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Introduction, establishment rate, pathways and impact of spiders alien to Europe

Wolfgang Nentwig

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Abstract A comprehensive analysis of spiders reported as alien for Europe over the last 200 years has yielded information for 184 spider species, which had been introduced at least once. The most common spider families are Theridiidae (27 species), Pholcidae (15), Salticidae (14), Sparassidae (14), Ctenidae (14), and Theraphosidae (13) but overall establishment rate was only 28 %. No ctenids or theraphosids established, and only one sparassid species, but many theridiids and pholcids. Most introduced species originated from South (34 %), Central (10 %) or North (12 %), America, Asia (19 %) and Africa (15 %). Only few of the South and Central American species could establish, while species from North America (36 %) and Asia (63 %) had much higher establishment rates. Over the last 200 years, introduction and establishment rates have been strongly increasing. Three pathways are responsible for the majority of introductions: fruit shipments (67 % of all cases), potted plants (16 %) and containers or packaging material (12 %). In contrast to fruit shipments, spiders introduced on plants or with containers have high establishment rates (65 and 47 %). Environmental impact of alien spiders can be expected on both insects (through predation) and spiders (through predation and competition), potentially leading to change of species composition and guild structure. Socio-economic impact includes reduction of marketability of horticultural products through excessive spinning activity which also may cause increased cleaning costs at facades and windows. Impact on human health may be caused by bites and subsequent need for medical treatments. For all these impact categories, however, only anecdotal evidence is given for alien spiders in Europe. This may change when spiders of medical importance such as the frequently introduced *Latrodectus* species will establish. Considering the current trends it is concluded that introduction and establishment rates of alien spiders will strongly increase in the next years unless preventive methods become more efficient.

Keywords Origin, contaminant · Environmental impact · Socio-economic impact · Human health

Introduction

Alien and invasive species are one of the main drivers of biodiversity decline, reducing ecosystem services worldwide (MEA 2005) and exerting an increasing impact to the environment and socio-economy (Vilà et al. 2010; Simberloff et al. 2013). The number of alien and invasive species is steadily increasing, mainly through continuous globalization with increasing transport of people and goods (DAISIE 2009; Hulme et al. 2009). This will also lead to an increased impact in the future ("invasion debt", Essl et al. 2011).

Alien species are transferred with direct or indirect human assistance from their area of origin into another

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biogeographical area (invaded area) (measured as introduction rate) where they may establish (establishment rate) and become invasive (e.g., Ricciardi et al. 2013; Jeschke et al. 2014). Invasiveness is usually defined as "having impact" on environment and/or socio-economy (Pyšek and Richardson 2010; Vilà et al. 2011). The probabilities of introduction, establishment and becoming invasive can be analysed with risk assessments, while impact is quantified in impact assessments, and often both are combined (Kumschick and Richardson 2013).

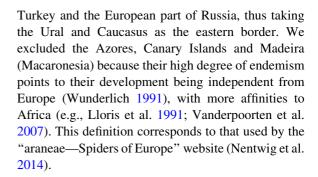
Research on higher taxa of alien and invasive species have so far focussed mainly on plants, vertebrates and selected invertebrates, while especially spiders have been neglected (DAISIE 2009; Langor and Sweeney 2009; Roques et al. 2010). Spiders are a large, diverse group of mainly generalist non-specialized predators, occurring in all terrestrial habitats and contributing considerably to biodiversity (Penny 2013; Nentwig et al. 2014). As alien and invasive species, spiders may be of considerable importance because they can reach high densities in natural and urban environments, which could affect native diversity (Hann 1990; Ruzicka 1995). Some spiders are also of medical concern because they can bite humans, which can potentially be lethal (Nentwig and Kuhn-Nentwig 2013).

The first notes mentioning records of alien spiders in Europe are about 200 years old and the first compilation of these records was given by Bonnet (1929). However, in the following decades mainly anecdotal reports appeared, and occasionally lists of species collected at border controls (interception data, e.g., Schmidt 1953–1971). Two recent publications concentrated on 47 established species and analyzed the areas of origin and the most probable invasion routes (Kobelt and Nentwig 2008; Nentwig and Kobelt 2010). Here we present a more comprehensive analysis of data for 184 spider species recorded as alien to Europe over the last 200 years. We calculate establishment rates, perform a pathway analysis, and present semi-quantitative data on their environmental and socio-economic impact.

Materials and methods

Biogeographical definition of Europe

Europe is defined biogeographically as the European continent and its islands, including Belarus, Ukraine,



Data collection

Information on spider species alien to Europe was obtained by

- A broad literature screening in the Web of Science and with Google Scholar. Search terms were spider and/or araneae and/or alien, exotic, non-native and/or Europe;
- A search in specialized databases for alien species, such as the DAISIE database (DAISIE 2015);
- (3) A search in specialized databases for spiders, mainly the World Spider Catalog (WSC 2015) and "araneae—Spiders of Europe" (Nentwig et al. 2014).

This search yielded information for a total of 233 species. In some cases it was not possible to find the earliest record for a given species for Europe. It can also not be excluded that older literature mentions unsuccessful introductions, but we did not detect such articles. Therefore, we consider these 233 species as a minimum number of species mentioned in the literature as alien to Europe.

Analysis of their taxonomic situation showed that six species had a dubious identity. The agelenid Agelena longipes Carpenter 1900 and the clubionid Clubiona facilis O. Pickard-Cambridge (1910) had only been caught once, described as a new species of alien origin, but were never recollected elsewhere in the world. These specimens need careful re-examination and are not considered here. Comparably, the salticid Philaeus superciliosus Bertkau 1883, has only been collected once, but could be a nomen dubium due to misidentification. The oonopid Orchestina dubia O. Pickard-Cambridge (1911) refers to a misidentified and mutilated specimen (Henrard, pers. comm.), while the European record of the gnaphosid Leptotopilos



pupa De Dalmas 1919 is a misidentification and this species does not occur in Europe (Levy 2009; Chatzaki, pers. comm.).

Forty-four species turned out to be of European origin and therefore cannot be considered as alien to Europe. This refers to many Mediterranean species that are widespread in Southern Europe. Nevertheless, they receive attention when they spread north and are first recorded, e.g., in Great Britain, Scandinavia or northeastern parts of Europe. The wasp spider Argiope bruennichi is a typical case where the spread of this Mediterranean species has been analysed in detail (Kumschick et al. 2011). For most of these species, their European origin is not in doubt, but in some cases, the native area is strongly debated. Here we assume European and mostly Mediterranean origins for the following species: *Oecobius cellariorum* (Dugès 1836), O. maculatus Simon 1870 and O. navus Blackwall 1859 (all Oecobiidae); Tapinesthis inermis (Simon 1882), Oonops domesticus De Dalmas 1916; O. pulcher Templeton 1835 and Silhouettella loricatula (Roewer 1942) (all Oonopidae); Holocnemus caudatus (Dufour 1820), H. pluchei (Scopoli 1763) and Pholcus opilionides (Schrank 1781) (all Pholcidae); Uloborus plumipes (Uloboridae). The gnaphosid Zelotes puritanus Chamberlin 1922 has a Holarctic distribution, from North America via South Siberia into the Ukraine. Because it is unclear if the European records of Z. puritanus represent the most westerly populations of this species, spreading since the late 1970s, or if these are introductions from North America, this species is not treated here as alien to Europe. On the other hand, the tetragnathid Tetragnatha shoshone, first described by Levi (1981) for North America and later detected in a few European locations (Uhl et al. 1992), is considered to be of North American origin.

After correcting our initial figure of 233 species for these five taxonomically doubtful species and for the 44 species of European origin, we ended up with 184 species, recorded at least once within Europe and of clearly non-European origin. For these species, we compiled the following data: year of first record, probability of establishment, current distribution, pathway of introduction and impact.

Impact scoring with GISS

Impact was calculated using the Generic Impact Scoring System GISS, initially developed by Nentwig et al. (2010) for mammals, but recently expanded to all major animal and plant taxa (Kumschick et al. 2015), including terrestrial arthropods (Vaes-Petignat and Nentwig 2014). The semi-quantitative GISS is based on an intensive literature search and relies on published information. It includes two main impact groups, environmental and socio-economic, each with six impact categories. Environmental impacts are classified as (1) on plants or vegetation (e.g., through herbivory), (2) on animals through predation or parasitism, (3) through competition, (4) transmission of diseases or parasites to native species, (5) hybridization, and (6) on ecosystems (e.g., through changes in ecosystem services). Socio-economic impact consists of impacts (1) on agricultural production, (2) animal production, (3) forestry production, (4) human infrastructure and administration, (5) human health, and (6) human social life (e.g., through restrictions in recreational activities). Within each of these 12 impact categories, impact is assessed on a scale of six impact levels, ranging from zero (no impact known, no impact detectable, or not applicable) to five (highest impact possible). Maximum impact of a given invasive species is 12 categories \times 5 points = 60 points. Each impact category and impact level is well described to avoid ambiguities between assessors as much as possible. For more details see Vaes-Petignat and Nentwig (2014).

Results

Introduction, establishment and origin

We collected data on 184 spider species introduced as alien to Europe, and belonging to 37 families (Table 1). The most common spider families were Theridiidae (27 species), Pholcidae (15), Salticidae (14), Sparassidae (14), Ctenidae (14), and Theraphosidae (13). From these, 51 species could establish selfmaintaining populations (=28 % establishment rate), belonging to 19 families. The most commonly established families were Theridiidae (13 species), Pholcidae (8), Linyphiidae (5), and Salticidae (4). In other families, establishment rates are extremely low, e.g., in Sparassidae (7 %). It is remarkable that in some families with many introduced species, none established, this is especially obvious in Araneidae, Corinnidae, Ctenidae and Theraphosidae.



Table 1 List of spider species introduced to Europe, their biogeographical origin, establishment in Europe, distribution in Europe (according to the geographical units at www. araneae.unibe.ch with a total of 64 units for Europe), pathway of introduction, and references

Family	Species	Family Species Authority Origin	Origin	Established	Distribution	Pathway	References
Amaurobiidae	Amaurobius similis	(Blackwall 1861)	North America	Yes	22		Nentwig et al. (2014)
Anapidae	Pseudanapis aloha	Forster 1959	Australia	Yes	2	Plants	Kielhorn (2009); Wilson (2012)
Anyphaenidae	Anyphaenoides octodentata	(Schmidt 1971)	South America	No		Fruits	Schmidt (1971)
Anyphaenidae	Hibana flavescens	(Schmidt 1971)	South America	No		Fruits	Schmidt (1971)
Anyphaenidae	Patrera ruber	F. O. Pickard-Cambridge (1900)	South America	No		Fruits	Schmidt (1971)
Araneidae	Alpaida trispinosa	(Keyserling 1892)	South America	No		Fruits	Schmidt (1971)
Araneidae	Araneus decaisnei	(Lucas 1863)	Asia	No		Plants	Bonnet (1930)
Araneidae	Dolichognatha quadrituberculata	(Keyserling 1883)	South America	No		Fruits	Schmidt (1971)
Araneidae	Kaira altiventer	O. Pickard-Cambridge (1889)	South America	No		Fruits	Schmidt (1971)
Araneidae	Neoscona crucifera	(Lucas 1838)	North America	No		Fruits	Schmidt (1971)
Araneidae	Neoscona nautica	(L. Koch 1875)	North America	No		Container	van Keer (2007)
Clubionidae	Clubiona abboti	L. Koch 1866	North America	No		Fruits	Bonnet (1930)
Clubionidae	Elaver lutescens	(Schmidt 1971)	South America	No		Fruits	Schmidt (1971)
Clubionidae	Elaver tigrinella	(Roewer 1951)	Central America	No		Fruits	Schmidt (1971)
Corinnidae	Castianeira scutata	Schmidt 1971	South America	No		Fruits	Schmidt (1971)
Corinnidae	Corinna anomala	Schmidt 1971	South America	No		Fruits	Schmidt (1971)
Corinnidae	Creugas gulosus	Thorell 1878	Tropics/subtropics	No			Wilson (2012)
Corinnidae	Falconina albomaculosa	(Schmidt 1971)	South America	No		Fruits	Schmidt (1971)
Corinnidae	Procopius luteifemur	Schmidt 1956	Africa	No		Fruits	Schmidt (1956c)
Corinnidae	Simonestus separatus	(Schmidt 1971)	South America	No		Fruits	Schmidt (1971)
Corinnidae	Trachelas daubei	Schmidt 1971	South America	No		Fruits	Schmidt (1971)
Corinnidae	Trachelas santaemartae	Schmidt 1971	South America	No		Fruits	Schmidt (1971)
Corinnidae	Trachelas uniaculeatus	Schmidt 1956	Macaronesia	No		Fruits	Schmidt (1971)
Ctenidae	Acanthoctenus sp.		Central America	No		Fruits	Binding (2011)
Ctenidae	Acanthoctenus spinipes	Keyserling 1876	Central America	No		Fruits	Schmidt (1971)
Ctenidae	Ctenus acanthoctenoides	Schmidt 1956	South America	No		Fruits	Schmidt (1971)
Ctenidae	Ctenus bicolor	(Bertkau 1880)	South America	No		Plants	Bonnet (1930)
Ctenidae	Ctenus velox	Blackwall 1865	Africa	No		Fruits	Schmidt (1957)



Table 1 continued

Family	Species	Authority	Origin	Established Dist	Distribution	Pathway	References
Ctenidae	Cupiennius coccineus	F. O. Pickard-Cambridge (1897)	Central America	No		Fruits	Schmidt (1971)
Ctenidae	Cupiennius foliatus	F. O. Pickard-Cambridge 1901	South America	No		Fruits	Schmidt (1971)
Ctenidae	Cupiennius getazi	Simon (1891)	Central America	No		Fruits	Essl and Rabitsch (2002); van Keer (2011)
Ctenidae	Cupiennius salei	(Keyserling 1876)	Central America	No		Fruits	Barth (2002)
Ctenidae	Isoctenus janeirus	(Walckenaer 1837)	South America	No		Fruits	Schmidt (1956c)
Ctenidae	Isoctenus minusculus	Keyserling 1891	South America	No		Fruits	Schmidt (1971)
Ctenidae	Phoneutria boliviensis	(F. O. Pickard-Cambridge 1897)	South America	S _O		Fruits	Schmidt (1956c, 1971); Essl and Rabitsch (2002); Jäger and Blick (2009)
Ctenidae	Phoneutria fera	Perty 1833	South America	No		Fruits	Schmidt (1953)
Ctenidae	Phoneutria nigriventer	(Keyserling 1891)	South America	No		Fruits	van Keer (2007, 2011)
Desidae	Badumna longinqua	(L. Koch 1867)	Australia	No		Plants	Kielhorn and Rödel (2011)
Dictynidae	Cicurina japonica	(Simon 1886)	Asia	Yes 4		Container	Wunderlich and Hänggi (2005)
Dictynidae	Dictyna foliacea	(Hentz 1850)	North America	No		Fruits	Bonnet (1930)
Dictynidae	Dictyna tarda	Schmidt 1971	South America	No		Fruits	Schmidt (1971)
Dictynidae	Emblyna sublata	(Hentz 1850)	North America	No		Fruits	Bonnet (1930)
Dictynidae	Lathys sp.		South America	No		Fruits	Schmidt (1971)
Dipluridae	Ischnothele digitata	(O. Pickard-Cambridge 1892)	South America	No		Fruits	Schmidt (1971)
Dipluridae	Masteria sp.		Tropics/subtropics	Yes 1			Neumann (2013)
Dysderidae	Dysdera aculeata	Kroneberg 1875	Asia	Yes 1		Soil	Deeleman-Reinhold and Deeleman (1988)
Eutichuridae	Cheiracanthium furculatum	Karsch 1879	Africa	No		Fruits	Bosselaers (2013); Bayer (2014)
Eutichuridae	Cheiracanthium inclusum	(Hentz 1847)	South America	No		Fruits	Bonnet (1930)
Eutichuridae	Eutichurus putus	O. Pickard-Cambridge 1898	South America	No		Fruits	Schmidt (1971)
Gnaphosidae	Drassodes neglectus	(Keyserling 1887)	North America	No		Fruits	Bonnet (1930)
Gnaphosidae	Drassylus novus	(Banks 1895)	North America	No		Fruits	Bonnet (1930)



Table 1 continued

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Scotophaeus gridelii Caporiacco 1928 Macaronesia No F Sosticus boricetuss (L. Koch 1872) Asia Yes 27 Sosticus boricetus (L. Koch 1872) Asia Yes 27 Urzezlotes nusticus (L. Koch 1872) Asia Yes 27 Zimiromis medius (K. Koch 1872) South America Yes 21 Erigone autumnalis Emerton 1882 North America Yes 2 F Hypselistes florens (O. Pickard-Cambridge 1875) North America Yes 7 P Mermessus naculatus (Banks 1892) North America Yes 7 P Mermessus naculatus (Banks 1892) North America Yes 7 P Asiaca erythrognatha (U. Pickard-Cambridge 1879) Unknown Yes 7 P Syricea sp. (O. Pickard-Cambridge 1879) Unknown Yes 10 P Nephila imaratu (Vinson 1863) Africa No No No Nephila	Gnaphosidae	Macarophaeus varius	(Simon 1893)	Macaronesia	No		Fruits	Schmidt (1971)
Scottophaeus mauchneri Schmidt 1956 Macaronesia No F Sosticus loricatus (L. Koch 1872) Asia Yes 27 Urozelotes nasticus (L. Koch 1872) Asia Yes 27 Zimiromis medius (Reyserling 1891) South America Yes 2 Erigone altuminalis Enerton 1882 North America Yes 3 F Hypselistes florens (O. Pickard-Cambridge 1875) North America No 7 P Mermessus denticulatus (Crosby 1924 North America Yes 7 P Mermessus maculatus (Banks 1892) North America Yes 10 Ostearius melanopygius (O. Pickard-Cambridge 1879) Unknown Yes 10 Ostearius melanopygius (O. Pickard-Cambridge 1879) Unknown Yes 10 Ostearius melanopygius (Vinson 1863) Africa No F Nephila inaurata (Vinson 1863) Africa No No Nephila sp. (Yaginuma 1970)	Gnaphosidae	Scotophaeus gridelii	Caporiacco 1928	Macaronesia	No		Fruits	Schmidt (1956a)
Sosticus loricatus (L. Koch 1866) Asia Yes 27 Urozelotes nasticus (L. Koch 1872) Asia Yes 21 Zimiromis medius (Keyserling 1891) South America No P Erigone alerris Crosby and Bishop 1928 North America Yes 2 Erigone alerris Emerton 1882 North America Yes 3 Hypselistes florens (O. Pickard-Cambridge 1875) North America Yes 7 P Mermessus denticulatus (Emerton 1882) North America Yes 10 Mermessus trilobatus (Emerton 1882) North America Yes 10 Oxtearius melanopygius (O. Pickard-Cambridge 1879) Unknown Yes P Lycosa erythrognatha (Uncas 1836) South America No P Syrisca sp. Nephila inaurata (Vinson 1863) Africa No Nephila sp. Tropicskubtropics No No Nephila sp. Tropicskubtropics No No Nest	Gnaphosidae	Scotophaeus mauckneri	Schmidt 1956	Macaronesia	No		Fruits	Schmidt (1971)
Urozelotes rusticus (L. Koch 1872) Asia Yes 21 Zimiromis medius (Keyserling 1891) South America Yes 2 Erigone aletris Crosby and Bishop 1928 North America Yes 3 Erigone autumnalis Emerton 1882 North America Yes 7 Hypselistes florens (O. Pickard-Cambridge 1875) North America Yes 7 P Mermessus radobatus (Crosby 1924 North America Yes 10 P Mermessus trilobatus (Emerton 1882) North America Yes 10 P Syrisca sp. Astica No No F P Lycosa erythrognatha (Vinson 1863) Africa No F Nephila inuurata (Vinson 1863) Africa No F Nephila inuurata (Yaginuma 1972) Asia Yes P Nephilaengys curentata (Yaginuma 1972) Asia Yes P Nesticella mogera (Yaginuma 1972) Asia Yes <td>Gnaphosidae</td> <td>Sosticus loricatus</td> <td>(L. Koch 1866)</td> <td>Asia</td> <td>Yes</td> <td>27</td> <td></td> <td>Nentwig et al. (2014)</td>	Gnaphosidae	Sosticus loricatus	(L. Koch 1866)	Asia	Yes	27		Nentwig et al. (2014)
Zinnironnis medius (Keyserling 1891) South America No F Erigone aletris Crosby and Bishop 1928 North America Yes 2 F Erigone autumnalis Emerton 1882 North America Yes 3 F Hypselistes florens (O. Pickard-Cambridge 1875) North America Yes 7 P Mermessus alenticulatus (Emerton 1882) North America Yes 7 P Mermessus rislobatus (Emerton 1882) North America Yes 10 P Ostearius melanopygius (O. Pickard-Cambridge 1879) Unknown Yes 76 P Syrisca erythrognatha (Uncas 1836) South America No F Syrisca erythrognatha (Vinson 1863) Africa No F Nephila inaurata (Vinson 1863) Africa No No Nephila sp. (Yaginuma 1970) Asia Yes P Nesticella brevipes (Yaginuma 1972) Asia Yes P Nesticella m	Gnaphosidae	Urozelotes rusticus	(L. Koch 1872)	Asia	Yes	21		Thaler and Knoflach (1995); Wilson (2012)
Erigone aletris Crosby and Bishop 1928 North America Yes 2 F Erigone autumnalis Emerton 1882 North America Yes 3 F Hypselistes florens (O. Pickard-Cambridge 1875) North America Yes 7 P Mermessus aenticulatus (Banks 1892) North America Yes 7 P Mermessus naculatus (Banks 1892) North America Yes 10 P Aermessus trilobatus (Crost erythrogantha (Unknown Yes 10 P Dycosa erythrognatha (Lucas 1836) South America No F Syrica sp. Nephila inaurata No Africa No F Nephila insurata (Vinson 1863) Africa No F Nephila isp. Nephila insurata Yes 1 Nephila isp. No Africa No Nephila isp. No Yes 1 Nephila isp. No Yes 1 Nephila isp. <td>Gnaphosidae</td> <td>Zimiromis medius</td> <td>(Keyserling 1891)</td> <td>South America</td> <td>No</td> <td></td> <td>Fruits</td> <td>Schmidt (1971)</td>	Gnaphosidae	Zimiromis medius	(Keyserling 1891)	South America	No		Fruits	Schmidt (1971)
Erigone autumnalis Ennerton 1882 North America Yes 3 Hypselistes florens (O. Pickard-Cambridge 1875) North America Yes 7 P Mermessus aenticulatus (Crosby 1924 North America Yes 7 P Mermessus maculatus (Banks 1892) North America Yes 10 Mermessus trilobatus (Emerton 1882) North America Yes 10 Ostearius melanopygius (O. Pickard-Cambridge 1879) Unknown Yes 26 P Syrisca sp. Nephila inaurata (Vinson 1863) Africa No F Nephila isaurata (Vinson 1863) Africa No No No Nephila sp. (Yaginuma 1970) Asia Yes 1 Nesticella brevipes (Yaginuma 1972) Asia Yes P Nesticella mogera (Yaginuma 1972) Asia Yes P	Linyphiidae	Erigone aletris	Crosby and Bishop 1928	North America	Yes	2	Fruits	Wilson (2012)
Hypselistes florens (O. Pickard-Cambridge 1875) North America No Mermessus denticulatus Crosby 1924 North America Yes 7 P Mermessus maculatus (Banks 1892) North America No Mermessus trilobatus (Emerton 1882) North America Yes 10 Ostearius melanopygius (O. Pickard-Cambridge 1879) Unknown Yes 26 P Lycosa erythrognatha (Lucas 1836) South America No F Syrisca sp. Nephila inaurata No No F Nephila inaurata (Vinson 1863) Africa No No Nephila sp. Asia Yes 1 Nesticella nevipes (Yaginuma 1972) Asia Yes P Nesticella mogera (Yaginuma 1972) Asia Yes P Theotima minutissima (Petrunkevitch 1929) Unknown Yes P	Linyphiidae	Erigone autumnalis	Emerton 1882	North America	Yes	3		Hänggi (1993); Pesarini (1996)
Mermessus denticulatus Crosby 1924 North America Yes 7 P Mermessus maculatus (Banks 1892) North America No Mermessus trilobatus (Emerton 1882) North America Yes 10 Oxtearius melanopygius (O. Pickard-Cambridge 1879) Unknown Yes 26 P Lycosa erythrognatha (Lucas 1836) South America No F Syrisca sp. Nephila inaurata (Vinson 1863) Africa No F Nephila inaurata (Vinson 1863) Africa No In Nephila sp. (Vinson 1863) Africa No In Nephila sp. (Yaginuma 1970) Asia Yes 1 Nesticella mogera (Yaginuma 1972) Asia Yes P Theotima minutissima (Petrunkevitch 1929) Unknown Yes P	Linyphiidae	Hypselistes florens	(O. Pickard-Cambridge 1875)	North America	No			Locket and Millidge (1953)
Mermessus maculatus (Banks 1892) North America No Mermessus trilobatus (Emerton 1882) North America Yes 10 Ostearius melanopygius (O. Pickard-Cambridge 1879) Unknown Yes 26 P Lycosa erythrognatha (Lucas 1836) South America No F Syrisca sp. Nephila inaurata (Vinson 1863) Africa No F Nephila inaurata (Vinson 1863) Africa No In Nephila sp. No Africa No No Nephila sp. No Asia Yes 1 Nesticella brevipes (Yaginuma 1970) Asia Yes 5 P Nesticella mogera (Yaginuma 1972) Asia Yes 5 P	Linyphiidae	Mermessus denticulatus	Crosby 1924	North America	Yes	7	Plants	Klein et al. (1995); van Keer (2007, 2010, 2011); Reiser (2013)
Mermessus trilobatus (Emerton 1882) North America Yes 10 Ostearius melanopygius (O. Pickard-Cambridge 1879) Unknown Yes 26 P Lycosa erythrognatha (Lucas 1836) South America No F Syrisca sp. Nephila inaurata (Vinson 1863) Africa No In Nephila inaurata (Yaginuma 1970) Asia Yes 1 Nesticella brevipes (Yaginuma 1972) Asia Yes 5 P Nesticella mogera (Yaginuma 1972) Unknown Yes 1 P	Linyphiidae	Mermessus maculatus	(Banks 1892)	North America	No			Holzapfel (1932)
Ostearius melanopygius (O. Pickard-Cambridge 1879) Unknown Yes 26 P Lycosa erythrognatha (Lucas 1836) South America No Syrisca sp. Nephila inaurata (Vinson 1863) Africa No madagascariensis Nephila sp. Nephila sp. Nephila sp. Nesticella brevipes (Yaginuma 1970) Asia Yes 1 Nesticella mogera (Yaginuma 1972) Asia Yes 7 Nesticella mogera (Yaginuma 1972) Asia Nest	Linyphiidae	Mermessus trilobatus	(Emerton 1882)	North America	Yes	10		Wilson (2012); Rozwalka et al. (2013)
Lycosa erythrognatha (Lucas 1836) South America No Syrisca sp. Nothila inaurata No Nephila inaurata (Vinson 1863) Africa No Nephila sp. Tropics/subtropics No Nephila sp. (Yaginuma 1975) Africa No Nesticella brevipes (Yaginuma 1972) Asia Yes 1 Nesticella mogera (Yaginuma 1972) Asia Yes 5 Theotima minutissima (Petrunkevitch 1929) Unknown Yes 1	Linyphiidae	Ostearius melanopygius	(O. Pickard-Cambridge 1879)	Unknown	Yes	26	Plants, packaging material	Ruzicka (1995); Wilson (2012); Rozwalka et al. (2013)
Syrisca sp. South America No Nephila inaurata (Vinson 1863) Africa No madagascariensis No Tropics/subtropics No Nephilengys cruentata (Fabricius 1775) Africa No Nesticella brevipes (Yaginuma 1970) Asia Yes 1 Nesticella mogera (Yaginuma 1972) Asia Yes 5 Theotima minutissima (Petrunkevitch 1929) Unknown Yes 1	Lycosidae	Lycosa erythrognatha	(Lucas 1836)	South America	No		Fruits	Schmidt (1953, 1971)
Nephila inaurata (Vinson 1863) Africa No madagascariensis Tropics/subtropics No Nephila sp. Tropics/subtropics No Nephilengys cruentata (Fabricius 1775) Africa No Nesticella brevipes (Yaginuma 1970) Asia Yes 1 Nesticella mogera (Yaginuma 1972) Asia Yes 5 Theotima minutissima (Petrunkevitch 1929) Unknown Yes 1	Miturgidae	Syrisca sp.		South America	No		Fruits	Schmidt (1971)
Nephila sp. Tropics/subtropics No Nephilengys cruentata (Fabricius 1775) Africa No Nesticella brevipes (Yaginuma 1970) Asia Yes 1 Nesticella mogera (Yaginuma 1972) Asia Yes 5 Theotima minutissima (Petrunkevitch 1929) Unknown Yes 1	Nephilidae	Nephila inaurata madagascariensis	(Vinson 1863)	Africa	No		Intentional release	Bonnet (1929, 1930)
Nephilengys cruentata (Fabricius 1775) Africa No Nesticella brevipes (Yaginuma 1972) Asia Yes 1 Nesticella mogera (Yaginuma 1972) Asia Yes 5 Theotima minutissima (Petrunkevitch 1929) Unknown Yes 1	Nephilidae	Nephila sp.		Tropics/subtropics	No			van Keer (2011)
Nesticella brevipes (Yaginuma 1970) Asia Yes 1 Nesticella mogera (Yaginuma 1972) Asia Yes 5 Theotima minutissima (Petrunkevitch 1929) Unknown Yes 1	Nephilidae	Nephilengys cruentata	(Fabricius 1775)	Africa	No			van Keer (2007, 2011)
Nesticella mogera (Yaginuma 1972) Asia Yes 5 Theotima minutissima (Petrunkevitch 1929) Unknown Yes 1	Nesticidae	Nesticella brevipes	(Yaginuma 1970)	Asia	Yes			Marusik pers. comm. (2014)
Theotima minutissima (Petrunkevitch 1929) Unknown Yes 1	Nesticidae	Nesticella mogera	(Yaginuma 1972)	Asia	Yes	vo	Plants	Snazell and Smithers (2007); Kielhorn (2009); Reiser (2013); Rozwalka et al. (2013)
	Ochyroceratidae	Theotima minutissima	(Petrunkevitch 1929)	Unknown	Yes	1	Plants	Kielhorn (2008)
Yes	Oecobiidae	Oecobius amboseli	Shear and Benoit 1974	Africa	Yes	3		[Jland (2013)



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Family	Species	Authority	Origin	Established	Distribution	Pathway	References
Oonopidae	Diblemma donisthorpei	O. Pickard-Cambridge 1908	Asia	No		Plants	Saaristo (2001); Wilson (2012)
Oonopidae	Heteroonops spinimanus	(Simon 1891)	Central America	Yes		Plants	Kielhorn (2008)
Oonopidae Oonopidae	Ischnothyreus lymphaseus Ischnothyreus neltifer	Simon 1893 (Simon 1891)	Asia Asia	o Z	_	Plants Plants	Stanon (1896a, b) Saaristo (2001)
Oonopidae	Ischnothyreus velox	Jackson 1908	Asia	Yes	2	Plants	Saaristo (2001); Snazell and Smithers (2007)
Oonopidae	Triaeris stenaspis	Simon 1891	Central America	Yes	∞	Plants	Simon (1896b); Koponen (1997); Snazell and Smithers (2007); Van Keer (2007, 2010); Kielhorn (2008)
Oxyopidae	Oxyopes kraepelinorum	Bösenberg 1895	Macaronesia	No		Fruits	Schmidt (1971)
Palpimanidae	Sarascelis luteipes	Simon 1887	Africa	No		Fruits	Schmidt (1971)
Philodromidae	Gephyrota viridipallida	(Schmidt 1956)	Africa	No		Fruits	Schmidt (1956c)
Philodromidae	Tibellus seriepunctatus	Simon 1907	Africa	No		Fruits	Schmidt (1956b)
Pholcidae	Artema atlanta	Walckenaer 1837	Asia	Yes	4	Container	Van Keer (2007); Lee (2005), Huber pers. comm (2014)
Pholcidae	Crossopriza lyoni	(Blackwall 1867)	Asia	Yes	-	Container	Van Keer (2007, 2010); Huber pers. comm. (2014)
Pholcidae	Metagonia bicornis	Keyserling 1891	South America	No		Fruits	Schmidt (1971)
Pholcidae	Metagonia duodecimpunctata	Schmidt 1971	South America	No		Fruits	Schmidt (1971)
Pholcidae	Metagonia flavipes	Schmidt 1971	South America	No		Fruits	Schmidt (1971)
Pholcidae	Metagonia lingua	(Schmidt 1956)	South America	No		Fruits	Schmidt (1971)
Pholcidae	Metagonia striata	Schmidt 1971	Central America	No		Fruits	Schmidt (1971)
Pholcidae	Micropholcus fauroti	(Simon 1887)	Asia/Near East	Yes	-	Container	Van Keer (2007, 2010, 2011); Huber pers. comm. (2014)
Pholcidae	Modisimus globosus	Schmidt 1956	South America	No		Fruits	Schmidt (1971)
Pholcidae	Pholcus phalangioides	(Fuesslin 1775)	Asia	Yes	53		Nentwig et al. (2014); Huber pers. comm. (2014)
Pholcidae	Psilochorus minimus	Schmidt 1956	South America	No		Fruits	Schmidt (1971)



Table 1 continued	per						
Family	Species	Authority	Origin	Established	Distribution	Pathway	References
Pholcidae	Psilochorus simoni	(Berland 1911)	North America	Yes	24	Packing material	Thaler and Knoflach (1995); Reiser (2013); Rozwalka et al. (2013); Huber pers. comm. (2014)
Pholcidae	Smeringopus pallidus	(Blackwall 1858)	Africa	Yes	1		Kielhorn (2008); Blick (2004); Huber (2012)
Pholcidae	Spermophora kerinci	Huber 2005	Asia	Yes	1	Plants	Snazell and Smithers (2007); Kielhorn (2009)
Pholcidae	Spermophora senoculata	(Dugès 1836)	Asia/Near East	Yes	25	Plants	Van Keer (2011); Huber pers. comm. (2014)
Pisauridae	Conykrya wolffi	Schmidt 1956	Africa	No		Fruits	Schmidt (1956b)
Prodidomidae	Zimiris doriai	Simon 1882	Asia	No		Container	Jäger (2005)
Salticidae	Aelurillis catus	Simon 1886	Africa	No		Fruits	Schmidt (1956a)
Salticidae	Breda milvina	(C. L. Koch 1846)	South America	No		Fruits	Schmidt (1971)
Salticidae	Eris riedeli	(Schmidt 1971)	South America	No		Fruits	Schmidt (1971)
Salticidae	Hasarius adansoni	(Audouin 1826)	Africa	Yes	18	Plants	Jäger (2000); Kielhom (2008); Van Keer (2010, 2011); Rozwalka et al. (2013)
Salticidae	Hypaeus benignus	(Peckham 1885)	South America	No		Fruits	Schmidt (1971)
Salticidae	Menemerus bivittatus	(Dufour 1831)	Africa	Yes	5		Wilson (2012)
Salticidae	Panysinus nicholsoni	(O. Pickard-Cambridge 1899)	Asia	Yes	2		Wilson (2012)
Salticidae	Phidippus johnsoni	(Peckham and Peckham 1883)	North America	No		Fruits	Wilson (2012)
Salticidae	Phidippus regius	C. L. Koch 1846	North America	No		Container	Schmidt (1971); van Keer (2010)
Salticidae	Phidipus audax	(Hentz 1845)	Central America	No		Fruits	Schmidt (1971)
Salticidae	Plexippus paykulli	(Audouin 1826)	Asia	Yes	11	Container	van Keer (2010, 2011); Wilson (2012)
Salticidae	Psecas rubrostriatus	Schmidt 1959	South America	No		Fruits	Schmidt (1971)
Salticidae	Siloca campestrata	Simon 1902	South America	No		Fruits	Schmidt (1971)
Salticidae	Thyene ocellata	(Thorell 1899)	Africa	No		Fruits	Schmidt (1971)
Scytodidae	Dictis striatipes	L. Koch 1872)	Asia	No		Container	Bonnet (1930)



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Family	Species	Authority	Origin	Established	Distribution	Pathway	References
Scytodidae	Scytodes fusca	Walckenaer 1937	Central America	Yes	3	Plants	Brignoli (1976); Reiser (2013); Šestáková et al. (2014)
Scytodidae	Scytodes immaculata	L. Koch 1875	Africa	Yes	1		Le Peru (2011)
Scytodidae	Scytodes longipes	Lucas 1844	Central America	No		Plants	Brignoli (1976)
Scytodidae	Scytodes venusta	(Thorell 1890)	Asia	Yes	1	Plants	Blick (2004)
Selenopidae	Selenops mexicanus	Keyserling 1880	Central America	No		Fruits	Schmidt (1971)
Sicariidae	Loxosceles laeta	(Nicolet 1849)	South America	Yes		Fruits	Huhta (1972)
Sparassidae	Barylestis montandoni	(Lessert 1929)	Africa	No		Fruits	Schmidt (1971); Jäger (2005)
Sparassidae	Barylestis occidentalis	(Simon 1887)	Africa	No			Schmidt (1971); Jäger (2005)
Sparassidae	Barylestis scutatus	(Pocock 1903)	Africa	No	I	Fruits	Forsyth (1962); Browning (1954); Schmidt (1971)
Sparassidae	Barylestis variatus	(Pocock 1899)	Africa	N _o		Fruits	Forsyth (1962); Browning (1954); Wilson (2012)
Sparassidae	Cerbalus cf. psammodes	Simon 1897	Asia	No			Jäger (2005)
Sparassidae	Heteropoda venatoria	(Linnaeus 1767)	Asia	Yes	7	Container, fruits, wool	Bonnet (1930); Schmidt (1956b); Jäger (2000); Van Keer (2007, 2010); Rozwalka et al. (2013)
Sparassidae	Olios antiguensis columbiensis	Schmidt 1971	Central America	S _o		Fruits	Schmidt (1971); Essl and Rabitsch (2002); Jäger (2005)
Sparassidae	Olios banananus	Strand 1915	Africa	No		Fruits	Schmidt (1957)
Sparassidae	Olios corallinus	Schmidt 1971	South America	No		Fruits	Schmidt (1971); Jäger (2005)
Sparassidae	Olios hirtus	(Karsch 1879)	Asia	No		Container	Jäger (2005)
Sparassidae	Olios rubripes	Taczanowski 1872	South America	No			Schmidt (1971); Jäger (2005)
Sparassidae	Olios rufus	(Keyserling 1880)	South America	No			Schmidt (1971); Jäger (2005)



Fable 1 continued	nued					
Family	Species	Authority	Origin	Established Distribution Pathway	Pathway	References
Sparassidae	Olios sanctivincenti	(Simon 1897)	Asia	No	Fruits	Forsyth (Forsyth 1962); Wilson (2012)

Family	Species	Authority	Origin	Established	Distribution	Pathway	References
Sparassidae	Olios sanctivincenti	(Simon 1897)	Asia	No		Fruits	Forsyth (Forsyth 1962); Wilson (2012)
Sparassidae	Tychicus longipes	(Walckenaer 1837)	Asia	No	Ç		van Hasselt (1872)
Tetragnathidae	Tetragnatha shoshone	(Levi 1981)	North America	Yes	10		Uhl et al. (1992); Komposch (1995)
Theraphosidae	Acanthoscurria sternalis	Tullgren 1905	South America	$_{ m o}^{ m N}$		Fruits	Schmidt (1971)
Theraphosidae	Brachypelma albopilosuum	Valerio 1980	Central America	No			van Keer (2011)
Theraphosidae	Cyriocosmus elegans	(Simon 1899)	Central America	No			Wilson (2012)
Theraphosidae	Cyrtopholis bartholomaei	(Latreille 1832)	South America	No		Timber	Bonnet (1930)
Theraphosidae	Grammostola cala	Chamberlin 1917	South America	No		Container	van Keer (2010)
Theraphosidae	Grammostola rosea	(Walckenaer 1837)	Central America	No			van Keer (2011)
Theraphosidae	Heterothele sp.		Africa	No		Fruits	Forsyth (1962)
Theraphosidae	Pamphobeteus nigricolor	(Ausserer 1875)	South America	No		Fruits	Schmidt (1971)
Theraphosidae	Paraphysa sp.		South America	No		Fruits	Schmidt (1971)
Theraphosidae	Phormictopus cancerides	Latreille 1806	Central America	No		Fruits	van Keer (2010)
Theraphosidae	Psalmopoeus plantaris	Pocock 1903	South America	No		Fruits	Schmidt (1971)
Theraphosidae	Psalmopoeus reduncus	(Karsch 1880)	South America	No		Fruits	Schmidt (1971)
Theraphosidae	Scodra sp.		Africa	$ m N_{o}$		Fruits	Forsyth (1962)
Theridiidae	Chrysso pulcherrima	(Mello-Leitao 1917)	South America	$N_{\rm o}$		Fruits	Schmidt (1956c, 1957)
Theridiidae	Chrysso spiniventris	(O. Pickard-Cambridge 1869)	Asia	Yes	1		Blick (2004)
Theridiidae	Coleosoma acutiventer	(Keyserling 1884)	South America	No		Fruits	Schmidt (1971)
Theridiidae	Coleosoma blandum	O. Pickard-Cambridge 1882	Asia	No		Plants	Simon (1896b)
Theridiidae	Coleosoma floridanum	Banks 1900	Asia	Yes	01	Plants	Koponen (1990); Knoflach (1999); Wilson (2012); Šestáková et al. (2014); Knoflach- Thaler pers. comm. (2014)
Theridiidae	Cryptachaea blattea	(Urquhart 1886)	Asia	Yes	'n	Plants	Sührig (2010); Van Keer (2010, 2011); Marriott (2012); Reiser (2013)
Theridiidae	Cryptachaea veruculata	(Urquhart 1885)	Australia	Yes	2		Blick (2004); Van Keer (2010, 2011)



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Family	Species	Authority	Origin	Established	Distribution	Pathway	References
Theridiidae	Hadrotarsus ornatus	Hickman 1943	Australia	Yes	1		Van Keer (2007)
Theridiidae	Latrodectus geometricus	C. L. Koch 1841	South America	No		Container	Van Keer (2007, 2011)
Theridiidae	Latrodectus hasselti	Thorell 1870	Australia	No		Container	Blick (2004); van Keer (2011)
Theridiidae	Latrodectus mactans	(Fabricius 1775)	North America	No		Fruits, container, cars, packing material	Ross (1988); van Keer (2007, 2010, 2011); Jäger (2009); Rozwalka et al. (2013)
Theridiidae	Nesticodes rufipes	(Lucas 1846)	South America	Yes	7	Crickets	Van Keer (2007); Gabriel (2010); Wilson (2012)
Theridiidae	Parasteatoda tabulata	Levi 1980	Asia	Yes	4		Moritz et al. (1988); Thaler and Knoflach (1995); Rozwalka et al. (2013); Knoflach-Thaler pers. comm. (2014)
Theridiidae	Parasteatoda tepidariorum	(C. L. Koch 1841)	South America	Yes	43	Plants	Bonnet (1930); Nentwig et al. (2014)
Theridiidae	Platnickina mneon	(Bösenberg and Strand 1906)	Africa	No		Fruits	Schmidt (1971)
Theridiidae	Rugathodes sexpunctatus	(Emerton 1882)	North America	Yes	-	Timber	Davidson (2012); Davidson and Merrett (2014)
Theridiidae	Steatoda grossa	(C. L. Koch 1838)	Asia	Yes	46	Fruits	Levi (1967); Kielhorn (2008); Wilson (2012)
Theridiidae	Steatoda nobilis	(Thorell 1875)	Macaronesia	Yes	10	Fruits, container, plants	Snazell and Jones (1993); Nolan (1999); Van Keer (2010, 2011); Kulczycki et al. (2012); Wilson (2012); Reiser (2013)
Theridiidae	Theridion bomae	Schmidt 1957	Africa	No		Fruits	Schmidt (1957)
Theridiidae	Theridion murarium	Emerton 1882	North America	No		Fruits	Bonnet (1930)
Theridiidae	Theridion musivivum	Schmidt 1956	Macaronesia	No		Fruits	Schmidt (1953, 1971)
Theridiidae	Theridion mysteriosum	Schmidt 1971	South America	No		Fruits	Schmidt (1971)
Theridiidae	Theridion purcelli	O. Pickard-Cambridge 1904	Africa	Yes	-1	Plants	Marusik pers. comm. (2014)



Family	Species	Authority	Origin	Established Distribution Pathway	Distribution	Pathway	References
Theridiidae	Theridion rubrum	(Keyserling 1886)	South America	No		Fruits	Schmidt (1971)
Theridiidae	Tidarren cuneolatum	(Tullgren 1910)	Macaronesia	No		Fruits	Schmidt (1971)
Theridiidae	Tidarren levii	Schmidt 1957	Africa	No		Fruits	Schmidt (1957)
Theridiidae	Yaginumena maculosa	(Yoshida and Ono 2000)	Asia	Yes 3			Kovblyuk et al. (2012)
Thomisidae	Bassaniana versicolor	(Keyserling 1880)	North America	No			O. Pickard-Cambridge (1911)
Thomisidae	Carcinarachne brocki	Schmidt 1956	South America	No		Fruits	Schmidt (1956c, 1971)
Thomisidae	Ozyptila georgiana	Keyserling 1880	North America	No		Fruits	Bonnet (1930)
Thomisidae	Synema trimaculosum	Schmidt 1956	South America	No		Fruits	Schmidt (1971)
Titanoecidae	Goeldia luteipes	(Keyserling 1891)	South America	No		Fruits	Schmidt (1971)
Titanoecidae	Goeldia patellaris	(Simon 1892)	South America	No		Fruits	Schmidt (1971)
Titanoecidae	Pandava laminata	(Thorell 1878)	Asia	Yes 2		Plants	Jäger (2008); Pfliegler et al. (2012)
Titanoecidae	Titanoeca guayaquilensis	Schmidt 1971	South America	No		Fruits	Schmidt (1971)

Most spiders introduced to Europe originate from South (34 %), Central (10 %) or North (12 %) America, so that in total 55 % of all introduced spider species came from the Americas. Asia contributed 19 % and Africa 15 %. However, only 5 % of the South American species and 17 % of those from Central America were able to establish. In contrast, species from North America (36 %) and Asia (63 %) had much higher establishment rates (Table 2).

The first records I found for the introduction of alien spiders to Europe go back to the first half of the nineteenth century. 1819 and 1831 are the first (known) recorded introductions, for *Plexipus paykulli* and Menemerus bivittatus, respectively (Nentwig and Kobelt 2010). The total of 184 species introduced during these 195 years refers to an average introduction frequency of 0.94 spider species per year. However, three different periods can be distinguished: 1819–1949 with a very low introduction rate of 0.3 species per year, 1950–1969 with 2.2 introductions per year, and 1970–2014 with 1.1 introductions per year (Fig. 1). While the introductions continuously increased over the last decades, the period 1950–1969 is special, mainly due to the intensive investigations of Schmidt on introductions via imported fruits (Schmidt 1956-1971).

Pathways

In 161 cases, the circumstances of the introduction of alien spiders were reported and this allows a detailed pathway analysis, following the pathway nomenclature of Hulme et al. (2008) (Table 3). Only one species

Table 2 Origin of spider species introduced to Europe and established there

Origin	Introduced	Established
Africa	27	8
Macaronesia	8	1
Asia	35	22
America North	23	8
America Central	18	3
America South	63	3
Australia	5	3
Tropics/subtropics	3	1
Unknown	2	2
Sum	184	51



Table 1 continued

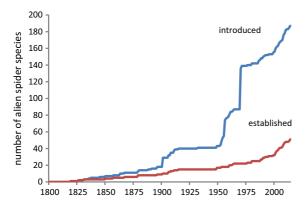


Fig. 1 Cumulative number of alien spider species introduced and established from 1800 to 2014

was introduced on purpose (*Nephila inaurata mada-gascariensis* at the end of the nineteenth century in France, for silk production, Bonnet 1929, 1930), while all other cases were unintentional, either as stowaways in or on transport vectors, or as contaminants of traded commodities. Only 19 cases of spider imports by means of containers or packaging material have been reported, but in 47 % of cases they led to the establishment of viable populations. Spiders as contaminants are most frequently found in fruit shipments (67 % of all cases), but only 5 % of the species were able to establish. Fruit shipments involved bananas in 86 % of cases. In 26 cases, potted plants contained spiders and their establishment rate was rather high (65 %). Among the remaining and relatively rare

categories, two need to be mentioned separately. There is an increasing market for food crickets which are shipped from the USA to Europe and vice versa. This led to the successful introduction of a theridiid, which made its way as predator in a shipment of its cricket prey (Gabriel 2010). Another species, the philodromid *Thanatus vulgaris*, was also shipped with food crickets from the USA to several European countries, but because this species is native to Europe, this represents a re-introduction of a species, earlier introduced to North America (Jäger 2002). The second category concerns the import of classic cars and used sport cars from the USA, where the cars quite often contained black widow spiders (Latrodectus mactans) in high numbers, also with cocoons (Van Keer 2010), but this has not led to the establishment of a European population so far.

Impact

Currently, our knowledge on the overall impact of spiders alien to Europe is low. Spiders exert environmental impact as predators. They prey on a wide range of invertebrates including other spider species, but only for a few species a high density in natural habitats has been reported. Such examples are the linyphiids *Mermessus trilobatus* and *Ostearius melanopygius* (Ruzicka 1995; Rozwalka et al. 2013) whereas in most cases evidence is merely anecdotal. Therefore, due to lack of data no further conclusion on the overall effect

Table 3 Pathways for the introduction of alien spider species to Europe according to the pathway nomenclature of Hulme et al. (2008)

Pathway	Motivation	Vectors	Introductions (number of species)	Established (%)
Release	Intentional		1	0
Escape from captivity	Unintentional		0	0
Contaminants of traded commodities	Unintentional	Fruits	108	5
		Potted plants	26	65
		Timber	3	33
		Food crickets	1	100
		Wool	1	100
		Soil	1	100
		Used cars	1	0
Stowaways in/at transport vectors	Unintentional	Container, packaging material	19	47

In a few cases more than one pathway was reported and they were counted separately. Total number of cases = 161



Table 4 Impact assessment of spiders alien to Europe according to the Generic Impact Scoring System (compare text)

Impact category	Impact description	Impact level (points)	Spider species	Reference
Environmental impacts				
Impacts on plants or vegetation through herbivory		No impact known (0)		
Impacts on animals through predation or parasitism	Predation on other spider species leading to local displacement of native species	Impact can be assumed but currently no impact known (0)		
Impacts on plants and animals through competition	Competing with other spiders for food, primarily in special habitats, such as caves, leading to local extinction of native species	Medium to major (3–5)	Pholcus phalangioides	Uhlenhaut (2001)
Impacts through transmission of diseases or parasites to native species		No impact known (0)		
Impacts through hybridization		No impact known (0)		
Impacts on ecosystems	Change of species composition, guild structure and/or food webs	Minor to medium (2–3)	Pholcus phalangioides	Uhlenhaut (2001)
Socio-economic impacts				
Impacts on agricultural production	Reduced marketability due to silk spinning activity in horticulture (ornamental plants)	Minor (1)	Mermessus denticulatus	Klein et al. (1995)
Impacts on animal production		No impact known (0)		
Impacts on forestry production		No impact known (0)		
Impacts on human infrastructure and administration	Increased cleaning costs for building facades and windows due to web spinning activity, including insecticide usage	Minor (1). This impact can be assumed but no example is known for Europe.		
Impacts on human health	Bites and associated health problems, including fear of spiders	Minor to major (1-4)	Latrodectus sp., Loxosceles laeta, Steatoda nobilis	Warrell et al. (1991)
Impacts on human social life		No impact known (0)		

of alien spiders on the native prey community can be drawn. This is different in habitats with a low diversity of spiders, such as caves or buildings, where the native species can easily be replaced by *Pholcus phalangioides*, one of the first invasive spiders in Europe, now considered to be typical for such habitats. In Europe, so far no native species has been replaced by this alien spider (category 1.2), but *Pholcus phalangioides* outcompeted native species locally in buildings (category 1.3), leading to a change of species composition and guild structure (Uhlenhaut 2001) (category 1.6, Table 4).

The socio-economic impact of alien spiders can affect agricultural production because intensive spinning activity on ornamental plants in horticulture can reduce marketability (Klein et al. 1995). Spiders can also increase the cleaning costs of buildings (facades and windows) and cause insecticide applications to facades to reduce their densities. According to pest-control companies, this happens frequently (pers. comm.) against spiders in general, but no example for spiders alien to Europe is currently known (Table 4). The most obvious impact of spiders can be caused by biting humans, which is also the best



documented impact. However, there are only a few European records for bites of spiders alien to Europe, for example the case of Steatoda nobilis (Warrell et al. 1991), which cannot seriously harm humans. There are, however, regular reports of three Latrodectus species, frequently introduced to Europe (Table 1), but they have not yet been able to establish populations, and there are also no reports about bites of these species in Europe. Loxosceles laeta is another potentially dangerous species for humans. It has been established in one building in Helsinki for 50 years, but has neither spread nor been reported to bite humans (Huhta 1972; Huhta pers. comm.; Pajunen pers. comm.) (Table 4). Impact on human health also includes fear of spiders, but no publications are available dealing with psychological consequences of alien spiders in Europe.

Discussion

Introduction, establishment and origin

A relatively large number of 184 species have been recorded as introduced to Europe from all other continents during the last 200 years. This number corresponds to 4 % of the European spider fauna (Nentwig et al. 2014). Moreover, only 28 % of these species were able to establish in Europe and even in the country with the highest number of alien species (Germany with 30 species), this amounts only to 3 % of the native spider fauna and thus could be considered as negligible.

The dates of introduction and establishment of a species in Europe are often difficult to confirm. For most data from Schmidt (1956–1970), we do not have a date of first introduction or specimen collection, but only a date for the publication. In addition, we usually have only interception dates (at border controls or from product screening) that mostly refer to unsuccessful introductions. Establishment dates logically follow successful introductions, but it cannot be estimated how much time has passed between both events. It is also unknown how many unsuccessful events preceded a successful establishment event. Furthermore, the detection of a successful establishment is often reported (usually, when the species could be identified by a specialist) while the extinction of a small population is typically not reported, which may happen quite frequently. The linyphiid *Hypselistes florens* has not been collected for 50 years and is supposed to be no longer present in England. In contrast to its detection (Locket and Millidge 1953), the disappearance has not been published. Also, the oonopid *Diblemma donisthorpei*, first mentioned and described as a new species in 1908 from its invaded area, a hot-house in Kew Garden, England (Pickard-Cambridge 1908), has probably not established (Harvey, pers. comm. 2014), but both species are still mentioned by Wilson (2012) as occurring in the country.

In many families, establishment probability was very low and most species failed to set up viable populations. In particular, species from tropical and subtropical climates have a rather low chance to establish in Europe, whereas conditions for species from North America and Asia are much better. This is also reflected by the size and physiological adaptability of the introduced species. While in general introduced species tend to be larger than their European close relatives (Kobelt and Nentwig 2008), most large species had a very low chance to establish. From the three families which comprise most of the large spider species (Ctenidae, Sparassidae and Theraphosidae), only one species out of 36 was able to establish (Heteropoda venatoria, in buildings), probably because they need tropical environments. On the other hand, from three families with medium-sized to small species (Pholcidae, Scytodidae, and Theridiidae) 24 out of 47 introduced species were able to establish. These families comprise many species welladapted to dry niches in their area of origin, which predisposes them for survival in Europe, specifically in buildings. Generally, establishment probability is higher for species from areas with a climate similar to Europe, but also an adaptation to specific microclimate conditions can offer an advantage. Alternatively, many species from seemingly unsuitable climates find suitable climatic niches in Europe, especially in hothouses of Botanical Gardens and Zoos, or inside normal buildings (e.g., Holzapfel 1932; Gabriel 2010; Šestáková et al. 2014). Thaler-Knoflach (2010) estimated that two-thirds of all alien spider species introduced to Central Europe live synanthropically.

All alien species have a defined area of origin, but in some cases this may be unknown. Those are named cryptogenic or cosmopolitan, underlining the lack of knowledge (DAISIE 2009). In a few cases, it was

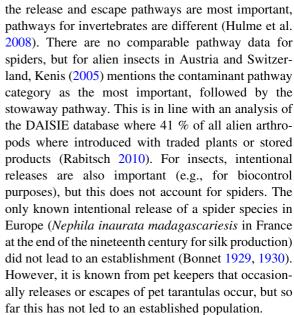


difficult to assign an area of origin to alien species in this study, but using expert opinion, the most probable area of origin could be estimated for all species but two. The linyphiid *Ostearius melanopygius* has been detected all over the world within a few decades (Ruzicka 1995) and for the ochyroceratid *Theotima minutissima* it is unknown whether it comes from America or Asia (WSC 2015 and references mentioned therein). Table 1 mentions their origins as unknown.

From a biogeographic perspective, Europe (as defined above) is treated here as a unit. This means that a species moving from one part of Europe to another part is not considered as alien because such a species is native to Europe. On the one hand, this makes sense because many species are widely distributed within Europe and are not restricted to one climate or habitat. On the other hand, an observer may find irritating the sudden appearance of a Mediterranean species in England or even Scandinavia where it never had been recorded previously. Climate change is real and its effects should not be underestimated. Spiders can disperse far more than the few metres a spider can walk during its lifetime. Many species balloon in a given developmental stage, and this enables them to spread over considerable distances. In the case of the wasp spider Argiope bruennichi (Araneidae), initially limited to the Mediterranean area and now occurring in England, Scandinavia and the Baltic states, human aid is clearly excluded, and this demonstrates how extensive natural spread in a spider can be (Kumschick et al. 2011). This concerns an extreme case, but many more Mediterranean species are spreading northwards and consequently, many examples for alien spiders mentioned by Thaler and Knoflach (1995) and Essl and Rabitsch (2002) refer to such natural spread. Also the Mediterranean species listed by Nentwig and Kobelt (2010) are not true alien to other parts of Europe and many of the species mentioned by Wilson (2011, 2012) as alien to the United Kingdom or by Nolan (2002) for Ireland are of European origin and not considered here.

Pathways

There are three main pathways for alien spiders to reach Europe, as contaminants with fruits, as contaminants with potted plants, and as stowaways with containers. While for terrestrial plants and vertebrates



For spiders, the contaminant pathway of traded commodities (mainly fruits and potted plants) concerns 88 % of cases and in 26 cases this lead to an established population. Therefore the contaminant pathway is much more important than the stowaway pathway with containers (12 % of cases, nine successful establishments). After the Second World War a tremendous increase of alien spider introductions was caused by fruit imports, mainly bananas, primarily from America and Africa. However, this is also due to the good documentation by the work of Schmidt (1953–1971) who for some time intensively collected spiders from fruit cargo landing in the harbor of Hamburg. The 1960s were also the time when the survival chances for alien arthropods rapidly declined during trans-Atlantic transports due to modified transport techniques, especially a modified and cool atmosphere with low O₂ contents of 2–5 %, high CO₂ contents of 2-5 % and up to 95 % nitrogen (Hallman 2007). So it can be assumed that the decline in records of alien spiders after 1971 was not primarily due to less collection and publication effort, but to modified transport conditions that were less suitable for the import of alien species. Nevertheless, recent reports of spiders imported with bananas (Jäger and Blick 2009) indicate that this pathway still exists. Among other fruits, table grapes are especially likely as a vector for spiders (Wilson 2012; Bosselaers 2013) and systematic investigations in South Africa and New Zealand have revealed frequent spider records from imported



table grapes, including four *Latrodectus* species (Ministry of Health 2002; Craemer 2006). Obviously this pathway still needs careful control.

Tropical plants, with soil in a pot, are imported for (1) typical botanical gardens and modern tropical show gardens, and (2) normal customers that usually buy potted plants for their houses. The establishment of a tropical garden is a rather rare event, however this artificial habitat tends to last for centuries. Therefore, these installations that import tropical plants by the container, can provide rather stable island habitats in an otherwise less suitable environment for tropical species (e.g., Holzapfel 1932; Koponen 1990, 1997). The Tropical World in Leeds, UK (Wilson 2011) and the Tropical Island near Berlin, Germany (Reiser 2013; Šestáková et al. 2014) or the Biodôme de Montréal, Canada (Paquin et al. 2008) indicate that it is still not possible to fill such buildings with plants without importing at the same time a series of alien spiders.

While it is well-known that plant pests are also imported with plant imports (Perrings et al. 2005; Rabitsch 2010) it has largely been overlooked that species from other trophic levels may also have a fairly good chance to be imported with plants, among them predators such as spiders. Spiders have the predisposition that they can survive harsh conditions in the cocoon stage, attached to a plant, and this brings a whole population at once into a new habitat. After a few decades of primary and secondary introductions, some theridiid species are now nearly globally distributed and for some species it is difficult to determine where they originated from (Levi 1967). Potted tropical plants can be bought today in garden centres, furniture or do-it-yourself supermarkets and even food super markets. Competition for low prices is high and standards of quality control are becoming increasingly less effective. In the 150 year period from 1844 to 1994, 16 spider introductions with plants were recorded (seven successful). Twelve introductions were recorded for the last 20 years (1995-2014) and 10 of them were successful. Not only the import of potted plants increased dramatically, but this has also led to much higher introduction and establishment rates of alien spiders.

The contaminant pathway concerns mainly fruit imports and potted plants. It is regulated by the responsibilities of exporters and importers, by international regulation and by quarantine procedures. Frame programs such as the International Plant Protection Convention (IPPC 2014) or the Plant Health Directive of the European Union (Plant Health Directive 2014) shall prevent introduction of pest organisms, and a positive side-effect could be the prevention of other organisms such as spiders. Obviously, this will not work sufficiently because more and more spider species are imported with traded plants and their products.

The stowaway pathway is also of increasing importance for spiders. This pathway concerns mainly containers and packaging material and is regulated by the responsibility of the carrier, by international regulation and quarantine procedures. For containers, this usually includes fumigation with phosphine, sulfuryl fluoride or methyl bromide (Hallman 2007). It can only be speculated here why this does not more efficiently prevent the introduction of spiders. Jäger (2005) mentioned the "forgotten" fumigation of a given container and it is possible that in many countries the fumigation standards are too low to be fully effective.

Impact

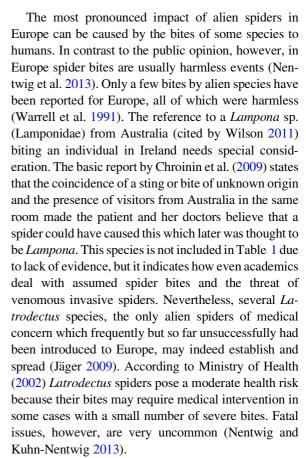
The environmental and socio-economic impact of alien spiders, as analysed with GISS, is very low. Scoring included only a few species, mainly due to lack of data, and no species reached an impact score of more than 4. High impact alien invasive invertebrates have impact scores in the range of 10–30 impact points (Vaes-Petignat and Nentwig 2014). In my interpretation, this does not allow the conclusion that alien spiders have a low impact, it only points to the considerable lack of knowledge we still have in this regard.

The most pronounced environmental impact of spiders is through the predation on other spider species, leading to the local disappearance of species or even extinction of all other spider species. However, besides anecdotal descriptions (e.g., Uhlenhaut 2001 for *Pholcus phalangioides* in a building), there are no analyses of the long term consequences of such massive changes in guild structure and reduction of native diversity. *Pholcus phalangioides* is an arane-ophagic species (Jackson and Brassington 1987) of Asian origin, now present in all European countries, often at high densities, and it can be assumed that its impact on the local spider community must be



considerable. Comparably, some alien linyphiids (Ostearius melanopygius or Mermessus trilobatus) with locally high densities will have some environmental effect, but this is yet to be investigated. Related to this is the local displacement of native species by invading species because they share the same niche, which usually concerns closely related species. There are no examples of such a displacement for Europe, but three well-investigated case studies concern theridiids and linyphiids: the North American Steatoda borealis replaced by the European S. bipunctata in anthropogenic habitats in eastern USA and Canada (Nyffeler et al. 1986), the endemic New Zealand Latrodectus katipo replaced by the South African Steatoda capensis (Hann 1990), and the North American Frontinella communis locally replaced by the European Linyphia triangularis (Bednarski et al. 2010).

The socio-economic impacts of alien spiders' spinning activity and subsequent reduced marketability of ornamental plants concerns only rare situations, at least no damage report from Europe could be found. In principle, however, this impact category has to be taken very seriously, as the description of Levi (1997) and Cárdenas-Murillo et al. (1997) for the European araneid Cyrtophora citricola shows. This species is alien and invasive in South America and is regarded there as a major pest in apple orchards and in coffee plantations because of its intensive web spinning activity. Another kind of impact refers to increased cleaning costs of buildings because of the high density and web spinning activity of spiders, particularly when these webs last for a long time [permanent cribellate catching webs of dictynids (Dictyna civica, Bonnet 1931; Samu et al. 2004) and pholcids (Holocnemus pluchei, Reiser 2013)]. Dust and dirt accumulating in the webs of these spiders can cause severe aesthetic and hygienic problems. However, all examples reported for Europe so far concern Mediterranean species spreading north. These species are of European origin and therefore not considered here, but H. pluchei is also known to cause considerable costs in its invaded area in North America (Vetter et al. 2011). It is further known that insecticides are also applied to reduce the density of spiders in buildings. The costs of insecticides (including costs of development, administration and undesired side-effects) are also typical economic costs of alien species, but there are no data available covering this topic.



Alien spiders could also be seen as having a negative impact on the well-being of many humans because they cause fear and disgust, especially if they are large and advertised as "dangerous" (Garcia-Palacios et al. 2002; Vernon and Berenbaum 2002). Often spider introductions are reported by the media, frequently in a style that provokes fear, but this is usually far from reality and cannot be considered here. So far, to the best of our knowledge, no publications are available dealing with the psychosomatic consequences of alien spiders in Europe.

Conclusions

Given the dynamics of introduction and establishment of alien spiders to Europe, the next decades will approach two species introductions per year (currently one) with nearly one newly species established per year (currently one per three years). The main driving force will be the increasing international trade volume, but also climate change will facilitate the establishment of more species



from warmer areas where most European trade partners are. This will also start a shift for many alien species from a synanthropic way of life to outdoors, as already observed by Thaler-Knoflach (2010) for a few species. It can also be assumed that a few species will be able to increase their densities, thus their potential impact on native ecosystems, human economy and human health may become more visible as discussed above.

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