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Steatoda nobilis, a false widow on the rise: a synthesis of past and current distribution trends

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Abstract

The Noble False Widow, *Steatoda nobilis* (Thorell, 1875) (Araneae, Theridiidae), is, due to its relatively large size and potential medical importance, one of the most notable invasive spider species worldwide. Probably originating from the Canary Islands and Madeira, the species is well established in Western Europe and large parts of the Mediterranean area and has spread recently into California and South America, while Central European populations were not known until 2011.

We report on long-time observations that reveal that at least two flourishing populations in Germany (Cologne) have been present for over five years, while in Ecuador one population has been observed between 2014 and 2018 and several other records were made in other parts of the country. Data obtained from the British Spider Recording Scheme demonstrate that the species moved significantly northwards since the report of the first populations in the very South of England, after several decades of relative stasis. The sudden northward expansion highly correlates with a massive rise in press coverage of the species.

In the Americas, *S. nobilis* is currently known from four countries (USA, Chile, Ecuador, Colombia), and available DNA barcoding data obtained for specimens from this area suggest that multiple introductions occurred within each country. Using ecological niche modeling, we identified suitable climate regions for the species and discuss possible reasons for its current spread. We propose that seaside cities and villages with a temperate oceanic or Mediterranean climate are especially favourable potential habitats for *S. nobilis* and will face the highest colonization pressure in the future, while tropical upland regions with temperate climates are also vulnerable to invasion by *S. nobilis*.

Keywords
alien species, araneism, biological invasion, citizen science, spider, steatodism

Introduction

With currently over 47 000 described species, spiders (Araneae) represent a hyperdiverse and extraordinarily variable arthropod group inhabiting nearly every terrestrial habitat on the globe (Mammola et al. 2017; World Spider Catalog 2018). Numerous species are successful alien colonizers (e.g., Kobelt and Nentwig 2008; Nentwig 2015) and spread, assisted by human activities, into natural and human-influenced habitats all around the world (e.g., Levi 1967; Pugh 2004; Nentwig 2015).

Members of the spider family Theridiidae, also known as tangle-web or cobweb spiders, are among the most successful alien spider species (Levi 1967; Nentwig 2015). Many alien theridiids live in and around human settlements (Kobelt and Nentwig 2008), and some particular species, e.g., *Nesticodes rufipes* (Lucas, 1846), *Steatoda grossa* (C.L. Koch, 1838), and *Parasteatoda tepidariorum* (C.L. Koch, 1841), are common house spiders in many parts of the world (Levi 1967). In some cases, alien theridiids seem to be able to replace native spider species of conservation importance (Hann 1990) or compete successfully against other native house spiders (Nyffeler et al. 1986), as well as threatening other arthropods through predation (Bryan et al. 2015) or even hybridizing with native species (Vink et al. 2008). Also, some theridiids of medical importance, e.g., black widow spiders of the genus *Latrodectus*, show a considerable range expansion due to human assistance. The infamous Australian redback spider, *Latrodectus hasselti* Thorell, 1870, successfully invaded New Zealand and Japan (Nihei et al. 2003; Vink et al. 2011), and the brown widow, *Latrodectus geometricus* C.L. Koch, 1841, a less dangerous relative (Müller 1993), was introduced into several countries and established on at least four continents (Vincent et al. 2008; World Spider Catalog 2018).

Steatoda nobilis (Thorell, 1875), one of the largest theridiids and sometimes called false widow or noble false widow, is often mistaken for a *Latrodectus* species. This species is able to inflict a painful bite often accompanied by swelling, erythema, and pruritus, but normally no systemic effects occur after a bite incident (Dunbar et al. 2017). The envenomation is partially comparable to that by *Steatoda grossa* (Isbister & Gray, 2003). Nevertheless, alleged *S. nobilis* bites are a stock feature especially of the British popular press (e.g., Christodoulou 2018), and reports of *S. nobilis* infestations have regularly resulted in public disruption (e.g., Associated Press 2015; Siddique 2018).

Probably native to the Canary Islands and Madeira and first described from the latter (Thorell 1875), *S. nobilis* dramatically expanded its range in the last 100 years. The main invasion pathways for several alien spider species are relatively well known (potted plants, fruits, containers, packing material, and feeder cricket boxes) (Nentwig 2015), and for *S. nobilis*, it was often suspected that current populations in Great Britain and Ireland are descendants of specimens imported to Europe with bananas and other fruit from the Canary Islands (e.g., Roberts 1995; Kulczycki et al. 2012).

Although alien populations of *S. nobilis* are known today from England, Ireland, several parts of the Mediterranean area, California, and Chile (Snazell and Jones 1993; Vetter et al. 2015; Taucare-Ríos et al. 2016; Dugon et al. 2017), no established population has ever been reported from Germany or other Central European countries. In the Mediterranean area and, e.g., California, nearly all records of *S. nobilis* are located in low altitudes, often near the coast (Kulczycki et al. 2012; Vetter et al. 2015; Morano et al. 2018), while the species is known to occur in natural habitats at altitudes up to 3200 m in their native range on Tenerife (Schmidt 1968).

Recently, we became aware of two established populations in Cologne, Germany, and collected *S. nobilis* in domestic settings in urban areas in the uplands of Ecuador. Both of these records are in accordance with the current spread of *S. nobilis* into new and sometimes unexpected habitats and areas all around the world. To further explore the distribution of *S. nobilis*, we collated all known distribution data together with a large citizen science dataset from Great Britain and performed several analyses of the current distribution trends on a global and local scale, including a global species distribution model. The aim of the work is to present a brief review of the invasion history of *S. nobilis*, describe current and potential future problems with this invasive species, and to identify regions which are suitable for future invasion.

Material and methods

Field surveys

Spiders were observed and collected by CW during several surveys at two localities in Cologne, Germany, in 2011–2017, with at least one survey per year. In Ecuador, several specimens were collected unsystematically by NR during a field trip in 2014. Collected specimens were identified using Snazell and Jones (1993) and the key in Nentwig et al. (2018). A male and a female found in October 2011 at locality 1 in Cologne (Tab. 1) were deposited in the collection of the State Museum of Natural History, Karlsruhe (**SMNK**). Two males and two females from Ambato were deposited at the Museo de Zoología (**QCAZ**) in Quito, Ecuador. Further material from Stuttgart, Germany, was also deposited at the SMNK.

Data review and analysis

To assess the global and local distribution as well as the invasion history of *Steatoda nobilis*, taxonomic and biogeographic literature was surveyed (Suppl. material 1: Table A1). Additional data were obtained from the British Spider Recording Scheme of

Table 1. Records of *Steatoda nobilis* in Germany.

Federal state	City	Location	Habitat	First collection	Status	Literature
BW	Stuttgart	48.8268N, 9.1677E	Wall of house	19.X.2018	?	Own data
NRW	Cologne	50.9657N, 6.8690E	Garden centre	10.X.2011	Established	Own data
NRW	Cologne	51.0139N, 6.9139E	Garden centre	XI.2011	Established	Own data
Berlin	Berlin	Not specified	Flower wholesale trade	2012–2013	Single observation	Reiser (2013)
BB	Not specified	Not specified	Garden centre	2012–2013	Single observation	Reiser (2013)
BW	Balingen	Not specified	Garden centre	2012–2013	Single observation	Reiser (2013)
Hamburg	Hamburg	Harbour area	Harbour buildings	Around 1954	Imports	Schmidt (1954, 1956)

the British Arachnological Society (British Arachnological Society 2018). We also performed a full-text search of the Lexis-Nexis database for all articles in UK newspapers mentioning "*Steatoda nobilis*". Subsequent analyses were done using the statistical software R 3.3.1 (R Development Core Team 2016). We used Spearman's rank correlation to analyse the relationship between number of records and number of press articles per year mentioning *S. nobilis.* To quantify the expansion of the species in Britain, the northerly distance of every grid record from Torquay, the site of the first and southernmost British *S. nobilis* record (Pickard-Cambridge 1879), was calculated using the function "distVincentyEllipsoid" in the R-package "geosphere" (Hijmans et al. 2017).

To further explore the global distribution of *S. nobilis* and its climatic drivers we performed additional analyses. We ran a principal component analysis (PCA) of bioclimatic variables (CHELSA climate data; Karger et al. 2017) to compare the native and invasive conditions in the environmental space. Based on these results we built a global species distribution model (SDM) using Maxent 3.4.1 (Phillips et al. 2017), a machine learning presence–background SDM which is widely used in macroecology (Merow et al. 2013). Detailed information about the PCA and the complete SDM analysis is provided in the Suppl. material 1. To test the predictions made by the climatic suitability model, a field survey was conducted in the city area of Granville, Normandy (France). The collected material was also deposited at the SMNK.

DNA barcoding data were obtained from the public section of the Barcode of Life Data System version 4 (BOLD), http://www.boldsystems.org/ (last accessed 1 May 2018). Specimens that were not determined to species in the database were identified on the basis of geographical and genetic proximity to identified specimens, as well as habitat information and habitus photographs available in BOLD.

Review and results

Global invasion history of *S. nobilis*

Steatoda nobilis was first described based on specimens from Madeira by Thorell (1875). Around the same time, a juvenile specimen of this species was collected by

Hamlet Clark in the neighbourhood of Torquay, England (Pickard-Cambridge 1879, as *Steatoda clarkii*). This record is often mentioned as the first record in Great Britain (e.g., Snazell and Jones 1993). However, this early record is slightly dubious, as in 1879 the Rev. Clark had already been dead for 12 years, and his lasting fame as a naturalist is based on his yachting trip (with John Gray) to Spain, Algeria, Brazil, and the Cape Verde Islands, during which he collected spiders for John Blackwall and, importantly, also made a brief onshore visit in Funchal, Madeira (in Tenerife, where the company also passed by, this was impossible due to quarantine restrictions) (Clark 1867). There is, thus, a distinct possibility of a mislabelling of the specimen, especially as Pickard-Cambridge explains that it was obtained together with many other spiders and had been "accidentally mislaid until very lately". Jackson (1907) reported on a specimen found on a cliff in Southern England "far from any house" and implied that an established population in England might exist. One of the earliest mentions of *S. nobilis* from the Canary Islands is found in Pickard-Cambridge (1908), who described specimens imported with Canarian bananas. Most probably *S. nobilis* was very regularly transported together with fruits from the Canary Islands to Great Britain, ever since Elder Dempster and Alfred Fyffe began the large-scale import of bananas and other fruits in the 1890s (Pickard-Cambridge 1908; Striffler and Moberg 2003).

In Germany, the species was one of the most frequently imported spiders with Canarian fruit arriving in the harbour of Hamburg at some point (Schmidt 1954, 1956), but there is no evidence *S. nobilis* ever became established in the Hamburg area. No further German specimens are deposited in the collection of the Zoological Museum of Hamburg, but three samples of imported specimens determined by Schmidt were transferred in 1988 to the collection of the Senckenberg Museum, Frankfurt (accession no. SMF 37425-115, 37426-115, and 37437-115; R. Klesser pers. comm.).

Although native to Madeira and the Canary Islands, *S. nobilis* was probably introduced on the Azores in the 20th century (Schmidt 1990). In the Mediterranean, it seems possible that populations of *S. nobilis* existed already before 1980: Pickard-Cambridge (1899) examined material from "Madeira and Spain" (the latter, however, could refer just to the Canary Islands), and Denis (1957) mentioned a juvenile specimen found in the Spanish Sierra Nevada determined as *Steatoda* sp. (as *Teutana*), which resembles *S. nobilis*. Additional records by Melic (1994), Vanuytven et al. (1994), and Snazell and Jones (1993) showed that *S. nobilis* was certainly already established at various places on the Iberian Peninsula in the early 1990s. A recent record of *S. nobilis* from the Normandy (Tab. 3) collected by TB, based on the predictions of the distribution model described below, represents the first clearly identified population from the French Atlantic Coast known to us (e.g., Emerit and Ledoux 2013; Courtial and Pétillon 2014).

The first record for Ireland was published by Nolan (1999), supporting the idea of a late establishment of *S. nobilis* in Western Europe. Today, the species is widespread on the island and common in many urban areas (Dugon et al. 2017).

In the Americas, the populations in California have to be established only recently. Vetter et al. (2015) pointed out that only very recently pictures and records of *S. nobilis* have been sent to an address originally used for records of *Latrodectus geometricus*, another alien theridiid which has settled in California. In Chile, records from four cities are currently known. Besides the records from Concepción and Temuco (Taucare-Ríos et al. 2016), observations of *S. nobilis* in Valdivia and Pucón are mentioned in Ceryngier et al. (2018). Concepción and Valdivia, both cities with large harbour areas, are separated by a distance of over 300 km. These records show that *S. nobilis* is widespread in Chile.

Steatoda nobilis has also been reported from Morocco (Denis 1962; Ledoux and Raphael 1998; Emerit and Ledoux 2013), which would be the only record for mainland Africa. However, Denis never formally published the numerous Moroccan records collected by Gattefossé (Emerit and Ledoux 2013). Additionally, the type locality of the closely related *Steatoda maura* (Simon, 1909) is located in Morocco (Simon 1909; Levy and Amitai 1982), and this species is mentioned as a possible synonym by Ledoux and Raphael (1998), without, however, giving arguments supporting this view. This synonymy had already been suggested by Wiehle (1934), without examining type material, but was convincingly refuted when Levy and Amitai (1982) examined and illustrated the types of *S. maura*. While this species is without doubt distinct, it is noticeably close to *S. nobilis* in terms of its genital morphology and overall habitus. Indeed, at the barcode level, the sequenced specimens most similar to *S. nobilis* are from BOLD:AAG5682 (distance 9.88%, reciprocal nearest neighbours in BOLD), three large adult females collected in Antalya and İzmir, Turkey. The photos provided by BOLD, together with the locality, indicate that these belong to *S. maura* (which has been reported from İzmir before; as *Lithyphantes gerhardti* from "Smyrna"; Wiehle (1934)). Therefore, material of *S. nobilis* from Morocco should be examined and compared to *S. maura*, but it still seems possible that *S. nobilis* is established in coastal cities of Morocco, as some other records originate from the very south of Spain (Morano et al. 2018). Incidentally, the relatively close genetic relation to the supposed *S. maura* also supports an origin of *S. nobilis* in the Macaronesian/North African region and not elsewhere (e.g., in the Americas). Interestingly, *S. maura* is not listed on current checklists of Turkey (e.g., Demir and Seyyar 2017). Based on the description of the only *S. nobilis* specimen by Türkeş and Mergen (2005, again listed by Türkeş and Mergen 2007) it is possible that these authors confused *S. maura* with *S. nobilis*, as the mentioned body length (6 mm) would be atypical for an adult specimen of *S. nobilis*. Additionally, the arachnological literature (Roberts 1995; Heimer and Nentwig 1991) used for identification by these authors does contain *S. nobilis*, but not *S. maura*. Another record of *S. nobilis* from India (Raiz Tabasum et al. 2018: 43) is based on a definite misidentification, like most of the species presented there (the associated image shows an unidentifiable theridiid, but certainly not a species of *Steatoda*).

First Central European populations of *S. nobilis*

Steatoda nobilis was collected and observed from autumn 2011 to October 2017 at two garden centres in Cologne, Germany, which are separated by a distance of about 7 km. The first specimen was sighted indoors on 10 October 2011 at a large garden centre located in the west of Cologne (Table 1). Subsequently, six adults and juveniles were collected the same day, but several more webs with the typical tubular retreat were located and indicated a high population density. A few weeks later (November 2011), the species was discovered indoors at the second locality (Table 1). On every visit over the subsequent years, several specimens and/or intact webs could be observed. At both localities, the species inhabited the gaps of the window profiles made of aluminium. Juveniles have been frequently observed on potted plants available for purchase. Since about 2014, the species seems to have colonized the outside walls of buildings at locality 1 as well as bushes in the parking lot. At locality 2, the species can be found on shelves in the outdoor area, as well as on an outdoor wall with common ivy. However, it is not known if these are permanent settlements, and the species possibly vanishes from adjacent outdoor habitats in cold winters. Additional singleton specimens were observed in garden centres in Balingen, Berlin and Brandenburg (Reiser 2013). We also searched for *S. nobilis* in about 10 other garden centres in Cologne and adjacent areas. No other specimens could be found. Although individual specimens of *S. nobilis* have been repeatedly found in Germany, the records from Cologne are the first evidence for established populations in Central Europe. Recently, on 19 October 2018, an adult male *S. nobilis* was collected on a wall near a garden centre in Stuttgart, Germany (Table 1, Fig. 5B).

First records of *S. nobilis* for Ecuador

We found *S. nobilis* in 2014 at several locations in the uplands of Ecuador (Table 2), at an average altitude of about 2800 m a.s.l. All records come from man-made structures in urban and rural habitats, mostly on walls along streets and on house walls, a similar microhabitat to that preferred by other invasive outdoor populations of *S. nobilis*, but in a rather different macrohabitat (Fig. 1). Adults of both sexes as well as juveniles were observed. The highest number of specimens could be found on a wall in Ambato-Montalvo. We revisited this population in February 2018, when several specimens of both sexes could be observed and collected again, which indicates an established population. In the population in Ambato, several females with egg sacs were observed.

Literature survey of the habitat preferences of *S. nobilis*

Together with these new populations, confirmed alien populations of *S. nobilis* are currently known from over 10 countries on four continents (Table 3, Suppl. material 1: Fig. A7). This allows a more detailed assessment of the habitat requirements of the species, which determine its invasive potential.

In Great Britain and Ireland, *S. nobilis* is very abundant in and around houses, and can be found on typical urban structures, e.g., in houses and on outside walls, concrete fences or hedges (Dugon et al. 2017; Snazell and Jones 1993). Dugon et al.

Table 2. Records of *Steatoda nobilis* in Ecuador.

Province	Location	Coordinates	Habitat	Date	Specimens	Leg.
Tungurahua	Ambato-Montalvo	−1.3266, −78.6257	Brick wall	10.X.2014	1 ♀	N. Reiser
Tungurahua	Ambato-Montalvo	−1.3256, −78.6270	Wall	17.X.2014	1 ♀	N. Reiser
Pichincha	Quito	−0.1857, −78.4781	Wall	07.XI.2014	1 juv.	N. Reiser
Tungurahua	Ambato-Montalvo	−1.3256, −78.6269	Wall	08.XI.2014	5 ♀, 2 ♂, juv.	N. Reiser
Pichincha	Quito	−0.1860, −78.4795	On house wall	10.XI.2014	1 ♀	N. Reiser
Pichincha	Quito	−0.2199, −78.5116	On house wall	10.XI.2014	1 ♂, 2 juv.	N. Reiser
Cotopaxi	Salcedo	−1.0446, −78.5902	House wall near Panamericana	14.XI.2014	1 ♂	N. Reiser
Tungurahua	Baños	−1.3970, −78.4231	Between drip rail/house wall	21.XI.2014	1 ♀	N. Reiser
Tungurahua	Ambato central	−1.2579, −78.6388	House wall	25.XI.2014	1 ♀, 1 juv.	N. Reiser
Tungurahua	Ambato-Montalvo	−1.3256, −78.6269	Wall	04.II.2018	5 ♀ , 1 ♂	J.F. Altamirano

Table 3. Global distribution of *Steatoda nobilis*. es = established and non-indigenous, ? = unclear status, ?? = unverified mentioning, pn = probably native, sp = single specimen record.

Country	Area	Literature	Status
Spain	Mainland	Denis 1957?; Melic 1994; Morano et al. 2018	es
	Balearic Islands	collection SMF	?
	Canary Islands	Pickard-Cambridge 1908; Schmidt 1990; Snazell and Jones 1993	pn
Portugal	Mainland	Snazell and Jones 1993; Morano et al. 2018	es
	Azores	Schmidt 1990; Wunderlich 1992; Borges and Wunderlich 2008	es
	Madeira	Thorell 1875	pn
France	South	Ledoux and Raphael 1998; Emerit and Ledoux 2013	es
	Corse	Canard 1989; Emerit and Ledoux 2013	es
	Atlantic coast	presented data	es
Italy	Mainland	Kulczycki et al. 2012	es
	Sicily	no published records	?
	Sardinia	Kulczycki et al. 2012	es
Great Britain		Pickard-Cambridge 1879; Snazell and Jones 1993	es
Ireland		Nolan 1999; Dugon et al. 2017	es
Germany		Table 1; Reiser 2013	es
Belgium		Van Keer 2010	?
Netherlands		Bink 2014; Van Helsdingen 2015	?
Turkey		Türkeş and Mergen 2005 (doubtful; see text)	sp
Iran		Zamani et al. 2015; pers. comm. Zamani	es
Morocco		Denis 1962	??
United States		Vetter and Rust 2012; Vetter et al. 2015	es
Chile		Taucare-Ríos et al. 2016; Ceryngier et al. 2018	es
Ecuador		Table 2; Faúndez et al. 2018	es
Colombia		Faúndez et al. 2018	es

(2017) showed that *S. nobilis* in Ireland seems to be restricted to man-made habitats and is currently not expanding into natural habitats such as forests or dunes. The habitat information based on about 400 records presented on the British Record Scheme website (British Spider and Harvestman Recording Scheme 2018) suggests a similar behaviour in Great Britain, but recently *S. nobilis* is spreading into semi-natural habitat

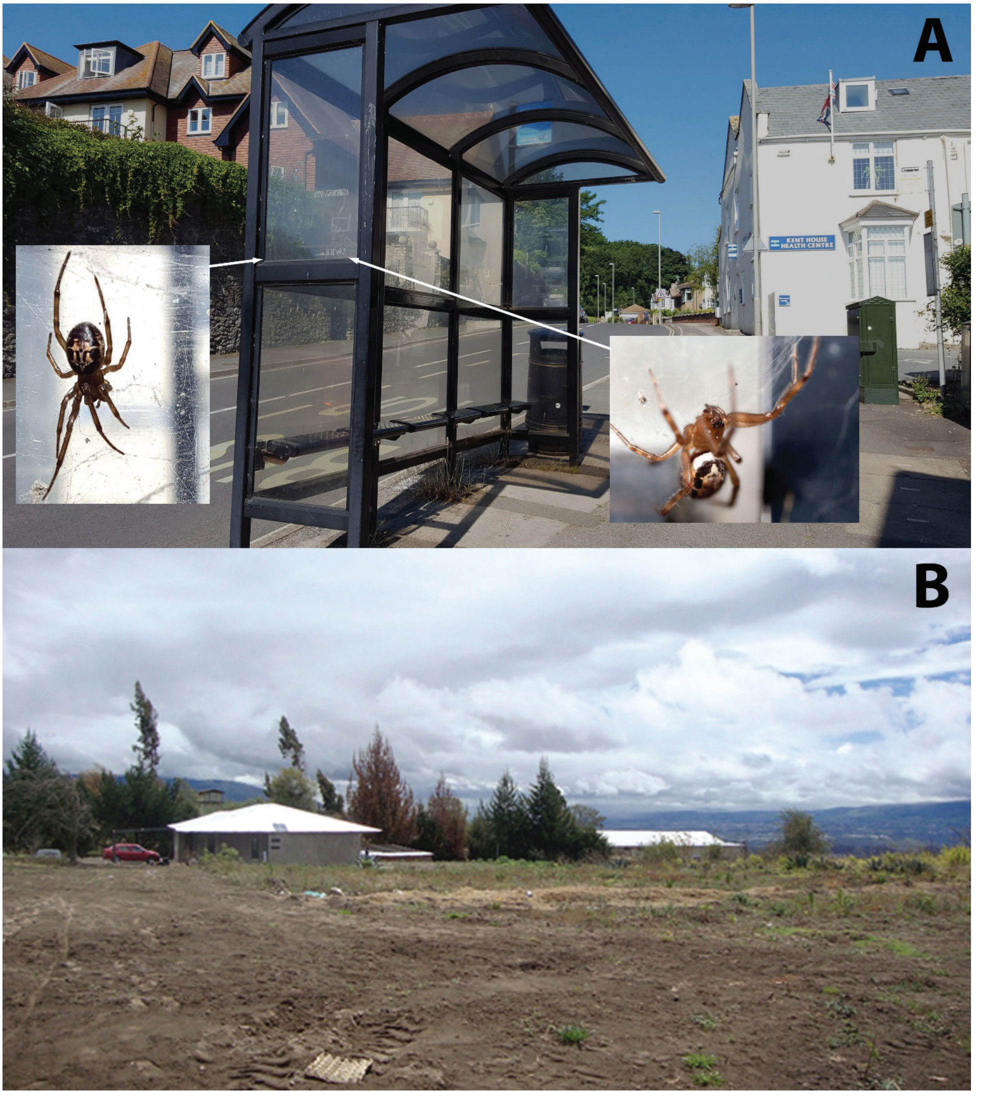

Figure 1. Diversity of habitats of *Steatoda nobilis* in its invasive range. **A** In the South of England, the species is not only abundant on stone walls and railings along the sea side, but also on man-made structures further inland, such as this bus stop in the coastal resort of Lyme Regis, Dorset, where its webs (inset) typically occur together with those of *Zygiella x-notata* (Araneidae) **B** Vicinity of the localities with records of *S. nobilis* in Ambato-Montalvo (Ecuador), August 2014.

in the southeast and is increasingly found in trees and scrubs in semi-natural habitats (P. Harvey pers. comm.).

In the Mediterranean, many of the *S. nobilis* observations were made in or around cities and villages (e.g. Kulczycki et al. 2012; Lecigne 2012; Melic 1994; Emerit and Ledoux 2013). However, several other specimens were collected in more natural habitats, e.g., a degraded pine forests near an urban area (Melic 1994), a (protected) marsh (Crespo et al. 2009), or dunes (Ledoux and Raphael 1998). An established population in Tehran, Iran (A. Zamani pers. comm.), is limited to urban areas.

In California (Vetter and Rust 2012; Vetter et al. 2015), most of the records were made randomly by citizens in their domestic environment and are therefore restricted to urban habitats, but it seems possible that *S. nobilis* is also spreading to more natural habitats in California. According to specimen data in the BOLD database (http://www.boldsystems.org/index.php/Public_BarcodeCluster?clusteruri=BOLD:ABA5272), five specimens of *S. nobilis* (1♀, 1♂, 3 immatures) were collected in 2011 at a dry dusty trail in Point Mugu State Park, south of Ventura, far from human habitation (specimen IDs BBUSE070-11, BBUSE071-11, BBUSE073-11, BBUSE105-11, BBUSE3156-12).

All records in Chile (Taucare-Ríos et al. 2016) and Ecuador were made in urban environments. The records in Ecuador may seem extraordinary, not just because of their localization in the inland of the country, but also because of the altitude of the records, at about 2600–2800 m for eight out of nine locations. However, records of *S. nobilis* in mountainous areas are known, e.g., from Spain (around 1000 m, Alicante; Morano et al. 2018) or Mount Teide, Tenerife (Schmidt 1968). Recently, Faúndez et al. (2018) published some records of *S. nobilis* from Ecuador collected in 2017 and 2018. Therefore, our specimens (Table 2) remain the oldest records of *S. nobilis* known from Ecuador.

On the Mediterranean mainland and in the Americas, over 50 % of all known localities are located within a distance of < 10 km to the coastline (Suppl. material 1: Fig. A5). This could be the result of several factors. Coastal regions often have the highest human population densities, which could result in more frequent collecting and reporting of *S. nobilis* by citizen scientists than in more rural areas (e.g. in California; Vetter et al. 2015). They are also often confronted with the highest propagule pressure of alien organisms due to long-distance trade and tourism, for example at the Italian localities discussed by Kulczycki et al. (2012).

All in all, *S. nobilis* seems to establish first in urban environments and is able to build up large populations in a short time. This generates further colonisation pressure on seminatural habitats in the environment of cities, finally leading to the establishment of populations outside the urban area.

Genetic structure of the New World populations of *S. nobilis*

To gain further insights into the most likely introduction routes of *S. nobilis*, we used publicly available DNA barcode sequences (~ 650 bp of the mitochondrial cytochrome c oxidase subunit I gene). We used barcodes for about 20 *S. nobilis* specimens from California and three specimens from Chile. The barcoded individuals are not identified to species in the BOLD database, but their distinct habitus, documented by photographs provided for many of the specimens, as well as their obvious abundance in synanthropic habitats in Southern California, nevertheless allow an unambiguous identification of the specimens. They form a single barcode cluster (BIN, BOLD:ABA5272, https://doi.org/10.5883/BOLD:ABA5272), without geographic structure, i.e. Chilean and Californian specimens share barcode haplotypes.

The genetic diversity of the Californian *S. nobilis* sample is relatively high, with an average pairwise distance of 0.78% and a maximum distance (within the Californian population) of 2.12%, compared to a median pairwise distance of 1.5% within *Steatoda* species with more than five published barcodes.

Dynamics of the expansion of *S. nobilis* in Great Britain

Additional insights into the changing invasive potential of *S. nobilis* can be gained from citizen science data obtained from the British Spider Recording Scheme. These show that *S. nobilis* is widespread in Great Britain and especially abundant in the southern half of the island, with scattered records along the northern coasts (British Spider and Harvestman Recording Scheme 2018; Suppl. material 1: Fig. A7). A comparison of the press coverage (number of articles in the Lexis-Nexis database which mention the scientific name) and the number of records in Britain show that both numbers closely correlate (Spearman's rank correlation, $p < 0.001$, $r = 0.78$) (Fig. 2). The total number of published press articles peaked in 2013 with 114 articles, followed by the highest amount of records in 2014 with over 150 observations of *S. nobilis* in Great Britain. In the following years, the number of records decreased slightly, in parallel with the number of articles. Examining the pattern of northward expansion of *S. nobilis* in Great Britain (Fig. 4), a long period of near-stasis following the initial establishment is quite notable; between 1984 and about 2010, despite thriving populations along the south coast and in the Thames estuary, no real change of the northern range boundary is evident at all (Fig. 4, Suppl. material 1: Fig. A6). Since about 2010, a persistent and accelerated expansion has occurred at a rate of at least 11 km/year when considering the contiguous range of the species and up to 95 km/year if the widely dispersed recent northernmost records are included (Fig. 4); the latter, however, are most likely the result of the long-distance transport of goods and materials and probably do not represent a real invasion front with established populations.

Niche exploration and distribution modelling

A principal component analysis of climate variables at native and invasive localities revealed that the two areas differ mainly in their annual temperature range and seasonality (Suppl. material 1: Fig. A1, Table A3). With the exception of the invasive locations in Ecuador, the native area shows a lower temperature range than the invasive area. A global prediction of potential occurrences of *S. nobilis* (Fig. 3) shows a relatively restricted area of suitable localities for the further spread of the species. In Europe, besides the known invasive areas the model especially predicts north and western parts of

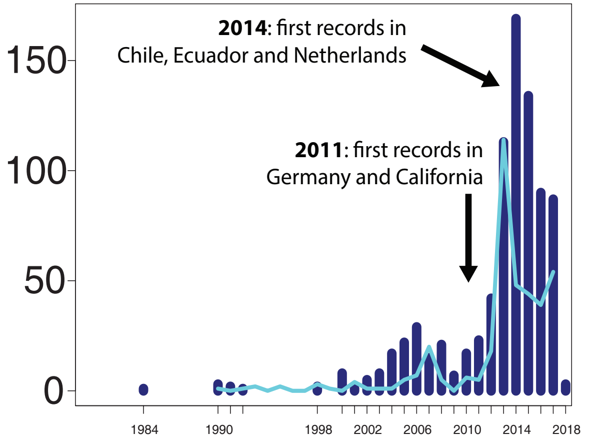

Figure 2. Increase in Spider Recording Scheme records for *Steatoda nobilis* in Britain parallels intensified press coverage in the local newspapers (dark blue bars = spider records, light blue line = number of press articles). The sudden massive increase in records seen in the last decade coincides with the first appearance of the species in various other countries far from the native range in the Macaronesian islands.

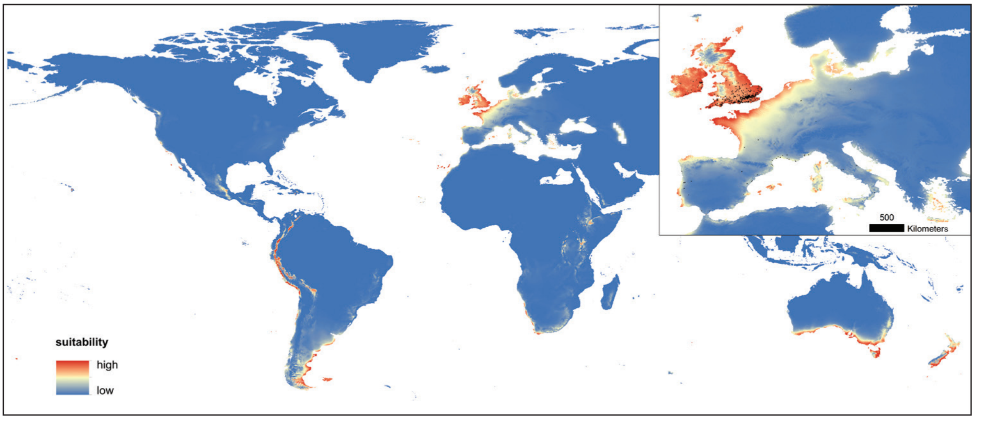

Figure 3. Global climatic suitability of *Steatoda nobilis***.** Mean Maxent prediction, black dots in insert depict known invasive populations in Europe (insert is not masking suitable areas).

France and some coastal areas of the North Sea as highly suitable. Some islands in the Aegean Sea and especially Crete might also be very suitable for *S. nobilis*. On a global scale, especially coastal regions with constant temperature regimes were predicted as suitable, e.g., in southern Australia and New Zealand.

To test our predictions, we conducted a field trip to Granville, Normandy (France). The coastline of the Normandy is predicted as a highly suitable area for *S. nobilis* by our model and has an oceanic climate similar to the south coast of England. Contrary to the latter, no populations of *S. nobilis* are yet known from the northern Atlantic coast of France near to the Channel Islands. Nevertheless, we were able to locate a local *S. nobilis* population in the city area of Granville and collected a single adult female

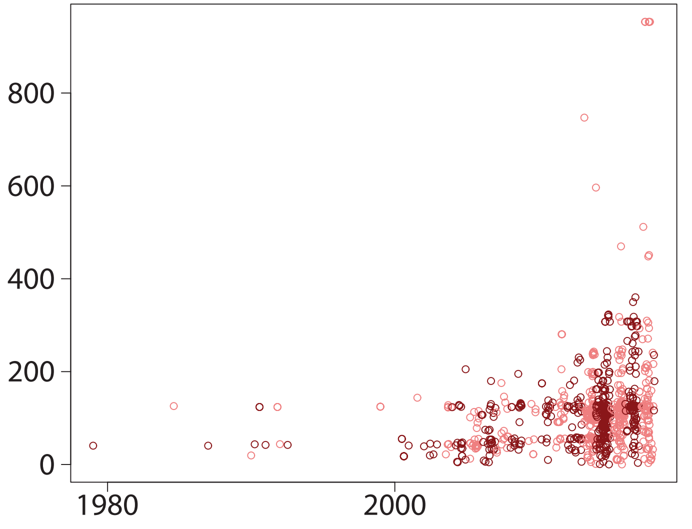

Figure 4. Northward distance (km) of recent records of *Steatoda nobilis* in Great Britain. Distances are calculated relative to the first known record in the country in Torquay, based on data in the SRS database and in Snazell and Jones (1993). Data from consecutive years are alternatingly coloured dark and light red.

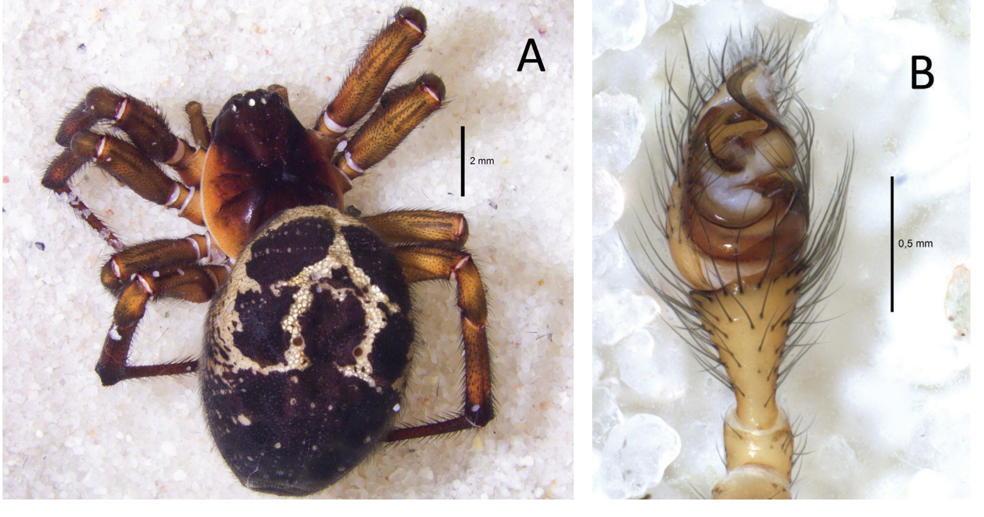

Figure 5. Habitus and male genitalia of *Steatoda nobilis*. **A** Female from Normandy, France **B** Male pedipalp in ventral view from Stuttgart, Germany.

(Fig. 5A) together with an egg sac behind a street sign next to a paved boardwalk (17.IX.2018, 48.8331N, -1.5879W, T. Bauer leg.). Webs of the species could also be found between sea defence rocks directly at the coastline (48.8342N, -1.5929W) as well as on trees in a small urban forest fragment (48.8334N, -1.5892W) next to the location of the female. Around 100 spiderlings emerged from the egg sac in captivity.

Discussion

Probable introduction pathways of *S. nobilis*

Steatoda nobilis seemed unable to establish viable populations in either Great Britain or Germany at the time of copious and untreated banana imports (= highest propagule pressure; Allendorf and Lundquist 2003). Although it is often suggested or indicated that the British *S. nobilis* populations are descendants of specimens imported with fruits from the Canary Islands (e.g., Roberts 1995; Kulczycki et al. 2012), this hypothesis is not well supported by current data. Since the 1960s, different phytosanitary treatments and transport techniques have become standard procedure in international trade and dramatically reduced the amount of alien spiders transported to Europe via shipping, especially after 1971 (Hallmann 2007; Nentwig 2015). Flourishing British populations of *S. nobilis* were not found until 1986 (Portsmouth area), followed by subsequent records and the observation of rapid colonization events (Snazell and Jones 1993). Great Britain has a long tradition in field arachnology, and it seems very unlikely that in the times of Bristowe (1941) and Locket and Millidge (1951, 1953, 1974) large populations of *S. nobilis* in domestic areas and harbours of the South of England would have been missed, especially as the urban and synanthropic spider fauna of Britain has traditionally received much closer attention than in other countries (e.g., Bristowe 1929, 1939). Therefore, it cannot be excluded that other introduction pathways, e.g., accidental imports by tourists (the Canary Islands are traditionally visited by British tourists every year, with several millions in 2016 alone (Patronato de Turismo Gran Canaria 2017)), specimens (or even populations) on returning cruise ships from Macaronesia, or the import of ornamental plants at least contributed to the establishment of *S. nobilis* in Great Britain.

The populations found in Cologne described in this work are most probably descendants of specimens introduced with potted plants. Very large amounts of cacti and other succulents are imported every year from the Canary Islands (e.g., by the grower "Canary Cactus"), but Kulczycki et al. (2012) pointed out that *S. nobilis* also achieves high population densities in Italian plant nurseries. Ornamental plants sold in garden centres in Germany are normally of various origins (e.g., Canary Islands, Iberian Peninsula, Dutch wholesalers); therefore, it seems currently impossible to determine the exact source of the German populations. Because we and Reiser (2013) only found scattered records/populations of *S. nobilis* among a large number of non-colonized garden centres (e.g., only two out of about 10 garden centres were colonized in Cologne), it can be tentatively concluded that *S. nobilis* is currently restricted to very few localities in Germany and that garden centres in Central Europe seem to be a potential habitat for this species.

In the Netherlands, a record from the Maasvlakte (Bink 2014) was possibly the result of an accidental introduction with armour rock for sea defences. Another record (juvenile female) from the Netherlands was made on 19 May 2016 at the coast in the Southwest (51.5879, 3.5667, leg. F. van de Putte, deposited at Naturalis Leiden after its final moult) under the bark of a tree in the neighbourhood of several camping areas, to which it was possibly introduced by tourists from France or England.

In South America, it seems possible that *S. nobilis* has been spread and/or is distributed by human assistance along the Panamericana Highway (the most important inland transportation route in South America), as two of the Ecuadorian locations (Ambato and Salcedo) are crossed by the route, and Temuco in Chile is situated on one of the two main southern branches of the route.

Distribution and outlook of *S. nobilis*

The climate exploration and the ability of the distribution model to explain the current distribution of *S. nobilis* with climate variables revealed that the general distribution is not decoupled from the regional climate. Even though most alien records of *S. nobilis* were located in urban environments, there is currently much evidence that the species is not restricted to urban areas and has already or will spread into seminatural or natural habitats in the invaded areas, e.g., in the South of England and France (Ledoux and Raphael 1998; P. Harvey pers. comm.). Additionally, if only local microclimates were relevant for the distribution of *S. nobilis*, we would expect a much more random establishment, similar to *Steatoda grossa*, another large theridiid, living mostly indoors in large parts of its cosmopolitan distribution (Heimer and Nentwig 1991; Le Peru 2011; World Spider Catalog 2018). We note that our modelling approach and the resulting map is a rather conservative prediction, which probably underpredicts the true potential distribution. SDMs calibrated in early stages of an invasion tend to underestimate the potential distribution, as not all suitable conditions are occupied yet and, therefore, only a part of the species' niche is captured by the model (Václavík and Meentemeyer 2012). However, the most recent findings of this species at locations (not used for modelling) in Normandy, France (Table 3, Fig. 5a) and Bogotá, Colombia (Faúndez et al. 2018), which were predicted as highly suitable by our model, corroborate the usefulness of our predictions. Our SDM identified several areas characterized by an oceanic climate on nearly all continents as habitat for *S. nobilis*. Especially parts of South Africa, the southern coastline of Australia and wide parts of New Zealand are highly suitable for *S. nobilis*. All three countries are heavily afflicted by invasive species (e.g., Hoffmann and Broadhurst 2016; Paterson et al. 2011; Aikio et al. 2010), and an invasion of *S. nobilis* could have unpredictable and severe consequences for the native fauna.

The rapid east–west spread of *S. nobilis* in Britain, followed by a much later substantial northward expansion especially since 2010, indicates that the range of *S. nobilis* initially was not constrained by limited dispersal ability. Interestingly, between 1984 and 2010 there was a period of well-known range expansions in other species (Parmesan and Yohe 2003). Recently, these ecological limitations seem to have been overcome rather suddenly by *S. nobilis*, leading to a rapid increase in population number and an expansion far beyond its original centres in the UK. The first period of stasis between 1985 and about 2010 can be interpreted as a typical lag-phase (a phase with little or no spread in the new environment), a phenomenon observed in many invasive species (Kowarik 1995; Crooks and Soulé 1999). What could have caused this accelerated spread? The northward expansion of adventive invertebrate species in Europe, and especially in the UK, is often attributed to the effects of climate change. However, the extent, unpredictability, and sudden rapidity of the expansion of *S. nobilis* all over the globe make this explanation unlikely. There is no indication that climate conditions across the UK have changed dramatically enough in the last 20 years, to turn much of the UK into favourable habitat for an originally Macaronesian species. Climate models for other species show a much more restricted expansion of the accessible range for this relatively brief period (e.g., Lundy et al. 2010), and such a more limited expansion would also agree with predictions made by climate modelling (Loarie et al. 2009). Also, the expansion persisted unimpeded through the very cold winter of 2010, while severe weather events like this would have halted and most likely reversed an expansion that was merely the result of global warming, as shown by Tinsley et al. (2015) for alien *Xenopus laevis* populations in Britain and predicted by Avery et al. (2010) for range expansions of alien Burmese pythons, *Python bivittatus*, outside of subtropical areas in the United States.

Could the observed distribution trends in Great Britain just be the result of greater awareness and thus more intense reporting, rather than of actual population growth and range expansion? Fig. 2 indeed shows that newspaper coverage and the number of *S. nobilis* records in the UK correlate quite closely. However, the causality seems to work both ways, with increased awareness contributing to some increase in reporting (although most non-expert reports of *S. nobilis* refer to a wide diversity of common house spiders, rather than actual false widows; Bee 2013; P. Harvey pers. comm.), while sustained and widespread coverage became only possible once the species had become common enough through large parts of the most populated areas of the UK leading to a larger number of reportable encounters. Moreover, the sudden expansion of the *S. nobilis* in the UK, after many years close to stasis, closely coincided with a wave of newly established populations in widely distant countries (Fig. 2) and a sudden rise of reports in Irish online spider groups (Dugon et al. 2017). In general, this indicates that the expansion is not a simple collection artefact based on increased awareness of naturalists and the public (Aikio et al. 2010), as the spread of *S. nobilis* was observed in different countries in the same time period and by different groups of naturalists and laypeople. Such lag-phases are also sometimes caused by a low number of specimens and populations connected to a slow growth rate in the beginning of an invasion (Crooks and Soulé 1999). After reaching a critical point in the exponential growth, the species becomes common and is spreading. However, this explanation seems unlikely because the first established populations of *S. nobilis* in Southern England were described as "flourishing" (Snazell and Jones 1993), indicating a high population density 30 years before the northward spread of the species. Together with the ability to build several egg sacs in one season (Snazell and Jones 1993), the colonisation pressure caused by the first *S. nobilis*-populations was probably very high already in the early years after the establishment.

Another possible reason for the spider's expansion success is evolutionary adaptation, e.g., an ecological niche expansion (Guisan et al. 2014) in the British populations. This has been suggested in *Argiope bruennichi* (Scopoli, 1772) and *Cheiracanthium punctorium* (Villers, 1789), two spider species which have naturally expanded their distribution in the last decades (Krehenwinkel and Tautz 2013; Krehenwinkel et al. 2015, 2016). The emergence of such adaptations can require extended times, leading to a characteristic lag phase of range expansion (Lee 2002; Aikio et al. 2010). Adaptive genetic variants could have entered the invasive populations by novel mutations (Jensen 2014), as part of the standing variation of native populations (Barrett and Schluter 2008), or by admixture of formerly isolated lineages in the course of the invasion (Nolte and Tautz 2010). However, to rigorously test the possibility of evolutionary adaptation driving the species' expansion, ecological experiments, e.g., reciprocal transplants and thermal tolerance tests (Krehenwinkel and Tautz 2013; Krehenwinkel et al. 2015), will be necessary.

The obvious prediction resulting from this assessment and our model is that the expansion of *S. nobilis* is likely to continue rapidly in the coming years. The western Mediterranean islands, parts of South Africa, southern Australia, and New Zealand will face the highest risk of colonisation in the future. It is possible that some of these areas, especially the western Mediterranean islands, are already inhabited by *S. nobilis* and the species has been overlooked, similar to the newly reported population in the Normandy, France. An intensified monitoring and search for *S. nobilis* in inhabited areas and regions predicted as suitable could therefore reveal the real distribution of the species.

As the DNA barcoding data indicate that *S. nobilis* is genetically very distinct from its congeners, it is unlikely that the species will hybridize with native species. This was observed for alien *Latrodectus hasselti*, which hybridized at least in one population with a native *Latrodectus* species in New Zealand (Vink et al. 2008). The barcode data also indicate that established populations in the New World are likely the result of multiple introductions (c.f. Kolbe et al. 2004), as the observed haplotype diversity (five distinct haplotypes with an average distance of 0.81%) seems inconsistent with a severe recent population bottleneck (e.g., a single founder female) for the populations in California and Chile. Similar deep genetic diversity is seen for populations of other invasive theridiids, such as *Parasteatoda tepidariorum* (BOLD:AAC0175, average distance=1.21%, maximum distance (globally)=3.61%, *n*=222) and *Steatoda grossa* (multiple BINs, *n* = 43), while *Nesticodes rufipes* (BOLD:AAG4814, average = 0.24%, maximum = 1.01%, *n* = 22) shows a much more homogeneous barcode gene pool. In comparison, 2009 specimens of the recently expansive *Argiope bruennichi* (BOLD:AAJ1655) (Araneidae) show an average barcode distance of only 0.37% (maximum = 2.63%), and 295 specimens of the invasive *Cheiracanthium mildei* (BOLD:AAB7601) (Cheiracanthiidae) are only slightly more diverse (average = 0.43%, maximum = 1.21%), thus exhibiting considerably less diversity than seen in the New World populations of *S. nobilis*. Nevertheless, *S. nobilis* competes with other spider species (Kulczycki et al. 2012) and could outcompete native species with a similar niche on the local scale and possibly threatens other arthropod species due to predation, similar to *Latrodectus hasselti* in New Zealand

(Bryan et al. 2015). It was observed that *S. nobilis* preys on a protected reptile species in Ireland (Dunbar et al. 2018), which shows that the spider is able to subdue small vertebrates. *Steatoda nobilis* can produce large amounts of offspring for a long period after mating, and adult females are extraordinarily long-lived and persistent (Locket 1979; Snazell and Jones 1993). Snazell and Jones (1993) reported on a female which lived for 5½ years in captivity. Therefore, an eradication of established populations seems impossible, especially as juvenile specimens are very hard to locate due to their cryptic lifestyle in crevices and holes (Snazell and Jones 1993; Kulczycki et al. 2012), and many populations are probably supported by repeated introductions, as shown by the barcode data. Additionally, their ability to balloon (Kulczycki et al. 2012) enables this species to overcome natural and anthropogenic barriers (e.g., rivers, streets) and to distribute over relatively large areas in a comparatively short time. Adjusted phytosanitary treatments of potted plants could potentially decelerate the spread of *S. nobilis* (and other alien spider species). As documented for Britain, the species is also able to cause public disruption and high economic costs in invaded areas, e.g., by increased consulting of pest management services in private homes or the closing of public institutions. Together with the potential ecological consequences of a further spread, *S. nobilis* has to be considered as one of the most invasive spider species in the world.

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Supplementary material 1

Dataset compilation, niche exploration, species distribution modelling, and additional analyses

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Data type: occurences, analyses, background information

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