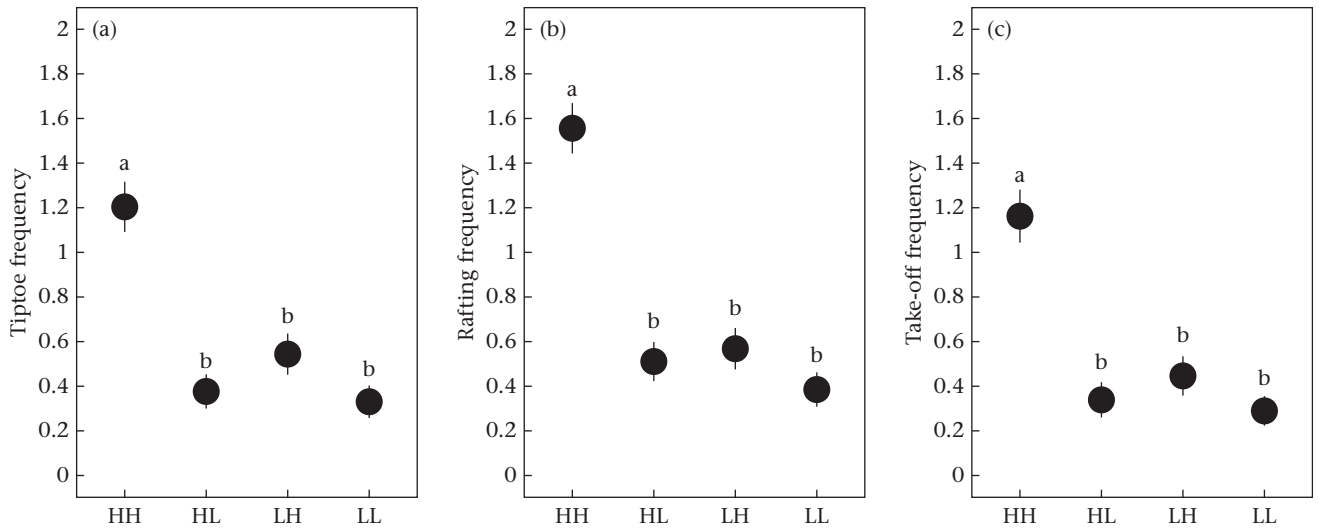


Figure 3. Effect of the parents' (F₁) dispersal ability on (a) tiptoe, (b) rafting and (c) take-off behaviour of the offspring generation based on their breeding groups (F₂: HH: high-dispersive parents; HL: high-dispersive dam and low-dispersive sire; LH: low-dispersive dam and high-dispersive sire; LL: low-dispersive parents). Means ± SE are presented. Differences between the groups are illustrated with letters based on the results from a Games–Howell post hoc test.

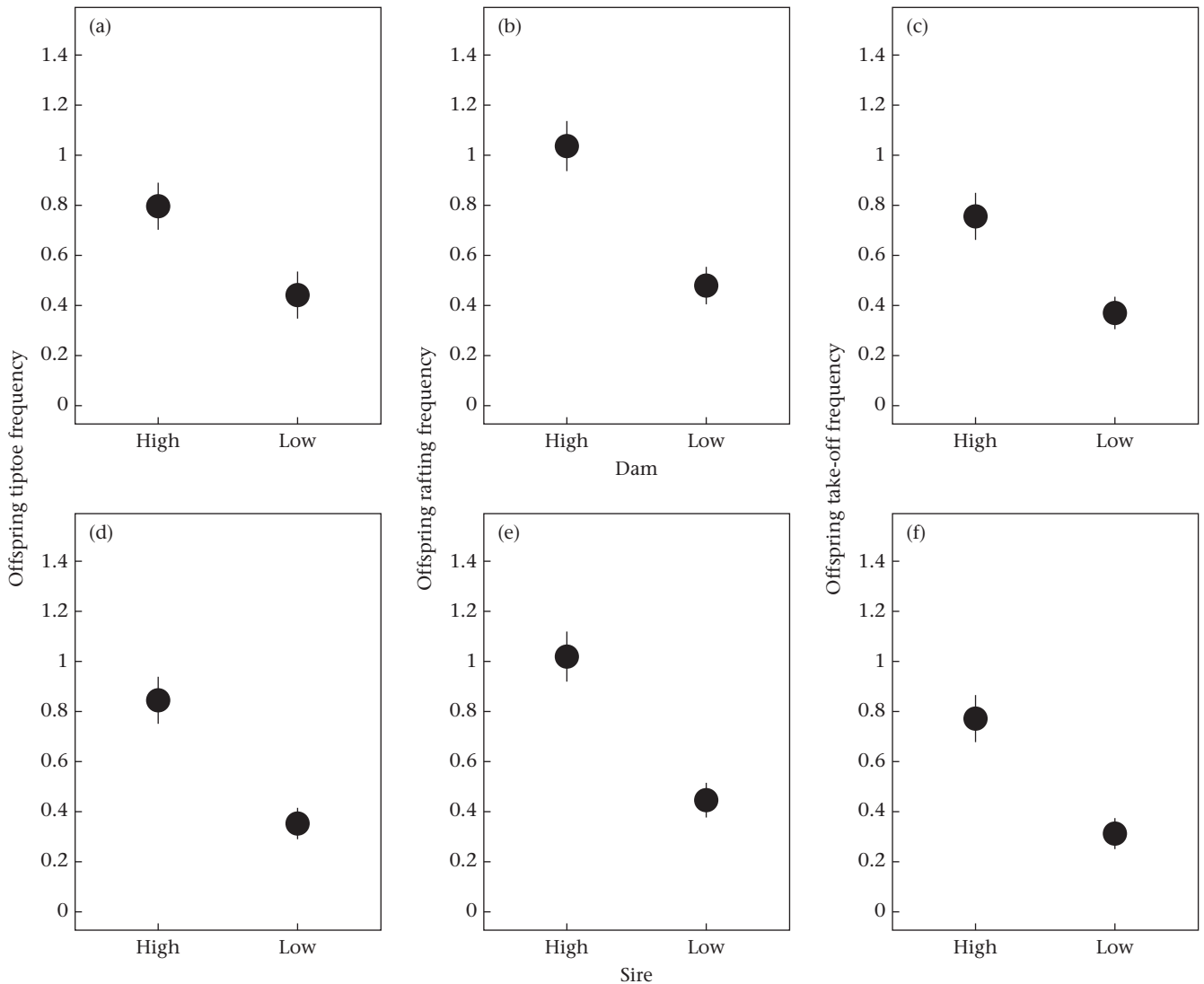


Figure 4. Frequency of (a, d) tiptoe, (b, e) rafting and (c, f) take-off behaviour based on (a, b, c) dam and (d, e, f) sire dispersal groups (High: high-dispersive; Low: low-dispersive). Means ± SE are presented.

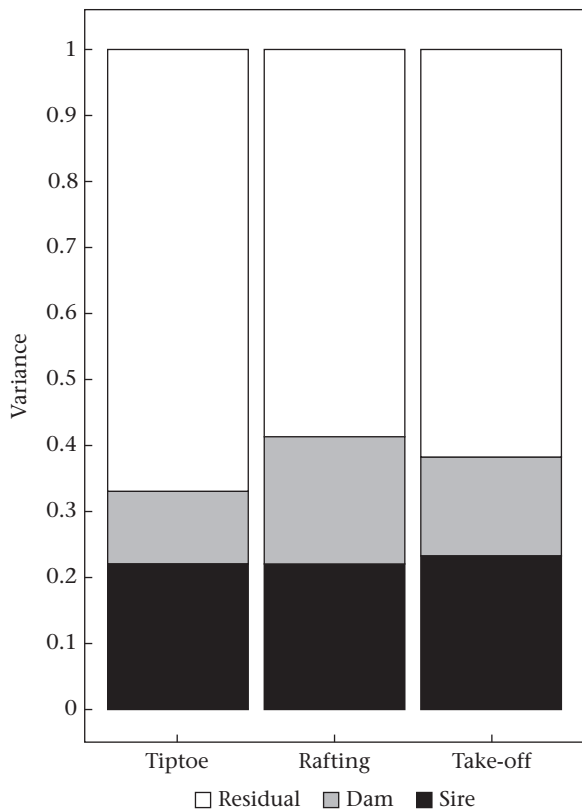


Figure 5. Variance components of tiptoe, rafting and take-off behaviour of 477 spiders from the offspring generation (F_2). Stacked bars represent the total variance consisting of residual, dam and sire components.

Table 2

The portion of the variation in tiptoe, rafting and take-off behaviour of 477 spiders from the offspring generation (F_2)

Dispersal traits	Dam	Sire	Residual
Tiptoe	0.113	0.218	0.67
Rafting	0.196	0.218	0.586
Take-off	0.154	0.231	0.616

sites, recessive genes are unmasked due to the increase in homozygosity (Charlesworth, 2003; Wang et al., 1999) and, thus, might become fixed and accumulate (Charlesworth, 2003; Mattila et al., 2012). Although recessive genes that give rise to homozygosity are scarce (e.g. Charlesworth & Charlesworth, 1987; Coleman, 1979; Ku et al., 2011), they might spread fast or dominate if their proportion is high. Such areas with a high proportion of homozygosity may be formed at the leading edge of an expanding range in species where individuals carrying recessively inherited genetic codes for high dispersal mate strictly among each other (Bonte et al., 2018; Shine et al., 2011) and hence reinforce the state of homozygosity. However, with time, the proportion of dominant low-dispersal genetic material might eventually increase in remote areas when low-dispersive individuals start to reach these areas and thus weaken the selection for high dispersal. This might explain the ephemeral character of highly dynamic ranges of some species (Chuang & Peterson, 2016). Further, our results suggest that variation in a single gene has a strong effect on the dispersal behaviour of *M. trilobatus*, which contrasts with the growing literature indicating the oligogenic inheritance of dispersal behaviour (reviewed in Saastamoinen et al., 2018). Molecular analysis incorporating behavioural experiments could clarify this question.

Dispersal behaviour of *M. trilobatus* was similarly heritable for females and males. However, female-biased, sex-specific heritability of tiptoe behaviour was recently revealed in a colonial spider, *Cyrtophora citricola*. Despite similar behaviour in both sexes, genetic variance contributed to the between-individual variation of tiptoe behaviour only in females (Yip et al., 2021). In contrast to *M. trilobatus*, *C. citricola* are mainly colonial spiders (Kullmann, 1959; Mestre & Lubin, 2011). In group-living spiders, females are often under selection for successful dispersal and establishment of new colonies (Berger-Tal et al., 2016; Lubin et al., 2009; Lubin & Bilde, 2007). In such group-living spiders, males may be less affected by selection, have more plastic strategies or alternatively be selected against high dispersal to maintain group cohesion. However, note that the populations tested in the study by Yip et al. (2021) were in their native range, and sex biases in dispersal heritability may largely affect the evolutionary dynamics of species' range expansions in populations in non-native ranges (e.g. in North America for *C. citricola*; Chuang & Riechert, 2021). Further, in solitary *M. trilobatus*, the heritability of dispersal behaviour for both sexes might also explain their rapid spread in Europe in a relatively short period. Subsequently, along with highly dispersing female offspring of highly vagile parents, highly dispersive male offspring could equally reach low-density sites and hence lower the risks of mate limitation and increase genetic diversity. However, note that in some female-biased dispersal systems, male genetic material can also disperse passively via females after successful mating (Lubin & Bilde, 2007).

The heritability of dispersal behaviour of *M. trilobatus* through both dam and sire could explain their rapid spread and colonization success in Europe. The species has undergone rapid range expansion in less than 50 years after it was first recorded in Germany (Dumpert & Platen, 1985; Hirna, 2017). Therefore, highly vagile individuals in the vanguard of their expanding range could mate at low-density sites and produce equivalently dispersive offspring leading to the accumulation of dispersive genotypes at the dynamic edge of this range (Bonte et al., 2018; Shine et al., 2011). Further, note that the dispersal propensity of *M. trilobatus* was approximately four times lower during the laboratory experiment than in native linyphiid species, namely *Agneta rurestris* and *Erigone dentipalpis* (Narimanov, Bonte et al., 2021). Hence, as dispersal is risky (Bonte et al., 2012), low dispersal could be advantageous in stable populations, whereas the recessive inheritance of high dispersal behaviour could boost vagility at the front of their expanding range. Consequently, the range of *M. trilobatus* in Europe might be spatially sorted with an accumulation of highly dispersive individuals at the front. Nevertheless, accelerated range expansions can also rapidly break off once the less dispersive individuals reach remote areas and mix with high dispersers (Chuang & Peterson, 2016). The phenotypic shift through space in voracity and exploration has been recently demonstrated for an invasive spider in the United States (Chuang & Riechert, 2021). However, the possible spatial sorting of invasive *M. trilobatus* in Europe requires further investigation.

Conclusion

The higher dispersal ability of the offspring from two high-dispersive parents compared to offspring of at least one low-dispersive parent indicates recessive inheritance of high dispersal in *M. trilobatus*. Further, the heritability of dispersal in invasive *M. trilobatus* implies the potential of selection for high dispersal at the invasion front of their expanding range. Thus, studies investigating the dispersal behaviour of spiders from the populations close to the edge and the core of the invasion range are needed to better understand the spatial distribution and the rapid spread of invasive *M. trilobatus* in Europe.

Author Contributions

Nijat Narimanov: Methodology (equal); Formal analysis (lead); Investigation (lead); Data curation (lead); Writing-original draft (lead); Writing-review & editing (lead); Visualization (lead); Project administration (lead).

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Data Availability

Data generated and analysed during this study are available from Figshare: <https://doi.org/10.6084/m9.figshare.16814836.v1>.

Declaration of Interest

The authors have no interest to declare.

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Appendix

Table A1

Sample sizes of the offspring generation (F_2) based on the breeding groups

Group	Females	Males	Total
HH	50	62	112
HL	54	55	109
LH	61	71	132
LL	65	59	124
Total	230	247	477

HH: high-dispersive parents; HL: high-dispersive dam and low-dispersive sire; LH: low-dispersive dam and high-dispersive sire; LL: low-dispersive parents.

Table A2

Repeatability estimates of 425 spiders from the parental generation (F_1)

Dispersal traits	R	SE	95% CI	P
Tiptoe	0.362	0.07	[0.287; 0.585]	< 0.0001
Rafting	0.297	0.036	[0.206; 0.344]	< 0.0001
Take-off	0.287	0.099	[0.217; 0.61]	< 0.0001

The individual behaviours were tested three times on consecutive days. CI: confidence interval. Significant correlations are shown in bold.



Figure A1. (a) Side view to the experimental set-up comprising the experimental frame with two interconnected and electrically grounded parallel metal electrodes, a table fan and a mesh to capture spiders. (b) Dispersal platform with a vertical stick made of moist plaster of Paris and connected to the bottom electrode via a wire.

Chapter 6

Accelerated invasion through the evolution of dispersal behaviour

Nijat Narimanov, Tobias Bauer, Dries Bonte, Lorenz Fahse & Martin H. Entling

Accelerated invasion through the evolution of dispersal behaviour

Abstract

Aim: The continuous spread of invasive species is attributed to demographic processes and high dispersal rates. Both can change and evolve during range expansion, eventually accelerating spread dynamics. Here, we document such an accelerated spread for one of the most invasive spiders in Europe, the dwarf spider *Mermessus trilobatus*, and test whether dispersal, reproduction or competing ability is at the source of this pattern.

Location: Europe.

Time period: 1978-2021.

Methods: First, we collected records from 21 countries across Europe to document the speed of progression of the invasion front over the last 45 years. Second, we collected live individuals from populations in the longest and more recently invaded areas and compared the dispersal propensity of offspring raised under standardised conditions. Third, we compare the reproduction and competing ability of the females derived from the populations of long-invaded areas against areas with the more recent establishment.

Results: The progression of the invaded range increased from about 150 km in the 1980s to some 400 km between 2010 and 2020. Dispersal-related behaviour was nearly twice as frequent in offspring from invasion front populations compared to the core area. By contrast, we found no differences in reproduction or competing ability among the studied populations. Further, neither joint inheritance nor trade-offs of dispersal, reproduction or competing ability were identified.

Main conclusion: As high dispersal is recessively inherited in *Mermessus trilobatus*, our results suggest that the accelerated invasion is due to the accumulation of dispersive but not more reproductive or competitive genotypes in newly colonised areas. Given the high climatic amplitude of the species in North America, we expect it to spread over the remaining parts of Europe and large parts of Asia in the coming decades. Accelerated range expansion through the evolution of dispersal behaviour could play a role in numerous arthropod invasions worldwide.

Keywords

Araneae; biological invasions; body size; colonisation; competition; dispersal; *Mermessus trilobatus*; range expansion; reproduction; spatial sorting

Introduction

Biological invasions play an increasing role in global biodiversity patterns and distributions (Simberloff et al., 2013). Non-native species become invasive after successful establishment and spread by overcoming novel biogeographical barriers and ecological pressures (Blackburn et al., 2011; Sakai et al., 2001). The introductions of species beyond their natural ranges are increasing worldwide (Seebens et al., 2018, 2021). Thus, predicting future patterns of biodiversity requires an understanding of the processes that are predominantly steering the spread.

The ranges of expanding species encompass the core, leading edge (front in the following) and intermediate areas (Chuang & Peterson, 2016). The core of the expansion range is considered the area of initial introduction with the highest density where introduced species reach a stable state of population dynamics (Chuang & Peterson, 2016; Phillips et al., 2010a, 2010b). In contrast, a highly dynamic front of the invasion range is often shaped by vagile individuals and characterised by a lower density and genetic diversity (Bridle & Vines, 2007; Chuang & Peterson, 2016; Phillips et al., 2010a; Shine et al., 2011). The accelerated invasion via accumulation of vagile genotypes at the leading edge of an expanding range can arise via spatial sorting when dispersal components of expanding species are heritable (Bonte et al., 2018; Phillips et al., 2010a; Shine et al., 2011). Consequently, individuals at the leading edge of the expanding ranges are often selected for dispersal-mediating traits (Bonte et al., 2018; Chuang & Peterson, 2016). In addition to dispersal, the speed of range expansions might also be determined by high reproductive rates (Fisher, 1937). Low density and subsequently reduced competition at the front of the expansion might result in local selection for individuals exhibiting high reproductive investments in the costs of low endurance and longevity, reinforcing further expansions (Brook & Bradshaw, 2006; Phillips et al., 2010a; Stearns, 1980). If competition with native species is retarding the spread of an invasive species, the evolution of higher competitiveness could overcome this limitation. This could be a third mechanism for accelerated range expansion over time. The three described mechanisms might also play differently when inherited jointly, facilitating the species' successful establishment and further spread (Alcock, 1998; Chuang & Peterson, 2016; Smallwood, 1993). Thus, joint inheritance and/or trade-offs of dispersal, reproduction and competition could equally play a substantial role in expanding species' range dynamics (Chuang & Peterson, 2016). Given the documented genetic background of dispersal (Saastamoinen et al., 2018) and its higher heritability when compared to other life-history traits (Dochtermann et al., 2019), selection for the increased dispersal and its more significant role in range expansion can be expected to be widespread but, hitherto, with only limited evidence.

The mean level of dispersal behaviour can differ between species' female and male individuals (Li & Kokko, 2019; Trochet et al., 2016). Several hypotheses have been developed to explain the mechanisms underlying sex-specific dispersal. For instance, inbreeding avoidance may fuel dispersal in either sex (Pusey, 1987), while mate competition for females might favour male-biased dispersal (Höner et al., 2007). Correspondingly, sex-specific dispersal can play an essential role in the range dynamics of expanding species (Dudaniec et al., 2021; Greenwood, 1980; Li & Kokko, 2019; Trochet et al., 2016). Higher mobility in males than females might contribute little to range expansions and could lower the speed of the spread, whereas a high female dispersal could accelerate the expansion (Miller & Inouye, 2013). Accelerated spread due to a female-biased dispersal is most plausible when the male genetic material can passively disperse with females after successful mating (Lubin & Bilde, 2007).

The literature on the demographic and phenotypic clines across the ranges of expanding species is growing; however, without a consensus (reviewed in Beissinger & Riddell, 2021; Chuang & Peterson, 2016; MacLean & Beissinger, 2017; also see Chuang & Riechert, 2021, 2022; McMahan et al., 2020; Mowery et al., 2021; Parker & Moczek, 2020; Wolz et al., 2020). Picking up signatures of spatial sorting is challenging. Such challenges can arise due to difficulties detecting front populations with low densities (Chuang & Petersen, 2016). Although the behaviour of some rapidly spreading species might not be shifted across their expansion, detection of the core-front differences can also be challenging due to the ephemeral nature of the dynamic fronts. For example, highly dynamic front populations shaped by strictly mobile individuals can reach their equilibrium state after a particular time, allowing less dispersive individuals also to reach these remote locations and mix with high-dispersers (Dytham, 2009; Hughes et al., 2007). Therefore, the age of the expansion might play a more significant role in the investigation of the spatial structure of expanding species (Chuang & Peterson, 2016). Subsequently, the ideal candidates to detect such spatial sorting would be the ranges having an accelerated nature of expansion (e.g., Lombaert et al., 2014; Phillips et al., 2010b).

As common and abundant predators, spiders play a central role in natural and agricultural ecosystems (Hogg et al., 2010; Michalko et al., 2019; Nyffeler & Birkhofer, 2017; Pétilion et al., 2020). Yet, the underlying mechanisms of invasions by spiders have only recently started to receive scientific attention (Bauer et al., 2019; Campbell et al., 2020; Chuang & Riechert, 2021, 2022; Mowery et al., 2021; Narimanov et al., 2021b, 2021c; 2022; Nentwig, 2015), most likely due to the prevalently synanthropic lifestyle and limited evidence for economic damage by spiders (Kobelt & Nentwig, 2008). To our knowledge, the range dynamics and evolution of rapidly spreading spiders are largely unexplored (Chuang & Peterson, 2016; but see Chuang & Riechert, 2021, 2022; Mowery et al., 2021; Wolz et al., 2020). The spatial sorting of invasive spiders has been studied only for the tentweb orbweaver spider (*Cyrtophora citricola*; a phenotypic shift in voracity, exploration and dispersal; Chuang & Riechert, 2021, 2022) and redback spiders (*Latrodectus hasselti*; higher dispersal ability in invasive populations; Mowery et al., 2021). Hence, most studies on invasive spiders' range dynamics compared life-history traits between native and invasive populations, but only a few effectively tested such variation during the course of the invasion (e.g., Chuang & Riechert, 2021, 2022). This is important since invasive populations may have strongly reduced genetic diversity (Colautti et al., 2014) and hence evolutionary potential compared to natural range expansions that are commonly studied under climate change (e.g., Krehenwinkel et al., 2015; Wolz et al., 2020). Although the role of genetic diversity in species range expansions has been experimentally demonstrated (Mortier et al., 2021), empirical evidence is still missing.

The North American dwarf spider *Mermessus trilobatus* (Emerton, 1882) (Araneae: Linyphiidae) is among the most abundant spiders in open habitats in Europe (Narimanov et al., 2021c; Schmidt et al., 2008) despite being inferior when compared with native sympatric species with respect to disturbance tolerance (Narimanov et al., 2021c), competing ability (Eichenberger et al., 2009) and release from a dominant generalist predator (Narimanov et al., 2021b). After the first record in South-West Germany in 1978 (Dumpert & Platen, 1985), the species has colonised a large part of Europe via aerial dispersal in less than five decades (Fig. 1; Feng et al., 2021; Grbić et al., 2021; Hirna, 2017). *Mermessus trilobatus* engages in aerial dispersal by performing a pre-dispersal behaviour. Two distinct types of pre-dispersal behaviour can be identified, namely tiptoeing and rafting. While tiptoeing, spiders release strands of silk in the air by climbing an elevated position, straightening their legs and lifting their abdomens (Bonte et al., 2009; Eberhard,

1987). For rafting, spiders first slide down on a silken line attached to the elevated position. They use the lines to release new threads in the air once the dispersal-facilitating forces are strong enough to bring the spiders aloft (Bell et al., 2005; Tolbert, 1977). The frequency of pre-dispersal behaviour in trials under standardised conditions can be used to detect spiders' motivation to disperse before the actual takeoff (Weyman, 1993; but see Lubin & Suter, 2013). Furthermore, *M. trilobatus* is an obligatory builder of horizontal sheet webs (Narimanov et al., 2021c). Spinning a web is associated with substantial energy investments. Spiders thus often take over existing webs of other individuals rather than spinning a new one (Ford, 1977). Further, existing webs are indicators of resource-rich foraging sites since sedentary spiders primarily concentrate in prey-rich areas for web building (Harwood et al., 2001). Hence, spiders also defend their webs due to associated high risks of re-location to prey-poor sites.

Here, we study the range dynamics of the highly invasive dwarf spider *Mermessus trilobatus* and the possible evolution of life-history traits behind these dynamics. First, we hypothesize that the range expansion of *M. trilobatus* in Europe has accelerated over time. Our second hypothesis is that the inherited mobility of *M. trilobatus* at the invasion front is higher than in core populations, potentially underlying the accelerated invasion. Alternatively, we expect reproductive output and/or competitiveness to be enhanced at the invasion front. Lastly, we expect that mobility, reproduction and competitiveness covary, either through the selective forces of the range-expanding population or due to trade-offs.

Materials and Methods

Invasion speed

We collected data on the time and location of *M. trilobatus* records in Europe by personally contacting arachnologists in 26 European countries (see Acknowledgements) and from databases and published records (Arachnologische Gesellschaft, 2021; Blick, 2000; Breuss, 1999; Čandek et al., 2013; Dumpert & Platen, 1985; Dolanský et al., 2009; Feng et al., 2021; GBIF.org; Grbić et al., 2021; Hänggi, 1990; Harvey, 2008; Hirna, 2017; Infofauna, 2021; Keer et al., 2006; Kovács et al., 2015; Lemke, 2018; Mezőfi & Markó, 2018; Nentwig et al., 2021; OpenObs, 2021; Spider Recording Scheme/British Arachnological Society, 2021; Waarneming.nl, 2021; Pantini & Isaia, 2019; Rozwałka et al., 2013, 2016; Šestáková et al., 2017; Szinetár et al., 2014; Thaler & Knoflach, 1995; Trigos-Peral et al., 2020; Van Helsdingen, 2021; Van Helsdingen & IJland, 2007; Wiśniewski, 2017). In total, we were able to collect around 4000 both published and unpublished records of *M. trilobatus* from 21 European countries (Fig. 1). We calculated the distance that the species moved for each record relative to the first record in Europe in 1978 (48°54'42.9"N, 8°23'56.8"E; Dumpert & Platen, 1985) using latitude and longitude data in decimals. The distance values were calculated as:

$$D = \left\{ \text{ACOS} \left[\begin{array}{l} \sin(\text{Lat}1) \times \sin(\text{Lat}2) + \cos(\text{Lat}1) \times \\ \times \cos(\text{Lat}2) \times \cos(\text{Lon}2 - \text{Lon}1) \end{array} \right] \right\} \times R,$$

where *Lat1* and *Lon1* are decimal coordinates of the species' first record in Europe in radians, *Lat2* and *Lon2* are the respective coordinates of the advanced record in radians, and *R* is the radius of Earth in km.

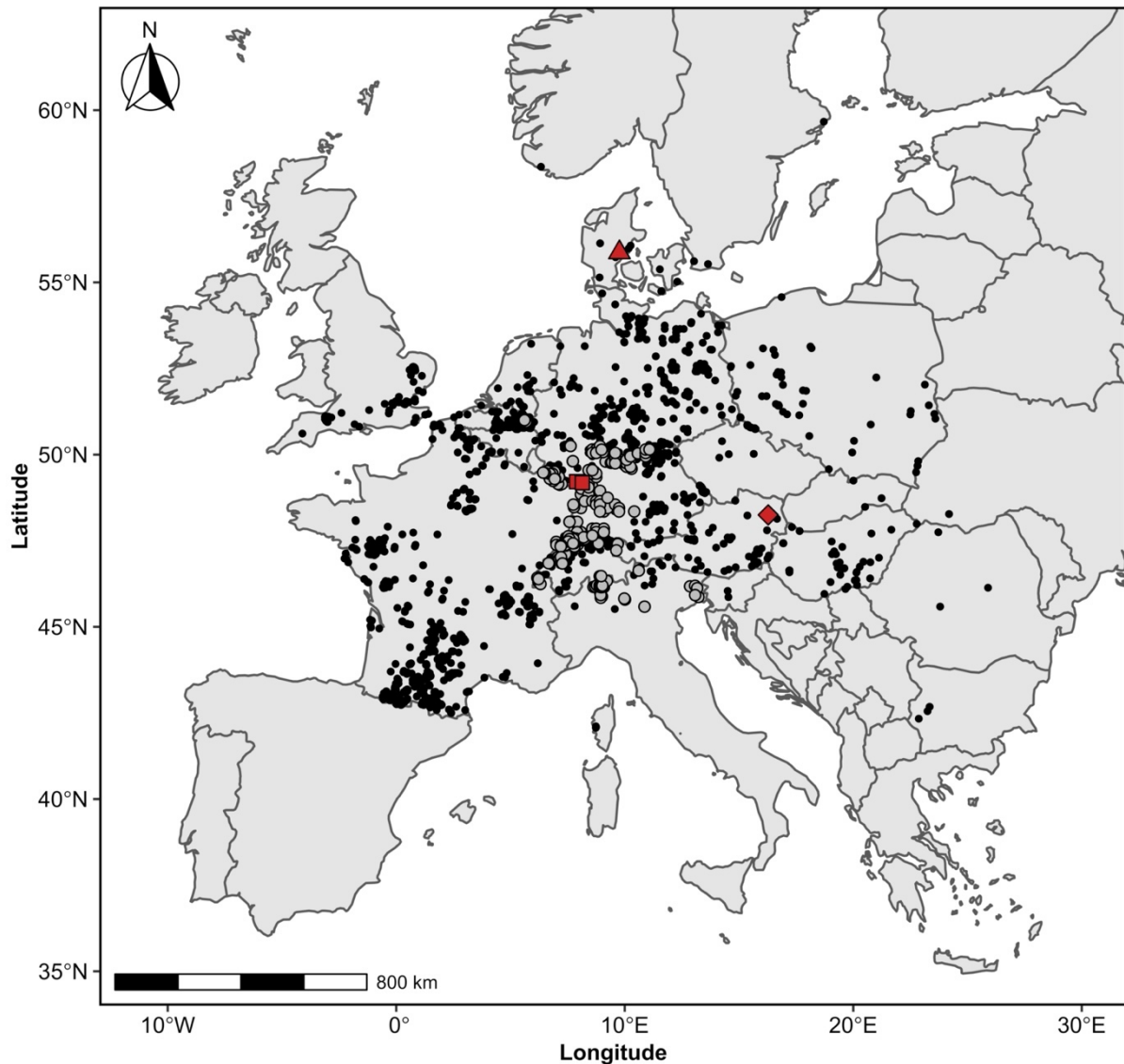


Figure 1: Collected records from 21 European countries and sampling locations of adult females of *Mermessus trilobatus* (F₀). Grey circles represent the records from 1978 to 2001, and black circles the records from 2002 to 2021. Red squares show the sampling areas close to the invasion core in Germany (Wilgartswiesen on the left and Landau on the right); red triangle shows the areas close to the invasion front in Denmark (Horsens) and red rhombus in Austria (Vienna). Coordinates of the exact sampling fields in Wilgartswiesen, Landau, Vienna and Horsens and their distances from the presumed centre of invasion are given in Table 1.

Sampling locations and generation rearing

We sampled spiders from four locations, namely in Wilgartswiesen (Germany), Landau (Germany), Vienna (Austria) and Horsens (Denmark), between June and July in 2020 and 2021 (Fig. 1; Table 1). The spiders were sampled with a vacuum sampler (modified STIHL SH86 blower; Stihl, Waiblingen, Germany). We collected mainly mated females (F₀). Mated females are identified by the presence of a mating plug, which is developed after the first mating to secure paternity (Narimanov et al., 2022; Uhl et al., 2010). Twenty-eight

sampled spiders in Landau and 16 in Wilgartswiesen represented individuals from the core populations due to the close distance to the presumed core of invasion (core populations in the following; Fig. 1; Table 1; Dumpert & Platen, 1985). We used 26 spiders sampled around Vienna and 16 from Horsens as populations closer to the edge of the expansion range (front populations in the following; Fig. 1; Table 1). The spiders were first recorded in Austria in 1998 (Breuss, 1999) and Denmark in 2014 (GBIF.org), indicating the more recent colonisation in Denmark. We sampled spiders in perennial hay meadows as the preferred habitat type by *M. trilobatus* (Narimanov et al., 2021c). All spiders were transferred singly into glass jars (405 ml) with a 1 cm layer of plaster of Paris to ensure a moist environment inside the glasses. All individuals were kept under standard conditions in climate cabinets (25°C, RH = ~65%, L:D = 16:8) and fed *ad libitum* with springtails (*Sinella curviseta*). We separated a new generation of spiders (F₁) from siblings at the early stage of development and accommodated them separately in 30 ml glass jars. We kept the spiders under conditions described above to avoid high mortality and minimise stress during development to ensure basic dispersal levels when adult (Bonte et al., 2008; De Meester & Bonte, 2010; Mestre & Bonte, 2012). In total, we were able to rear nearly 1000 F₁ offspring.

Table1: Geographical coordinates of the collected sites and the year when all *Mermessus trilobatus* individuals were sampled. The distances are calculated relative to the first record of the species in Europe in 1978 (Dumpert & Platen 1985).

Location	Area	Latitude	Longitude	Distance (km)	Year
Austria	Pötzleinsdorf	N48° 14' 58.0"	E16° 16' 46.3"	584	2020
Austria	Pötzleinsdorf	N48° 14' 45.2"	E16° 16' 37.2"	584	2020
Austria	Neuwaldegg	N48° 14' 33.9"	E16° 15' 38.8"	583	2020
Austria	Neuwaldegg	N48° 14' 31.2"	E16° 15' 28.5"	583	2020
Austria	Orth a.d. Donau	N48° 08' 08.0"	E16° 39' 54.2"	614	2020
Austria	Klosterneuburg	N48° 18' 53.2"	E16° 19' 41.7"	586	2020
Germany	Landau	N49° 12' 03.0"	E8° 08' 49.2"	37	2020
Germany	Landau	N49° 12' 16.2"	E8° 06' 22.3"	39	2020
Germany	Landau	N49° 12' 02.7"	E8° 08' 57.6"	37	2020
Germany	Offenbach	N49° 12' 05.8"	E8° 10' 11.4"	36	2020
Germany	Landau	N49° 11' 59.7"	E8° 09' 18.3"	37	2020
Germany	Landau	N49° 11' 57.6"	E8° 09' 30.2"	36	2020
Germany	Wilgartswiesen	N49° 12' 57.1"	E7° 53' 28.3"	50	2021
Germany	Wilgartswiesen	N49° 13' 04.9"	E7° 53' 27.8"	50	2021
Denmark	Horsens	N55° 52' 08.0"	E9° 46' 03.7"	779	2021
Denmark	Horsens	N55° 52' 23.2"	E9° 47' 48.4"	780	2021

Dispersal experiments

We used dispersal platforms to test spiders' propensity for aerial dispersal. The dispersal platforms were made of plaster of Paris and shaped as a disk with a 2.5 cm diameter. We placed a 7-cm tall wooden stick in the middle of the platform to provide a suitable position to disperse. In order to prevent spiders from escaping, we set the platforms in the middle of 7-cm diameter petri dishes filled with water. We placed a table fan (diam. = 10 cm, 2.5 W) beside the arena at the distance of 0.8 m to provide a suitable airflow for dispersal (1 ± 0.1 m/s; Entling et al., 2011) and measured the wind velocity using a hot-wire anemometer (VOLTCRAFT PL-135). We used an electrically grounded experimental

frame to shield the trial area from ambient electric fields and hence to reduce their potential impact on spiders' dispersal behaviour (for more details, see Narimanov et al., 2021a, 2022).

In order to estimate the propensity of individual dispersal behaviour, we tested each spider three times during three consecutive days. We placed a spider on the dispersal platform and observed the behaviour for ten minutes in each trial. The trial was ended after ten minutes or if the spider took off. We washed the platforms with water between the trials in order to remove the silk and possible chemical cues. The spiders were offered no food for three days before the experiments to standardise the hunger level. We recorded the frequency of tiptoe, rafting and take-off behaviour. The behaviour was analysed blind to spiders' originating locations (Wilgartswiesen, Landau, Vienna or Horsens) and previous performances. We tested 857 adult F₁ individuals in total (see Table 2 for sample sizes). A subset of high and low dispersive individuals derived from Landau and Vienna populations was used for breeding an F₂ generation for the experiments reported elsewhere (Narimanov et al., 2022).

Table 2: Sample sizes of spiders tested for dispersal behaviour and body size measurements (in brackets) based on their originating locations.

Location	Origin	Females	Males	Total
Wilgartswiesen	core	111 (110)	103 (103)	214 (213)
Landau	core	105 (100)	109 (103)	214 (203)
Vienna	front	107 (100)	105 (103)	212 (203)
Horsens	front	111 (110)	106 (106)	217 (216)

Body size measurements

The body size of each F₁ spider was measured after all three dispersal trials. We measured the prosoma widths of adult F₁ individuals. Individuals' prosoma widths can be used as an estimate of body size since it is independent of the current feeding condition (Moya-Laraño et al., 2008). Thus, we anaesthetised the spiders with a CO₂ dispenser and measured the broadest part of the prosoma from the dorsal side with the aid of a stereomicroscope. In total, we measured 835 spiders (see Table 2 for sample sizes).

Reproductive output

We mated adult F₁ females with F₁ males from the same location, avoiding direct inbreeding, and counted the total number of egg sacs that each female produced until the natural death. We opened each female's first four egg sacs after successful mating and counted the number of eggs produced. We estimated the reproductive output by multiplying the mean number of eggs per sac times the total number of egg sacs produced from 30 females from Landau, 45 from Vienna, 56 from Wilgartswiesen and 65 from Horsens.

Web competition experiments

We tested females originating from core populations against front females in each trial. Thus, we tested pairs of F₁ females from Landau and Vienna in web takeover trials in 2020. Similarly, we tested pairs of adult females from Wilgartswiesen and Horsens in 2021. We randomly assigned spiders and tested each spider twice, once as a host (the web owner) and once as an intruder (added spider). We kept the pairs unchanged during the second trial. We let spiders build a web in 405 ml glass jars with a 1 cm layer of moistened

Plaster of Paris on the bottom and five vertical sticks to facilitate web building. We fed all spiders *ad libitum* to standardise the feeding and web conditions. We put the intruder on the host's web on the opposite side of the host's position. We observed spiders during 30 minutes and registered behaviour, namely, (I) takeover of the web by the intruder (the only spider that stayed on the web was an intruder); (II) defence of the web by the host (the only spider that stayed on the web was a host); (III) no visible interaction between the spiders (as in Eichenberger et al., 2009). We stopped the trials when the first or the second behaviours mentioned above was recorded or after 30 minutes when no interaction was detected. Additionally, we scored each female based on their web competing success. We added one to the score when a spider defended or took over the web. Since each spider was tested twice during our experiments, the scores ranged from 0 (complete losers) to 2 (ultimate winners). The behaviour was registered blind to the originating location of spiders and their IDs. The difference in prosoma width was calculated as the intruder's respective value minus the host. Consequently, we obtained positive values when the intruder was larger than the host and negative values when the host was larger than the intruder. In total, we had 222 trials. We tested 36 adult females from Landau against 36 from Vienna and 75 females from Wilgartswiesen against 75 from Horsens.

Statistical analysis

All analyses were performed in R 4.1.2 (R Core Team, 2021).

Invasion speed

To investigate the speed of invasion, we modelled the spread distances by fitting a linear model from the stats package (R Core Team, 2021), including the year of records as the explanatory variable. Note that only the years in which the maximum distance increased (N = 17, red filled circles in Fig. 2) were considered in the model. To test whether the monomials with a degree larger than one help to explain the response variable in our model, we applied the specification test (Ramsey RESET test; Ramsey, 1969) to the linear model.

Dispersal behaviour

We modelled tiptoe, rafting and dispersal frequencies by fitting generalized linear mixed-effects models with negative binomial distribution as the most appropriate and flexible for the count data (glmer.nb from the lme4 package; Bates et al., 2015; O'Hara & Kotze, 2010). We analysed explanatory variables, namely location (Wilgartswiesen, Landau, Vienna, Horsens), sex (female, male) and interaction of location and sex (location \times sex) as fixed predictors by applying ANOVA χ^2 - test from the R package car (Fox & Weisberg, 2019) to the glmer.nb models. We included the sex and the interaction term in the model to account for sex-biased dispersal (higher dispersal rates of males than females in *M. trilobatus*; Narimanov et al., 2022) and its possible impact on the expansion velocity (Miller & Inouye, 2013). Spiders originating from Landau and Vienna were tested in 2020 and those from Wilgartswiesen and Horsens in 2021. Thus, to account for the possible year effect, we included the year of measurements (2020, 2021) as random factors in our models.

Body size

We modelled prosoma width measurements by fitting a linear mixed-effects model (LMM) from the lme4 package (Bates et al., 2015) in R. We analysed location (Wilgartswiesen, Landau, Vienna, Horsens), spiders' sex (female, male) and interaction of location and sex (location \times sex) as fixed predictors using ANOVA χ^2 - test from the R package car (Fox & Weisberg, 2019) on LMM model. We included the interaction term in the model to account for possible sex-specific size dimorphism between the core and front

of the expansion range. Different people measured spiders in different years (Landau and Vienna in 2020; Wilgartswiesen and Horsens in 2021). Thus, to account for possible observer bias and the year effect, we included the year of measurements (2020, 2021) as random factors in our model.

Reproductive output

Here, we also fitted a linear mixed-effects model (LMM) from the lme4 package (Bates et al., 2015) in R. We included females' location (Wilgartswiesen, Landau, Vienna, Horsens), their prosoma widths, as well as their tiptoe, rafting and dispersal frequencies as fixed predictors in the models. We included spiders' frequencies for dispersal behaviour to investigate possible correlations or trade-offs between their reproductive investments and dispersal ability. Due to the skewed shape of the distribution, we log-transformed the response variable to match the requirements of normal distribution (Zuur et al., 2010). We applied ANOVA χ^2 - test from the R package car (Fox & Weisberg, 2019) to the LMM model. Similar to web competition assays, the number of eggs produced by females was measured in different years by two different observers (Landau and Vienna in 2020; Wilgartswiesen and Horsens in 2021). Thus, we included the year of measurements (2020, 2021) as random factors to account for the observer bias and the year effect.

Web competition

We individually modelled the response variables, namely web defence, web takeover and no interaction outcome, by fitting generalized linear mixed-effects models (GLMM) for a binomial response from the lme4 package (Bates et al., 2015) separately for the experiments conducted in 2020 (Vienna vs Landau) and 2021 (Horsens vs Wilgartswiesen). We analysed location (Vienna vs Landau or Horsens vs Wilgartswiesen) and the difference in prosoma widths as fixed predictors using ANOVA χ^2 - test from the R package car (Fox & Weisberg, 2019) on GLMM models. We included individual IDs as random factors since each individual was tested twice (intruder, host). To investigate a possible correlation or trade-offs among web competition (web competing scores), dispersal ability (frequencies to tiptoe, rafting and take-off) and the reproductive output (the mean number of eggs per sac times the total number of egg sacs produced), we also modelled spiders scores fitting generalized linear models with a negative binomial distribution (glm.nb from the MASS package; Venables & Ripley, 2002).

Results

Invasion speed

Invasive *M. trilobatus* has first expanded its range by nearly 500 km during the first two decades of invasion (by 2001; Fig. 1; Fig. 2). In the following two decades, the species has reached the most distant locations of approximately 1350 km, thus nearly doubling the speed of its expansion (by 2021; Fig. 1; Fig. 2). The specification test for the linear regression model showed that including monomials with a degree larger than one significantly increased the model's power (RESET = 23.02, df1 = 1, df2 = 14, $P = 0.0003$); hence, a linear model would be misspecification. Thus, the maximum distances increase superlinearly with time (red curve in Fig. 2).

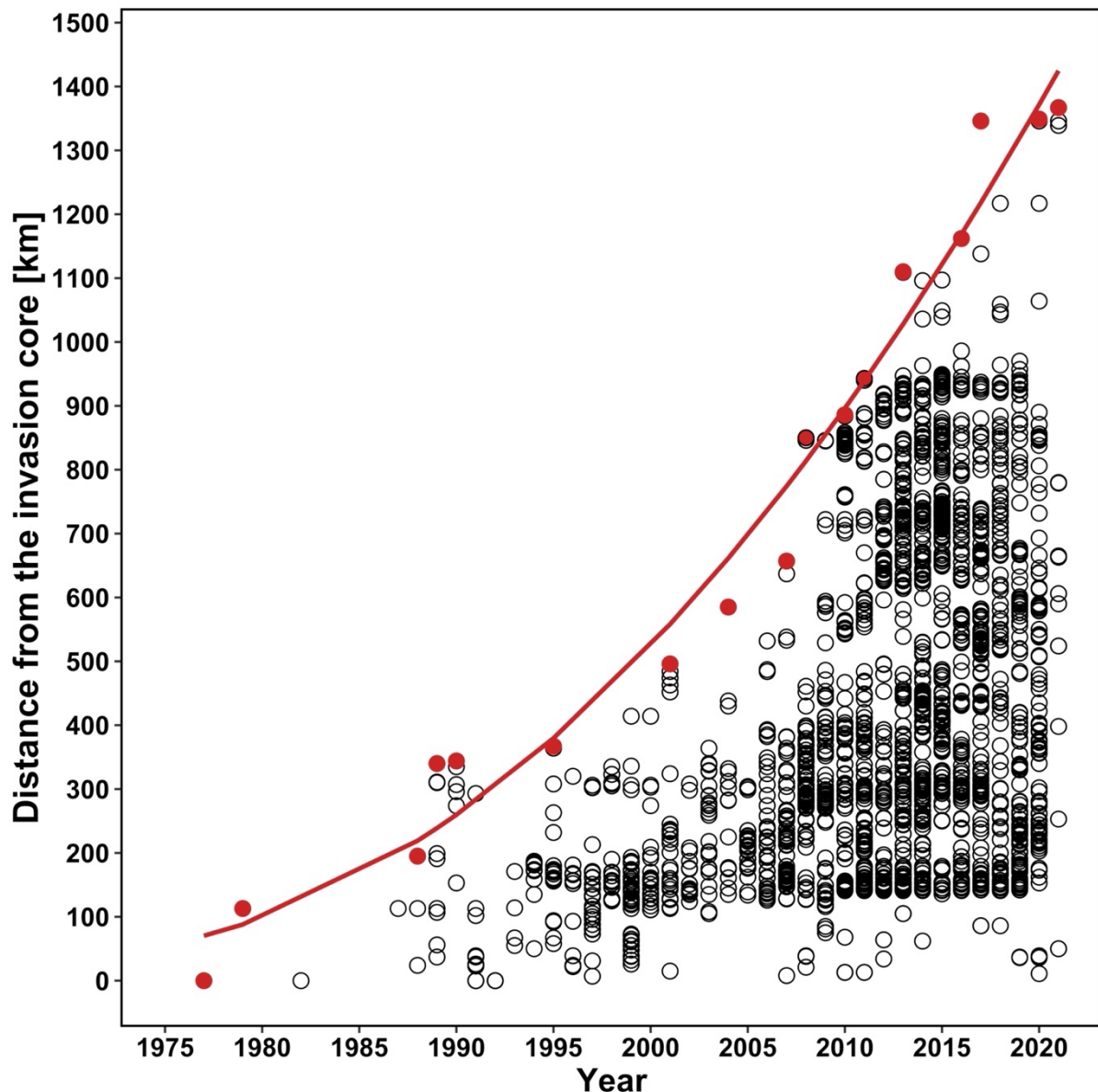


Figure 2: Distances of *Mermessus trilobatus* records from the location of its first record in Europe in 1978 (Dumpert & Platen, 1985). Filled red circles represent the maximum distances for the years in which the invasion front advances. The red curve represents a quadratic model fitted to the records when the front advanced (red filled circles; $r^2 = 0.98$, $y = 2028858 - 2060.2 \times \text{year} + 0.52 \times \text{year}^2$).

Dispersal behaviour

Spiders' dispersal behaviours differed significantly between the sampling locations, increasing from the old toward the newly colonised areas (Fig. 3; Table 3). Individuals originating from the areas with recent spread had nearly twofold higher dispersal rates than those from the long-invaded core areas (Fig. 3). Overall, male individuals showed a higher propensity of dispersal traits than females, whereas both sexes showed a similar increase in dispersal behaviour across locations (Table 3). We found no effects of spiders' prosoma widths on their dispersal behaviour (Table 3).

Table 3: Outputs for logistic regression models predicting the frequency of dispersal traits.

Measurement	Predictor	χ^2	df	<i>P</i>
Tiptoe	location	18.58	3	< 0.0001
	sex	13.92	1	< 0.0001
	location × sex	2.9	3	0.41
	prosoma width	2.9	1	0.09
Rafting	location	25.23	3	< 0.0001
	sex	9.53	1	0.002
	location × sex	2.85	3	0.41
	prosoma width	0.62	1	0.43
Take-off	location	20.08	3	< 0.0001
	sex	23.37	1	< 0.0001
	location × sex	2.35	3	0.5
	prosoma width	0.93	1	0.33

Significant correlations are shown in bold.

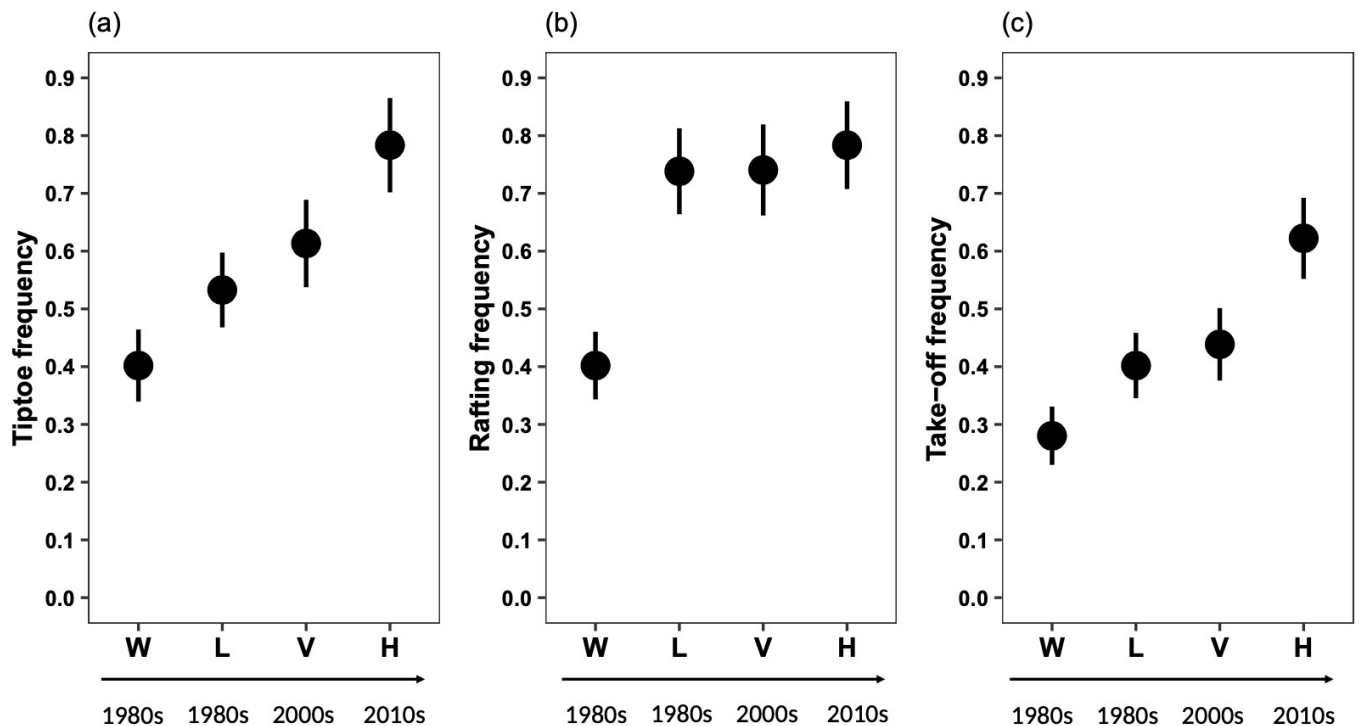


Figure 3: Frequencies of (a) tiptoe, (b) rafting and (c) take-off behaviour based on spiders originating locations (core: W = Wilgartswiesen, L = Landau; front: V = Vienna, H = Horsens) and the decades when the species was first found in the area. Means \pm SE are presented.

Body size

Spiders' prosoma widths did not differ based on their originating locations ($\chi^2 = 1.0$, $df = 3$, $P = 0.8$), whereas males had larger prosoma widths than females ($\chi^2 = 592.63$, $df = 1$, $P < 0.0001$; males' mean value = 0.71; females' mean value = 0.66). We found no evidence for sex-specific core-front size dimorphism in *M. trilobatus* (location \times sex; $\chi^2 = 1.31$, $df = 3$, $P = 0.73$).

Reproductive output

Female individuals from all four locations invested similarly into reproduction ($\chi^2 = 1.65$, $df = 3$, $P = 0.65$). Spiders' prosoma widths had no effect on their reproductive output ($\chi^2 = 2.75$, $df = 1$, $P = 0.1$). Furthermore, females' reproductive output was not correlated with their dispersal behaviour (tiptoe: $\chi^2 = 0.35$, $df = 1$, $P = 0.55$; rafting: $\chi^2 = 0.09$, $df = 1$, $P = 0.76$; take-off: $\chi^2 = 1.46$, $df = 1$, $P = 0.23$).

Web competition

The rates of web defence, web takeover and no interaction were not affected by the spiders' origin (Vienna vs Landau: $\chi^2 = 0.00$, $df = 1$, $P = \text{n.s.}$; Horsens vs Wilgartswiesen: $\chi^2 = 0.00$, $df = 1$, $P = \text{n.s.}$). Similarly, there was no effect of the difference in prosoma widths on the web defence (Vienna vs Landau: $\chi^2 = 1.28$, $df = 1$, $P = 0.26$; Horsens vs Wilgartswiesen: $\chi^2 = 0.85$, $df = 1$, $P = 0.36$), web takeover (Vienna vs Landau: $\chi^2 = 0.00$, $df = 1$, $P = \text{n.s.}$; Horsens vs Wilgartswiesen: $\chi^2 = 0.01$, $df = 1$, $P = 0.91$) or the probability of no interaction outcome (Vienna vs Landau: $\chi^2 = 1.28$, $df = 1$, $P = 0.26$; Horsens vs Wilgartswiesen: $\chi^2 = 0.74$, $df = 1$, $P = 0.39$). Spiders' web competing scores were neither correlated with their ability to disperse nor with the reproductive output (tiptoe: $\chi^2 = 0.36$, $df = 1$, $P = 0.55$; rafting: $\chi^2 = 0.13$, $df = 1$, $P = 0.72$; take-off: $\chi^2 = 0.97$, $df = 1$, $P = 0.33$; reproductive output: $\chi^2 = 1.22$, $df = 1$, $P = 0.27$).

Discussion

With increasing rates of biological invasions worldwide (Seebens et al., 2018, 2021), it is essential to understand the mechanisms behind the range dynamics of expanding species (Travis & Park, 2004). Here we show that selection for mobile, but not more reproductive or competitive genotypes at the expansion front of one of the most invasive spiders in Europe gives rise to an accelerated range expansion by now more than 1300 km in under 45 years. Furthermore, this study also confirms the highly dynamic character of the invasion fronts, highlighting the importance of the time since establishment for studies of range expansions.

Mermessus trilobatus individuals derived from the populations in Horsens were more likely to disperse than those from the core populations, with intermediate levels for the Vienna population. Interestingly, the higher mobility in Horsens than Vienna corresponds with a more recent establishment in Denmark than Austria (first records in 2014 and 1998, respectively; Breuss, 1999; GBIF.org). The dispersal behaviour is highly heritable in these invasive spiders. Furthermore, the high dispersal is recessively inherited and phenotypically expressed only in offspring of strictly two high dispersive parents (Narimanov et al., 2022). It is thus possible that high-dispersers, carriers of the homozygous recessive allele responsible for high dispersal, shape the vanguard of the invasion front and reach the distant location first. In such low-density areas, high-dispersers mate among each other, producing equally vagile offspring and hence driving the spread even further (i.e., Olympic Village effect; Chuang & Peterson, 2016; Shine et al., 2011). However, with time passing, the low-dispersers, the carriers of dominant low dispersive genetic material, would also reach these remote areas and mix with high-dispersers. Therefore, high dispersal would eventually be masked by dominating low dispersive allele, bringing the fronts' dynamics into a stable state after the selection for high dispersal is over. From an evolutionary perspective, this could benefit the expanding species by allowing the populations to settle in the novel areas (Dytham, 2009; Hughes et al., 2007; Narimanov et al., 2022).

Both the range dynamics and the prevalence of highly mobile genotypes at the invasion front indicate an accelerated rate of range expansion of *Mermessus trilobatus* in Europe. Such accelerated invasion has been demonstrated in cane toads, *Rhinella marina*, expanding in Australia (Phillips et al., 2010b; Shine et al., 2021; Urban et al., 2008). However, invasion dynamics in this species were heterogeneous on the regional scale and depended on the environmental factors determining dispersal behaviour (Urban et al., 2008). Apart from the genetic background underlying the dispersal ability, many environmental factors can influence the range dynamics of expanding species. For instance, Allee effects (Allee, 1931) might hinder the spread due to the low densities and mate limitation at the expansion edges (Travis & Dytham, 2002). However, as indicated by the frequency of mating plugs, no differences in female fertilisation rates were detected among the four populations of *Mermessus trilobatus* studied here. Contrary to Allee effects, the increased relatedness (i.e., kin competition) at the expansion front may further reinforce the expansion rate if the organisms possess the abilities to recognise a kin (Van Petegem et al., 2018). Additionally to kin recognition, positive density-dependence of dispersal (De Meester & Bonte, 2010) can fuel the expansion rate throughout the invasion history. Subsequently, the speed of invasion of *M. trilobatus* in Europe might also differ on the regional scale. Hence, more complex model simulations considering all possible ecological and geographical factors are needed to fully understand the nature of *M. trilobatus*' expansion in Europe.

Both females and males of *M. trilobatus* are similarly sorted across their expansion range with increased evolution for high dispersal ability at the front areas. Such similarities between the sexes, despite different dispersal propensities, do not come as a surprise since the dispersal behaviour of this species proved as highly heritable through dam and sire for both female and male offspring (Narimanov et al., 2022). This absence of sex-biased expansion might have contributed to the accelerated spread (Miller & Inouye, 2013), lowering the risks of mate limitation and maintaining the genetic diversity.

Our results show that the accelerated spread of invasive *M. trilobatus* is driven strictly by their dispersal behaviour and not by competing ability for webs or reproductive output. Compared to native sympatric species, these invasive spiders are poor competitors for webs due to their relatively small size compared to native Linyphiidae (Eichenberger et al., 2009). However, within the species, large-bodied conspecifics are superior in taking over foreign webs (Samu et al., 1996; Wise, 1993). Thus, the absence of size dimorphism between core and front populations of *M. trilobatus* in Europe can explain similar competing abilities between core and front female individuals. The lack of increased investments into reproduction at the edge could be explained by *M. trilobatus*' ability to overcome Allee effects at the front areas. Females of this species develop a mating plug after the first mating (Narimanov et al., 2022) and are capable of long-distance dispersal (Van Wingerden, 1980; Weyman et al., 2002). The species, hence, might not be limited by mates at the front areas with low density since the male genetic material can also travel with females after successful mating. Moreover, similar to a rapidly expanding spider, *Argiope bruennichi*, no correlation among dispersal, competition and reproduction traits in *M. trilobatus* shows that dispersal has evolved independently from other surviving-facilitating traits (Bonte & Dahirel, 2017; Wolz et al., 2020) in the course of the invasion of this species in Europe.

Conclusion

Records of *Mermessus trilobatus* across Europe illustrated an at least twofold increase in the progression rate of the invasion front over the last 45 years. Spiders from the areas with the most recent spread were selected for the higher propensity of dispersal behaviour but not reproductive output or competing ability. The ongoing spatial selection resulting in an evolved increase in dispersal ability combined with the high heritability of dispersal in *M. trilobatus* (Narimanov et al., 2022) contributed to its accelerated spread in Europe. As the evolution of dispersal behaviour is little studied in arthropods, it might play a role in other invasions by non-native arthropods worldwide.

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Author contributions

Nijat Narimanov: Conceptualisation (supporting); Methodology (equal); Formal analysis (lead); Investigation (lead); Data curation (lead); Writing-original draft (lead); Writing-review & editing (lead); Visualisation (lead); Project administration (lead).

Tobias Bauer: Investigation (supporting); Writing-review & editing (supporting).

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Data availability statement

The data will be uploaded to the *Figshare* data repository when the manuscript is accepted for publication.

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Conflict of interest disclosure

The authors have no interest to declare.

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Chapter 7

Synthesis and outlook

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Ecological factors

We found no evidence for the ruderal strategy or the enemy release as the driving mechanisms behind the invasion success of *Mermessus trilobatus* in Europe. Our experiments showed that densities of invasive *M. trilobatus* decreased rapidly after soil disturbance in grasslands, whereas no native linyphiid showed a comparable decline. Furthermore, invasive linyphiid was almost three times more susceptible to the abundant native predator, *Pachygnatha degeeri*, than a native linyphiid species. Thus, invasive *M. trilobatus* is naïve towards generalist predators in European grasslands. Despite these ecological pressures in its exotic range, *M. trilobatus* could still colonise a large part of Europe in under five decades, most likely due to high reproduction. High reproductive investments trading off the low competing ability (Eichenberger et al., 2009) and increased susceptibility to local predators might explain the striking invasion success of *M. trilobatus* in its invaded range. The experiments comparing the reproduction of *M. trilobatus* to native linyphiids are ongoing and beyond the scope of this thesis (but stay tuned!).

Soil disturbance sensitivity of *M. trilobatus* could be related to the destruction of the webs during tillage since *M. trilobatus* is an obligatory web builder. However, it is important to note that soil tillage did not decrease the densities of other obligatory web builders during our experiments. Thus, other factors, such as microclimate or prey availability, might underly the sensitivity of *M. trilobatus* to soil disturbance in grasslands. Furthermore, Eichenberger and colleagues (2009) compared the web competing ability of invasive *M. trilobatus* and five native sympatric species with a similar hunting strategy. *Mermessus trilobatus* proved itself as a poor competitor due to its relatively small body size. Consequently, the preference of the habitats with lower densities of better competing species was expected for our invasive species. Nevertheless, neither invasive *M. trilobatus* nor any other obligatory web builders showed any preference towards disturbed sites. On the contrary, the free hunters, namely *Oedothorax apicatus* and *O. fuscus* (Cardoso et al., 2011), showed a relatively high preference for disturbed grasslands (Chapter 2: Fig. 1). Thus, investigations of possibly higher pressures from free hunting linyphiids (*O. apicatus* and/or *O. fuscus*) on *M. trilobatus* deserve scientific attention.

Only one predator species, namely *P. degeeri*, was used in our predator susceptibility experiments. This might represent the disadvantage of the study since the invasive spiders could be released from other predators. Nevertheless, our trial experiments with wolf spiders (Araneae: Lycosidae) and black garden ants (*Lasius niger*) resulted largely in failure for predators to consume neither invasive nor native linyphiid spiders. However, this is particularly surprising for wolf spiders since other spiders make up a substantial portion of the lycosids' diet (Nyffeler et al., 1994). The reason for such a failure could be, in opposite to *P. degeeri*, the inability of lycosids and ants to climb and invade the linyphiids' webs. Thus, *P. degeeri* is an ideal candidate as an abundant generalist predator of linyphiids in European grasslands, which is not found in the native range of *M. trilobatus* (Millidge, 1987; Nentwig et al., 2021; World Spider Catalog, 2021). Nevertheless, this invasive species might still be released from parasites, parasitoids and/or pathogens (reviewed in Durkin et al., 2021) in Europe, facilitating its colonisation success. Thus, further experiments on this topic are warranted.

Dispersal experiments

Meteorological factors trigger spiders' dispersal behaviour (Bell et al., 2005; Cho, 2021; Sheldon et al., 2017), including atmospheric electric fields (Morley & Robert, 2018). Although strong electric fields employed in our experiments elicited tiptoe behaviour in spiders, the successful take-off was driven by the presence of wind. In spiders, mechanosensory hairs (trichobothria) are used to perceive the surrounding environment, including detecting the air movement facilitating the flight (Barth, 2002; Reissland & Görner, 1985). Spiders' ability to detect the atmospheric electric fields and distinguish the signal of strong electric fields from those of the wind was tested in the study of Morley & Robert (2018). The authors studied the response of front metatarsus trichobothria to the light wind of 0.5 m/s strength and electrical stimuli with 0.1 Hz and 0.01 Hz square waves to imitate the rapid change in electric fields in the air. As a result, the authors concluded that despite sharing a common peripheral receptor, air movement and electric fields generated different mechanical responses in spiders. It is essential to note that the values of electric fields used in these analyses and also in our experiments (6.25 kV/m) are equivalent to the values of the exposed positions such as tree crowns ~ 20 m above the ground (Morley & Robert, 2018) or electric fields in disturbed weather (>2 kV/m in heavy shower/thunderstorm; Bennett & Harrison, 2007). The wind velocity of 0.5 m/s used in experiments by Morley & Robert (2018) to stimulate spiders' trichobothria is not equivalent to the strength of the wind during disturbed or stormy weather (the Beaufort Scale; *Royal Meteorological Society*). Moreover, linyphiid spiders employed in these experiments widely balloon in fair weather conditions (Vugts & Wingerden, 1976) and with the wind speed threshold of 4 to 5 m/s (Simonneau et al., 2016). Further, these spiders are primarily found in open habitats where the values of atmospheric electric fields can vary between +0.05 and +0.3 kV/m (Bennett & Harrison, 2007), with simulated maximum values reaching only up to 1 kV/m (Morley & Gorham, 2020). Thus, studies comparing the trichobothria response of spiders to the wind and electric field stimulus matching similar and realistic for spiders' dispersal weather conditions are highly encouraged. Furthermore, our experiments found significantly distinct tiptoe behaviour under electric field treatment strictly for *Erigone dentipalpis* and not for *Agyneta rurestris* or *Mermessus trilobatus* (Chapter 4: Fig. S1 in Supplementary materials). Interestingly, all 36 spiders used in the experiments by Morley & Robert (2018) belonged to the genus of *Erigone*. This is, hence, possible that mostly *Erigone* spp. have evolved to distinguish the rapid change of atmospheric electricity. In contrast, *Erigone* spp. could also be simply unable to distinguish the stimulus of strong electric fields from those of wind and try to disperse by performing tiptoe behaviour in conditions with strong electric fields but no airflow. Further multispecies studies incorporating weaker values of electric fields strength under different wind velocities are needed to fully understand the role of atmospheric electricity in the dispersal of spiders and other passively dispersing arthropods.

Accelerated spread and genetics of dispersal

Invasive *Mermessus trilobatus* has spread into at least 21 European countries, travelling up to 1400 km from the area of the first record in Europe (Dumpert & Platen, 1985). The invasion speed of this species has accelerated during its invasion, making its remarkable colonisation success possible under 50 years (Chapter 6: Fig. 1; Feng et al., 2021; Grbić et al., 2021; Hirna, 2017). Accumulation of high dispersive populations at the front areas

with the recent spread shows a temporal character of its spatial sorting in Europe and highlights the role of recessive inheritance of high dispersal in this species. Hence, low dispersive individuals (carriers of dominant low dispersal allele) might reach the front areas following high dispersers (carriers of recessive high dispersal allele) after a certain period and thus bring the dynamics of the front to the stable state by mating with high dispersers (i.e., recessive high dispersal allele will be masked by the dominant low dispersal allele). Thus, our results suggest that variation of a single gene has a strong effect on the dispersal behaviour of *M. trilobatus*, which contrasts with the numerous studies demonstrating the oligogenic architecture underlying dispersal (reviewed in Saastamoinen et al., 2018). However, note that the significant effect of a single gene in traits' heritable variation has also been reported in other taxa, namely the lifespan and egg hatching rate in Glanville fritillary butterfly (*Melitaea cinxia*; Klemme & Hanski, 2009) and the presence of an escape tunnel in burrows of oldfield mice (*Peromyscus polionotus*; Weber et al., 2013). Thus, molecular analyses (e.g., Quantitative trait locus analysis; Miles & Wayne, 2008) incorporating dispersal experiments can help to identify a single gene in the dispersal behaviour of *M. trilobatus*. Moreover, when identified, the gene responsible for high dispersal in this species might be used to address a number of questions. For example, by examining a high number of individuals from distant locations in the native and invaded range, we could better understand the spatial dynamics of the dispersal alleles. Furthermore, we could “rewind time” and analyse the genetic material of specimens kept in private and museum collections, providing more detailed answers on the nature of its spread in Europe, identifying whether the high dispersal allele was present from the beginning of its invasion history and how its dominance developed over time. This knowledge might have implications for other taxa and dispersal-mediated traits by providing opportunities to study the population dynamics of the species of interest on the spatial and temporal scales.

During this research, a single introduction of the species in the 1970s in the Upper Rhine valley near Karlsruhe (Dumpert & Platen, 1985) was presumed. Although the concentric range expansion, the spatial sorting and concentration of dispersive genotypes at the front areas with the most recent spread might indicate a single introduction of *M. trilobatus* in Europe, further introduction events of this species cannot be excluded. Genomic admixture from previously separated populations of the wasp spider, *Argiope bruennichi*, has fuelled the north-poleward expansion of this Mediterranean spider (Krehenwinkel et al., 2015). Hence, in *M. trilobatus*, secondary introductions might have occurred during the last 50 years, and these new introduction events could add some genetic diversity to the invasive populations. Consequently, genome-wide analysis of *M. trilobatus* individuals from their native range (United States, Canada; Millidge, 1987) and individuals collected from the distant location and large areas in Europe might clarify this question and better explain the dynamics of *M. trilobatus*' spread in Europe also on the local scale.

Community scale: Abundance and impact

Apart from the rapid spread, *Mermessus trilobatus* was characterised as one of the most abundant spiders in parts of Europe (Schmidt et al., 2008). For example, in the same meadows where spiders were sampled in Landau, Germany for the experiments in this project (Chapters 3, 4 & 5), *M. trilobatus* accounted for ~36.7% of all adult spiders with an average of 10.4 adult individuals per square metre in summer of 2011. All other linyphiid species had abundances lower than 1.3 individuals per 1m² (data from Martin Entling). Thus, such a high dominance of this invasive species could have indicated the

replacement of native linyphiids in the long-established areas (~40 km distant from the presumed centre of invasion; Dumpert & Platen, 1985). Nevertheless, we observed a drastic decrease in the abundances of *M. trilobatus* in the same meadows in Landau during the summers of 2019 and 2020. Instead of approx. 10.4 individuals per square metre, we found only 0.54 adult *M. trilobatus* in 1m². Such a drastic drop in abundances after a certain period in the invasion core could be explained by the native predator naïveté (Cox and Lima, 2006) at the beginning of the invasion history. In other words, native predators might not recognise *M. trilobatus* as a potential prey at first and eventually adapt to this novel prey (Hawkes, 2007), lowering the abundance of the invasive prey after a certain time. Further studies comparing susceptibility of *M. trilobatus* to common predators from the populations where *M. trilobatus* has never been found could clarify this question. Nevertheless, the extremely dry summer in 2018 and its consequences in central Europe (Ionita et al., 2021) could have played a more significant role in the decrease in abundances of *M. trilobatus* around Landau since a sharp drop in the abundance of another linyphiid species, *Erigone dentipalpis*, was also observed in the area when compared with data from 2011 (Martin Entling, personal observation). Additionally, the abundance of *M. trilobatus* in meadows around Vienna in the summer of 2020 was similar to those in Landau (~0.5 per 1m²). Thus, extreme local climatic changes in central Europe can explain the current rarity of this species in grasslands. Hence, faunistic studies quantifying the abundances of *M. trilobatus* across spatial and temporal scales are needed to understand the population dynamics of this invasive spider species in Europe and associated possible impacts to the native ecosystems. However, at this stage, due to the current relative low abundance, poor competing ability with native linyphiids (Eichenberger et al., 2009), and high susceptibility to a native predator species, the impact of *M. trilobatus* on the native communities in Europe seems to have rather a positive nature (increasing the local biodiversity), or at least the negative impact appears to be unlikely. Nevertheless, the absence of the data does not mean the lack of the effect, and thus, studies analysing the impact of *M. trilobatus* on the native communities across its exotic range are highly encouraged.

Similar invasions

The mechanisms of invasions studied in this project can be alternatively applied to a number of invasive arthropods with similar life-history traits as *Mermessus trilobatus*. For instance, Bell and colleagues (2005) created a catalogue of 400+ ballooning species of spiders, spider mites and moth larvae, some of which might be introduced to the novel areas and can be prone to show similar to *M. trilobatus* or even different ecology and evolution during their establishment and spread in the exotic ranges. As an example of spiders, sympatric species of *M. trilobatus*, namely *Agyneta rurestris* and *Erigone dentipalpis*, were first recorded in North America in 2009 and 2014, respectively (Drapeau Picard, 2021; GBIF.org). These linyphiid species are non-native to North America and have been introduced to the area via human transport. Compared to *M. trilobatus*, both *A. rurestris* and *E. dentipalpis* exhibit higher dispersal propensity during the lab experiments (Chapter 4: Fig. S1 in Supplementary materials; Entling et al., 2011) and, hence, have a potential to rapidly colonise the unoccupied territories. Furthermore, *E. dentipalpis* is superior in competing for webs than *M. trilobatus* (Eichenberger et al., 2009). The species, hence, might rapidly spread and dominate in the native range of *M. trilobatus* by eventually replacing some native species. However, as many non-native species, these species might also fail to establish in North America and remain in low abundances in grasslands. For instance, *E. dentipalpis* was first recorded in Australia

already in 1991 with no further records until 2008 when two individuals were sampled (possible reintroduction after 17 years; GBIF.org). Thus, *E. dentipalpis* might be unable to establish and spread in Australia due to potential novel ecological pressures in the invaded range. However, note that the species might simply be understudied in the area and/or collected specimens could be unreported. Consequently, future studies incorporating the knowledge gathered during this project are warranted to investigate the establishment, spread and impact on invaded ecosystems of other invasive arthropods around the globe.

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Appendix

Status and author contributions of publications included in the thesis

Curriculum vitae

Declaration

Status and author contributions of publications included in the thesis

Chapter 2

Narimanov, N., Kempel, A., Van Kleunen, M., & Entling, M.H. (2021). Unexpected sensitivity of the highly invasive spider *Mermessus trilobatus* to soil disturbance in grasslands. *Biological Invasions*, 23(1), 1–6.
<https://doi.org/10.1007/s10530-020-02348-9>

See Chapter 2 for author contribution statements.

Chapter 3

Narimanov, N., Hatamli, K., & Entling, M.H. (2021). Prey naïveté rather than enemy release dominates the relation of an invasive spider toward a native predator. *Ecology and Evolution*, 11(16), 11200–11206. <https://doi.org/10.1002/ece3.7905>

See Chapter 3 for author contribution statements.

Chapter 4

Narimanov, N., Bonte, D., Mason, P., Mestre, L., & Entling, M.H. (2021). Disentangling the roles of electric fields and wind in spider dispersal experiments. *The Journal of Arachnology*, 49(3), 380–383. <https://doi.org/10.1636/JoA-S-20-063>

NN and MHE conceived the idea; NN, MHE, PM, DB and LM designed the methodology; NN and PM collected the data; NN analysed the data and wrote the first draft of the manuscript. All authors contributed critically to the drafts.

Chapter 5

Narimanov, N., Bonte, D., & Entling, M.H. (2022). Heritability of dispersal in a rapidly spreading invasive spider. *Animal Behaviour*, 183(1), 93–101.
<https://doi.org/10.1016/j.anbehav.2021.11.002>

See Chapter 5 for author contribution statements.

Chapter 6

Narimanov, N., Bonte, D., Bauer, T., Fahse, L., & Entling, M.H. (under review). Accelerated invasion through the evolution of dispersal behaviour.

See Chapter 6 for author contribution statements.

Curriculum vitae

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Education

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Academic work and Internship

04. 2019 - present **Scientific Assistant**, iES Landau Institute for Environmental Sciences, Department of Ecosystem analysis, University of Koblenz-Landau
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German	C1	C1	B1	B1
Russian	C2	C2	C2	C2
Azerbaijani	C2	C2	C2	C2

A1 and A2: Basic user; B1 and B2: Independent user; C1 and C2: Proficient user

[Common European Framework of Reference for Languages](#)

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Publications

1. Mestre, L., **Narimanov, N.**, Menzel, F., & Entling, M.H. (2020). Non-consumptive effects between predators depend on the foraging mode of intraguild prey. *Journal of Animal Ecology*, 89(7), 1690–1700.
<https://doi.org/10.1111/1365-2656.13224>
2. **Narimanov, N.**, Kempel, A., Van Kleunen, M., & Entling, M. (2021). Unexpected sensitivity of the highly invasive spider *Mermessus trilobatus* to soil disturbance in grasslands. *Biological Invasions*, 23(1), 1–6.
<https://doi.org/10.1007/s10530-020-02348-9>
3. **Narimanov, N.**, Hatamli, K., & Entling, M.H. (2021). Prey naïveté rather than enemy release dominates the relation of an invasive spider toward a native predator. *Ecology and Evolution*, 11(16), 11200–11206.
<https://doi.org/10.1002/ece3.7905>
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<https://doi.org/10.1636/JoA-S-20-063>
5. **Narimanov, N.**, Bonte, D., & Entling, M.H. (2022). Heritability of dispersal in a rapidly spreading invasive spider. *Animal Behaviour*, 183(1), 93–101.
<https://doi.org/10.1016/j.anbehav.2021.11.002>

Reviewer for international journals

- 01.2021: *The Journal of Arachnology* [[Web link](#)]
- 10.2021: *Biological Invasions* [[Web link](#)]

**Declaration according to §8 of the Promotionsordnung des
Fachbereichs 7: Natur- und Umweltwissenschaften der Universität
Koblenz-Landau, Campus Landau vom 14.06.2013 i.d.F. vom
19.08.2014**

Erklärung des Doktoranden darüber,

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ob er die gleiche oder eine andere Abhandlung in einem anderen Fachbereich oder einer anderen wissenschaftlichen Hochschule als Dissertation eingereicht hat, ggf. mit welchem Erfolg; - *nicht zutreffend*

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Landau, 21. Januar 2022



Nijat Narimanov