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Distribution patterns of established alien land snail species in the Western Palaearctic Region

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Abstract

Established alien land snail species that were introduced into the Western Palaearctic Region from other regions and their spread in the Western Palaearctic are reviewed. Thirteen of the 22 species came from North America, three from Sub-Saharan Africa, two from the Australian region, three probably from the Oriental Region and one from South America. The establishment of outdoor populations of these species was usually first seen at the western or southern rims of the Western Palearctic. Within Europe, the alien species usually spread from south to north and from west to east. The latitudinal ranges of the alien species significantly increased with increasing time since the first record of introduction to the Western Palearctic. The latitudinal mid-points of the Western Palaearctic and native ranges of the species are significantly correlated when one outlier is omitted. There is a general trend of poleward shifts of the ranges of the species in the Western Palaearctic compared to their native ranges. There are three reasons for these shifts: (1) the northward expansion of some species in Western Europe facilitated by the oceanic climate, (2) the impediment to the colonisation of southern latitudes in the Western Palaearctic due to their aridity and (3) the establishment of tropical species in the Mediterranean and the Middle East. Most of the species are small, not carnivorous and unlikely to cause serious ecological or economic damage. In contrast, the recently introduced large veronicellid slugs from Sub-Saharan Africa and the giant African snail *Lissachatina fulica* could cause economic damage in irrigated agricultural areas or greenhouses in the Mediterranean and the Middle East.

Keywords

Europe, Gastropoda, introduced species, Middle East, Mollusca, North Africa, non-native

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Introduction

An increasing number of species are being spread beyond their native ranges, usually by humans, sometimes intentionally, but often accidentally with commodities or travellers (van Kleunen et al. 2015; Seebens et al. 2017). The spread of species across biogeographical barriers results in global biogeographic homogenisation (McKinney and Lockwood 1999). The distributions of alien species are primarily explained by the prevailing climate and, to a lesser extent, by distance and trade relationships (Capinha et al. 2015). Alien species may disturb local ecosystems and may contribute to the extinction of native species (McKinney and Lockwood 1999; Clavero and Garcia-Berthou 2005). They may become pests and cause economic impacts (Pimentel et al. 2005; Vilà et al. 2010; Haubrock et al. 2021) and they may even be directly or indirectly harmful to human health as parasites, vectors or hosts (Hulme 2014). Therefore, the spread of alien species should be prevented; they should be monitored and, if necessary, controlled or eradicated (Butchart et al. 2010). However, for many taxa, especially invertebrates, we even lack an overview of the alien species and their distributions. Despite efforts to compile lists of alien species (e.g. DAISIE (2009)), a well-documented inventory of alien invertebrate species is not even available for Europe.

Molluscs are amongst the little-known taxa. In this paper, I focus on land snails. Land snail species play a variety of roles in ecosystems (Barker 2001). The greater majority of land snail species are detritivores, feeding on decaying plant material. They make an important contribution to decomposition, the nutrient cycle and soil formation (Meyer et al. 2013). Some also feed additionally or exclusively on living plant tissues (Godan 1983; Barker 2002). Others are facultative or obligate carnivores (Barker and Efford 2004). The different functional groups can pose different concerns if they are intentionally or unintentionally introduced into regions beyond their native ranges. Whereas the detritivores are of least concern, the herbivores may become agricultural and horticultural pests (Godan 1983; Barker 2002). Carnivorous land snails have been intentionally introduced in various regions as biological control agents for herbivorous snails. There are strong indications that they have not been effective in regulating the targeted pest snails (Cowie 2001; Gerlach et al. 2021). Instead, the introduction of carnivorous snails has often had fatal consequences for the native snail fauna. The extreme case is the *Euglandina rosea* (Férussac, 1821) species complex, known commonly as the rosy wolfsnail. This species complex has been introduced to many islands of the Pacific and Indian Oceans, as well as the Caribbean and southern and eastern Asia from the 1950s onwards as a biological control agent for the invasive giant African snail, *Lissachatina fulica* (Bowdich, 1822) (Griffiths et al. 1993; Civeyrel and Simberloff 1996; Lowe et al. 2000; Gerlach et al. 2021). However, the introduced *Euglandina* species prefer to prey on smaller native species than on *L. fulica* (Griffiths et al. 1993). The introduction of the *Euglandina* species has probably caused extinctions of at least 134 endemic land snail species (Régnier

et al. 2009). Moreover, some land snails may act as intermediate hosts of pathogen species like the rat lungworm, *Angiostrongylus cantonensis* (Chen, 1935) (Grewal et al. 2003), which may cause meningitis (Kliks and Palumbo 1992; Prociv et al. 2000; Barratt et al. 2016). Therefore, it is important to compile available information about alien land snail species as a basis for decisions on further measures to control or eradicate introduced populations.

In this study, the distribution and spread of land snail species that were introduced into the Western Palaearctic Region from other regions and that have established self-sustaining outdoor populations within the Western Palaearctic is reviewed. Current knowledge about the timing of introduction of the species into the Western Palaearctic Region and their spread within the region is summarised from the scattered literature. The latitudinal ranges of the established alien species in the Western Palaearctic Region are compared with the latitudinal extent of their native ranges.

Methods

Records of land snail species introduced to the Western Palaearctic Region from other regions after 1492 that have established self-sustaining outdoor populations and their distribution in the Western Palaearctic were compiled from literature, GBIF.org (2022) and the online collection database of the Steinhardt Museum National Natural History Collections (https://smnh.tau.ac.il/en/research/collections-database/). Introductions of species that occur only in greenhouses, plant nurseries or in flowerpots were not considered. Whether populations occurred outdoors is usually stated in publications, but is often less clear in datasets retrieved from GBIF.org (2022). It was not possible to further restrict the outdoor habitats where the introduced species occurred; i.e. they may be restricted, for example, to permanently irrigated, anthropogenic habitats like gardens. The Western Palaearctic as considered here includes Europe, the Azores, Madeira, Canary Islands (but not Cape Verde), Africa north of the Sahara, the Caucasus region and the Middle East eastwards to western Iran (but not the Arabian Peninsula, which forms a transitional zone to the Ethiopian region). Only the first reports of established outdoor populations of introduced species at the country level are compiled. With the exception of the Macaronesian archipelagos, islands are not listed separately from the countries to which they belong.

Data on the native ranges of the alien species were mainly taken from GBIF.org (2022), Hubricht (1985) and additional papers listed under the respective species. The boundaries of the native ranges are often fuzzy, as species also expand beyond their native ranges in the regions where they originated.

Latitudinal limits, latitudinal extent and latitudinal mid-point of the native range of each species and its range in the Western Palearctic were calculated as described by Guo et al. (2012).

Results

List of established alien land snail species in the Western Palaearctic Region

Laevicaulis alte (Férussac, 1822) (Veronicellidae; Fig. 1A)

Origin: Tropical Africa (Forcart 1953).

First record for the Western Palaearctic Region: Egypt, 2018 (Ali and Robinson 2020).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Egypt.

References for identification: Forcart (1953).

Remarks: *Laevicaulis alte* has been spread by humans throughout the tropics (Robinson 1999; GBIF.org 2022). Given that most *Laevicaulis* species are restricted to Africa, it has been assumed that *Laevicaulis alte* originated in Africa (Forcart 1953). The species has only recently been found in the Western Palaearctic (Ali and Robinson 2020), but was already known for a longer time from anthropogenic habitats in the transitional zone to the Ethiopian region in the southern Arabian Peninsula (El-Alfy et al. 1994; Neubert 1998).

Laevicaulis stuhlmanni (Simroth, 1895) (Veronicellidae; Fig. 1B)

Origin: Eastern Democratic Republic of the Congo, Uganda, Rwanda, Burundi, Kenya, Tanzania (Forcart 1953; Verdcourt 2006).

First record for the Western Palaearctic Region: Egypt, 2016 (Ali 2017a, b).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Egypt, Libya.

References for identification: Forcart (1953).

Remarks: This East African species was reported from a garden in Cairo (Ali 2017a, b). Samples from Libya initially identified as *Laevicaulis striatus* (Simroth, 1896) (Liberto et al. 2021) were later also identified as *L. stuhlmanni* (Ali et al. 2022).

Allopeas clavulinum (Potiez & Michaud, 1838) (Achatinidae; Fig. 1C)

Origin: Oriental Region?

First record for the Western Palaearctic Region: Israel, 2011 (Mienis et al. 2012).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Israel.

References for identification: Pilsbry (1946); Kerney et al. (1983); Horsák et al. (2020).

Remarks: The delimitation of this species is unclear (see Horsák et al. (2020)). Some considered *A. mauritianum* (Pfeiffer, 1853) to be a synonym of *A. clavulinum* (Kerney et al. 1983; Griffiths and Florens 2006; Horsák et al. 2020), while others considered them distinct species (Pilsbry 1946; Gittenberger and van Bruggen 2013). *Allopeas clavulinum* is a common greenhouse species (Kerney et al. 1983; Horsák et al.

2020). Its association with ornamental plants can easily result in its introduction to countries with suitable environmental conditions. It has also been spread by humans throughout the tropics (Robinson 1999). Its origin is sometimes given as East Africa (Kerney et al. 1983; Robinson 1999; Griffiths and Florens 2006), although it is not known from mainland East Africa (Connolly 1925; Verdcourt 2006). Molecular genetic investigations may help to reveal the geographic origin of the species. Although *A. clavulinum* and its presumed synonym *A. mauritianum* (Pfeiffer, 1853) were originally described from the Mascarene Islands, it should be re-considered whether it originated in Southeast Asia, where the species is widespread, but usually considered introduced (Nurinsiyah and Hausdorf 2019).

Allopeas gracile (Hutton, 1834) (Achatinidae; Fig. 1D)

Origin: Oriental Region?

First record for the Western Palaearctic Region: Iraq, 2008 (Naser 2010).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Canary Islands, Iraq.

References for identification: Pilsbry (1946); Horsák et al. (2020).

Remarks: *Allopeas gracile* has been distributed throughout the tropics by humans (Pilsbry 1946; Robinson 1999). For a long time, it has been supposed that *A. gracile* originated in the Neotropics (Pilsbry 1946; Solem 1964; Neubert 1998; Robinson 1999; Brodie and Barker 2011). However, Christensen and Weisler (2013) argued for an Old World origin of *A. gracile* because there are several Quaternary and archaeological records of *A. gracile* from southern Asia, the Middle East, Africa and Pacific islands, but none from the Americas.

Allopeas gracile has been recorded from irrigated agricultural land in Iraq (Naser 2010), a typical habitat for introduced tropical species for which the climate in the Mediterranean and Middle East is warm enough, but usually too dry. It has also been recorded from nurseries in Egypt (Ali and Robinson 2020) and Israel (Vaisman et al. 2020). It is unclear whether specimens of *A. gracile* from an alluvial sediment in Spain (identified as *Subulina octona*; Quiñonero-Salgado and López-Soriano (2020)) originated from an outdoor population or from a greenhouse. It can be expected that *A. gracile* will colonise irrigated outdoor habitats in these and additional Mediterranean countries.

Lissachatina fulica (Bowdich, 1822) (Achatinidae; Fig. 1E)

Origin: East Africa (Bequaert 1950; Mead 1961).

First record for the Western Palaearctic Region: Israel, 2010 (Mienis 2010).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Israel.

References for identification: Bequaert (1950).

Remarks: *Lissachatina fulica* is a tropical species that has been spread by humans throughout the tropics and has become a major pest (Mead 1961; Robinson 1999). In Israel, it occurs in gardens that are regularly irrigated during the dry season (Mienis 2010).

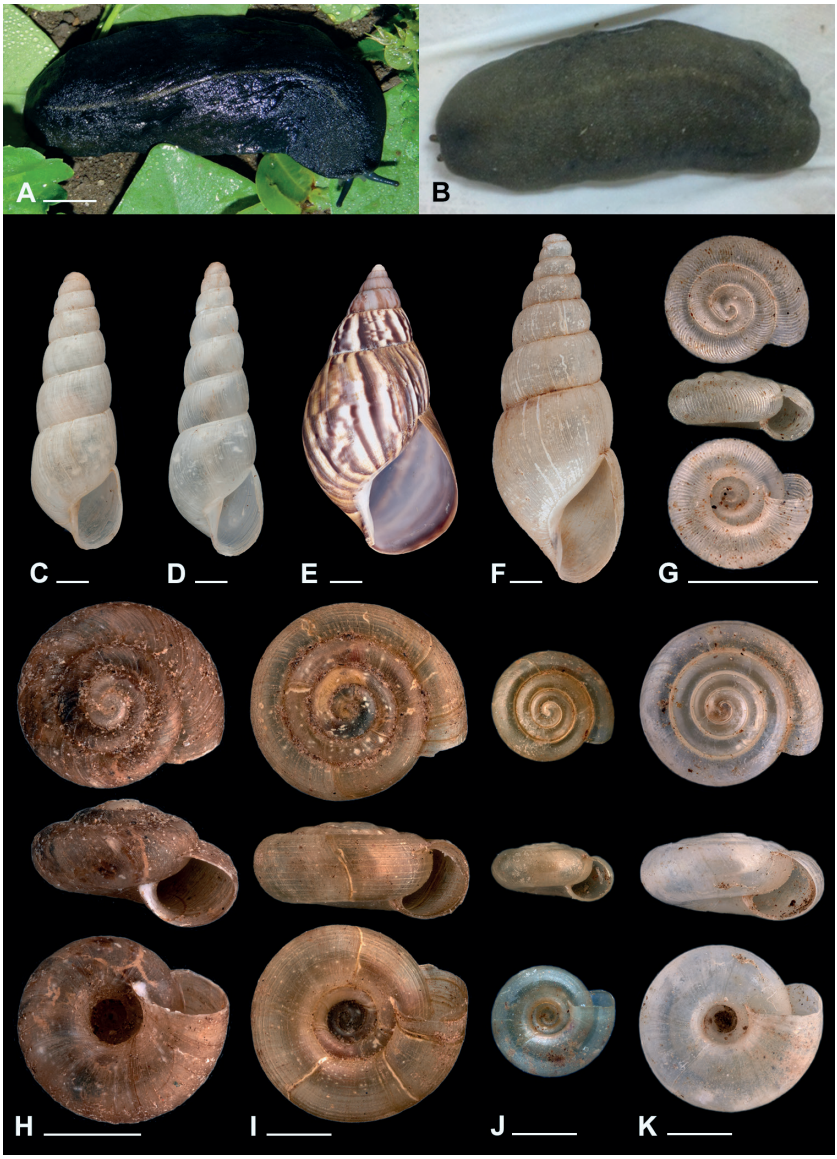

Figure 1. Alien land snail species in the Western Palaearctic Region **A** *Laevicaulis alte* (Férussac, 1822), Egypt, Abu Rawash (reproduced from Ali and Robinson (2022), courtesy of R. F. Ali) **B** *Laevicaulis stuhlmanni* (Simroth, 1895), Egypt, El Zamalek (reproduced from Ali et al. (2022), courtesy of R. F. Ali) **C** *Allopeas clavulinum* (Potiez & Michaud, 1838), Netherlands, Delft, botanical garden (ZMH 50896) **D** *Allopeas gracile* (Hutton, 1834), Canary Islands, Tenerife, Santa Cruz de Tenerife, Parque García Sanabría (ZMH 122731) **E** *Lissachatina fulica* (Bowdich, 1822), Colombia, Tolima, Honda (ZMH 76101) **F** *Paropeas achatinaceum* (Pfeiffer, 1846), Indonesia, Java, Pacitan, Poko (ZMH 133608) **G** *Discocharopa aperta* (Möllendorff, 1888), Indonesia, Java, Karangpaci, Green Canyon (ZMH 133063) **H** *Paralaoma servilis* (Shuttleworth, 1852), Spain, Vilanova de la Muga (ZMH 99005) **I** *Helicodiscus parallelus* (Say, 1821), USA, Salem (ZMH 45981) **J** *Lucilla scintilla* (Lowe, 1852), Austria, Wildon, debris of Kainach River (ZMH 89156) **K** *Lucilla singleyana* (Pilsbry, 1889), Russia, Armavir, debris of Urup River (ZMH 100266). Scale bars: 10 mm (**A, E**); 1 mm (**C–D, F–K**).

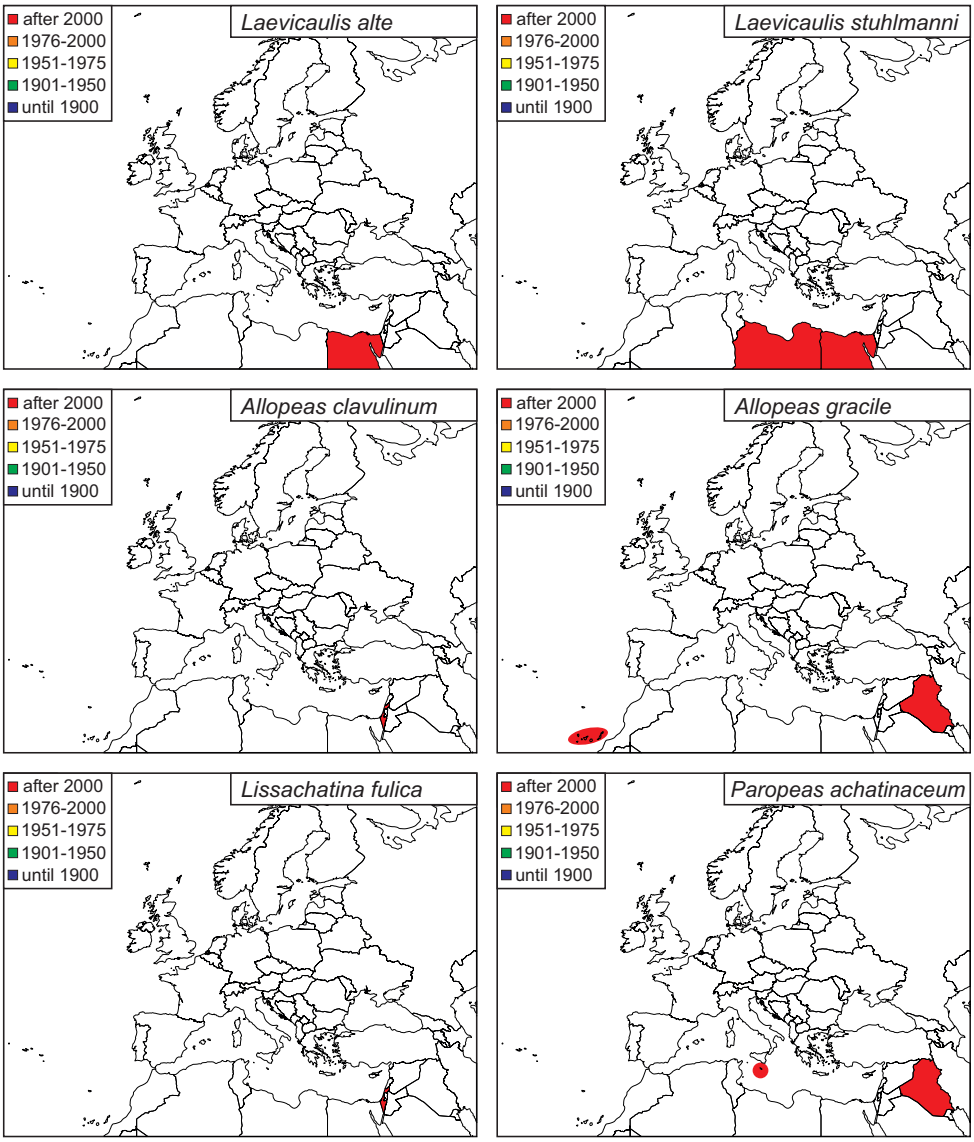

Figure 2. Maps showing the distributions of established alien land snail species in the Western Palaearctic Region and the period of the first records at the country level. Base map courtesy of Vemaps.com (https://vemaps.com/).

Paropeas achatinaceum (Pfeiffer, 1846) (Achatinidae; Fig. 1F)

Origin: Oriental Region.

First record for the Western Palaearctic Region: Iraq, 2017 (Hussein et al. 2018).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Iraq, Malta.

References for identification: Horsák et al. (2020).

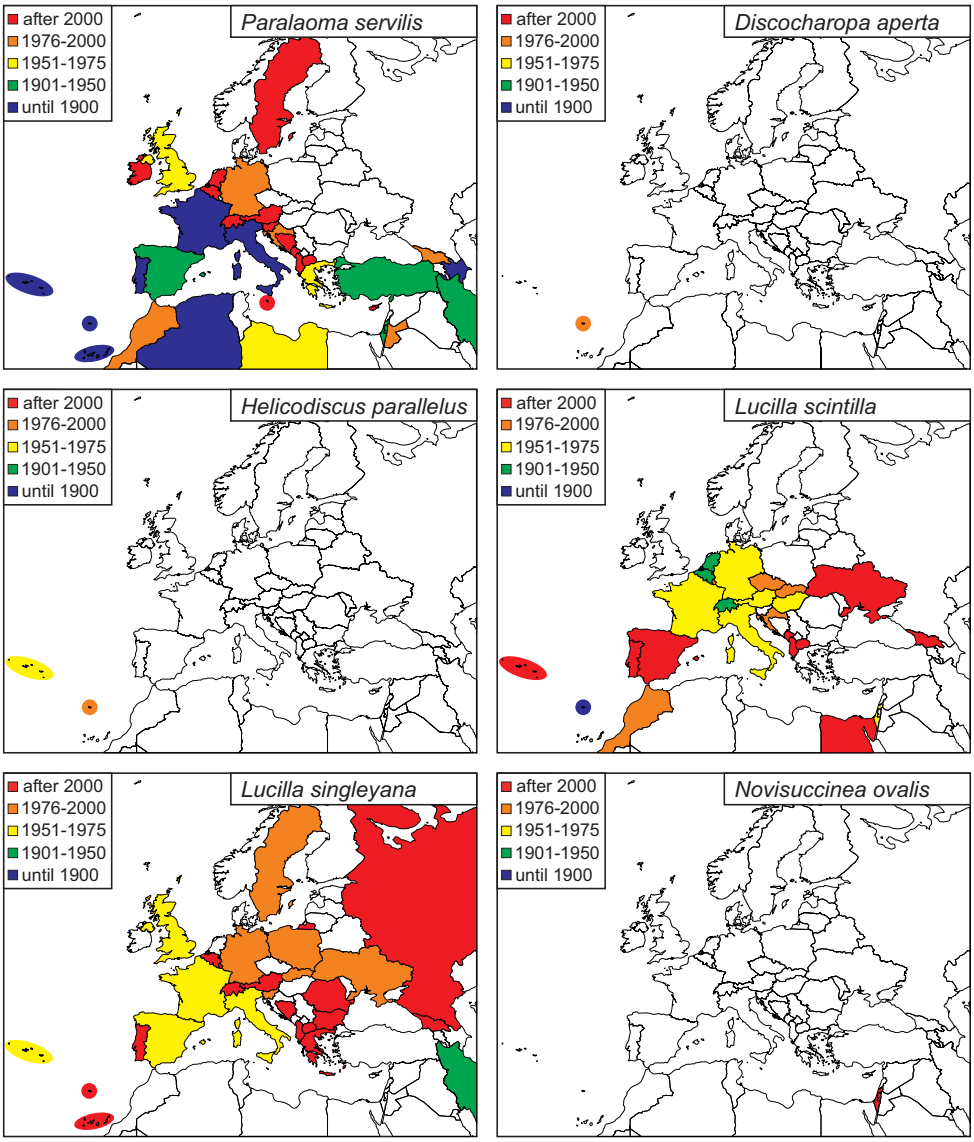

Figure 2. Continued.

Remarks: *Paropeas achatinaceum* is a Southeast Asian species that had probably already spread to Mauritius, Sri Lanka and Japan at the end of the 19th century (Boettger 1891 as *O. clavulinum* non Potiez & Michaud, 1838, according to Germain (1921), as *O. javanicum* (Reeve, 1849)). In the early 20th century, it was introduced to various Pacific Island groups (Brook 2010). In the Americas, it was established in Florida in 2001 (Robinson & Slapcinsky 2005) and in Guadeloupe in 2011 (GBIF.org 2022). All

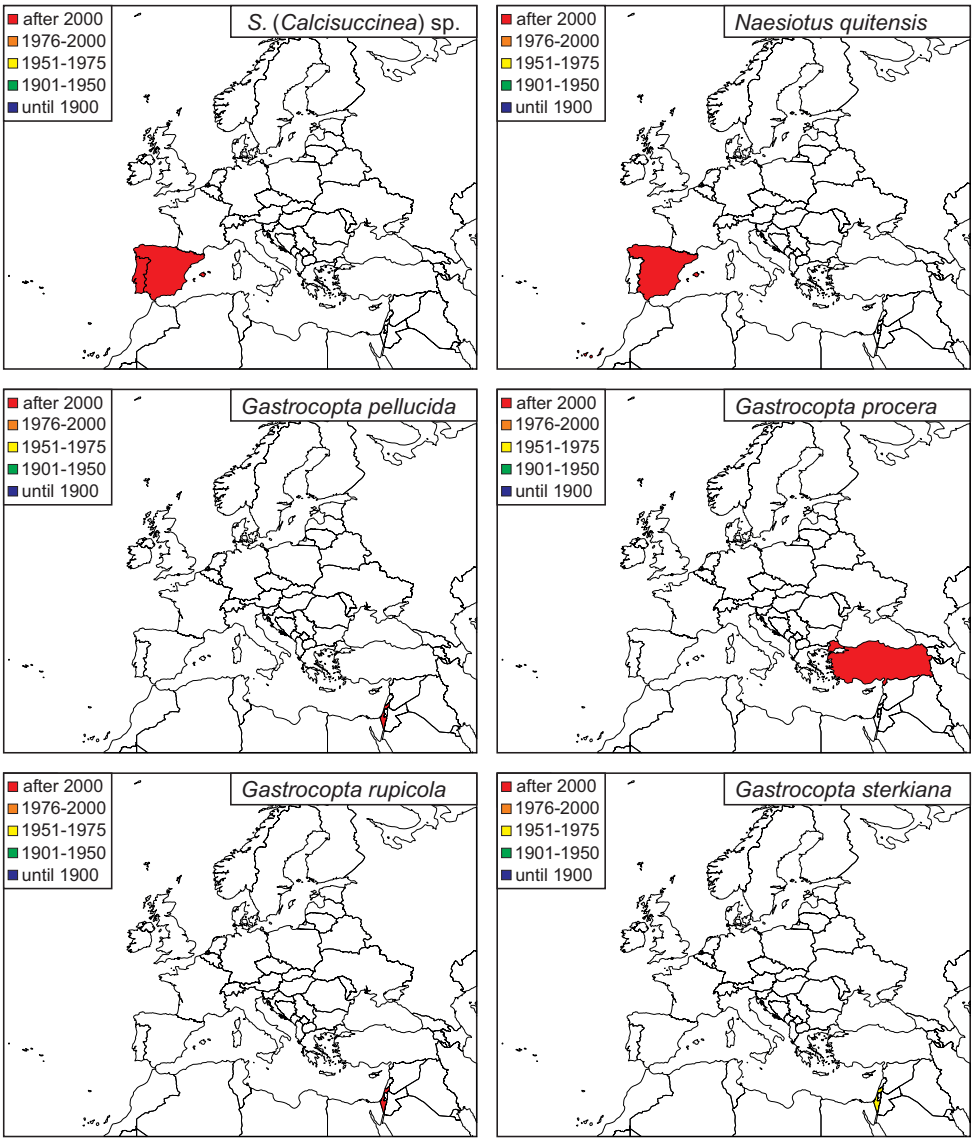

Figure 2. Continued.

of these introductions occurred on islands or coastal regions, which is consistent with Naggs' (1994) statement that *Paropeas achatinaceum* "has notably failed to penetrate inland on any major land mass". In contrast, the first record from the Western Palaearctic in Baghdad, Iraq (Hussein et al. 2018), is the most inland occurrence. The record of this species at high altitudes in Nepal (Budha et al. 2015) is even more surprising and should be checked.

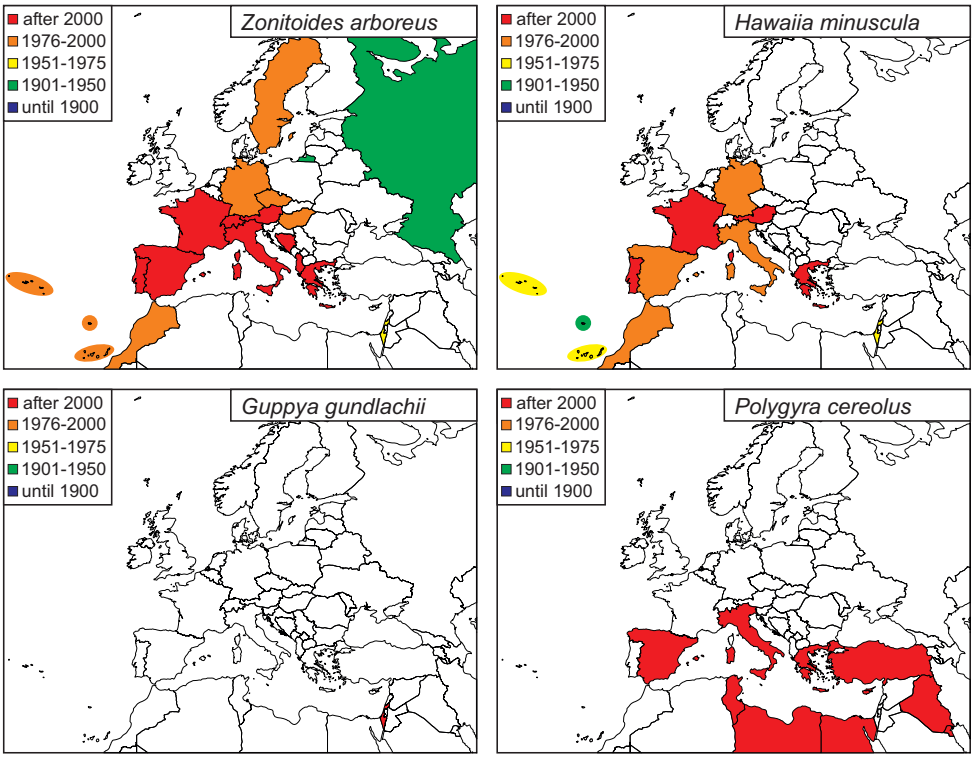

Figure 2. Continued.

Paralaoma servilis (Shuttleworth, 1852) (Punctidae; Fig. 1H)

Origin: Australia, New Zealand.

First record for the Western Palaearctic Region: Madeira, 1831 (Lowe (1831); as *Helix pusilla* Lowe, 1831).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Albania, Algeria, Andorra, Austria, Azerbaijan, Azores, Belgium, Bosnia and Herzegovina, Canary Islands, Croatia, Cyprus, France, Georgia, Germany, Greece, Iran, Ireland, Israel, Italy, Jordan, Libya, Madeira, Malta, Montenegro, Morocco, Netherlands, North Macedonia, Palestine, Portugal, Slovenia, Spain, Sweden, Switzerland, Turkey, United Kingdom.

References for identification: Kerney et al. (1983).

Remarks: Although *Paralaoma servilis* and several of its synonyms were originally described from different regions of the Western Palaearctic in the 19th century, it turned out to be an introduced species. It is now known from all continents, except Antarctica. *Paralaoma servilis* originated in New Zealand or/and Australia, where most of the other *Paralaoma* species occur and from where it is known from Pleistocene (Price and Webb 2006) and Holocene deposits (Jones 1984; McFadgen 1997; Brook 1999; Brook and Goulstone 1999).

Discocharopa aperta (Möllendorff, 1888) (Charopidae; Fig. 1G)

Origin: From the Philippines and Indonesia to Australia and the Society Islands (Solem 1982).

First record for the Western Palaearctic Region: Madeira, 1983 (Gittenberger and Ripken 1983).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Madeira.

References for identification: Solem (1982).

Remarks: *Discocharopa aperta* has been reported from Madeira only twice (Gittenberger and Ripken 1983; Seddon et al. 1986), but is more common on the island (M. Horsák, pers. comm.).

Helicodiscus parallelus (Say, 1821) (Helicodiscidae; Fig. 1I)

Origin: North America (Pilsbry 1948; Hubricht 1985).

First record for the Western Palaearctic Region: Azores, 1969 (Backhuys 1975).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Azores, Madeira.

References for identification: Pilsbry (1948); Kerney et al. (1983).

Remarks: *Helicodiscus parallelus* has been reported from greenhouses in many European countries (Kerney et al. 1983), but outdoor populations have been observed only in the Azores and in Madeira. Sysoev and Schileyko (2009: fig. 54F) figured a shell probably of *Helicodiscus parallelus* as '*Helicodiscus singleyanus*'. The shell was collected in 1969 in Ukraine (Balashov and Gural-Sverlova 2012), but it was not stated whether this was from a greenhouse or from outdoors.

Lucilla scintilla (Lowe, 1852) (Helicodiscidae; Fig. 1J)

Origin: North America (Pilsbry 1948; Hubricht 1985; Horsák et al. 2009).

First record for the Western Palaearctic Region: Madeira, 1852 (Lowe 1852).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Albania, Austria, Azores, Belgium, Croatia, Czech Republic, Egypt, France, Georgia, Germany, Hungary, Israel, Italy, Luxembourg, Madeira, Montenegro, Morocco, Netherlands, North Macedonia, Portugal, Slovakia, Spain, Switzerland, Ukraine.

References for identification: Horsák et al. (2009).

Remarks: Falkner et al. (2002) suggested that *Lucilla scintilla* is a European native not conspecific with any North American species. In contrast, Horsák et al. (2009) considered both European *Lucilla* species to be non-native introductions of North American species and synonymised *Helicodiscus singleyanus inermis* Baker, 1929 with *Lucilla scintilla* (Lowe, 1852). Hotopp et al. (2010) accepted this synonymy and used the name *Lucilla scintilla* for the North American species. Older identifications of shells as *H. singleyanus* or *H.* (*singleyanus*) *inermis* in literature were partly based on other criteria than those established by Horsák et al. (2009) and have to be checked. Here, some older literature records of *H. singleyanus* and

H. (*singleyanus*) *inermis* are preliminarily re-assigned following the lists of countries in the IUCN Red List evaluations of *L. singleyana* by Allen (2017) and *L. scintilla* by Seddon (2018).

Lucilla singleyana (Pilsbry, 1889) (Helicodiscidae; Fig. 1K)

Origin: North America (Pilsbry 1948; Hubricht 1985; Horsák et al. 2009).

First record for the Western Palaearctic Region: Iran, 1912 (GBIF.org 2022).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Albania, Austria, Azores, Belgium, Croatia, Czech Republic, France, Georgia, Germany, Hungary, Israel, Italy, Luxembourg, Madeira, Montenegro, Morocco, Netherlands, North Macedonia, Portugal, Slovakia, Spain, Switzerland, Ukraine.

References for identification: Horsák et al. (2009).

Remarks: Concerning the delimitation of the *Lucilla* species and the classification of older literature records, see remarks under *Lucilla scintilla*. The first record of *Lucilla singleyana* in the Western Palaearctic dates back to the Mission to Persia of Jacques de Morgan (1889–1912). The sample from Ardabil in Iran was identified by J. Gerber in 2018 (GBIF.org 2022).

Novisuccinea ovalis (Say, 1817) (Succineidae; Fig. 3A)

Origin: North America (Pilsbry 1948; Hubricht 1985).

First record for the Western Palaearctic Region: Israel, 2001 (https://smnh.tau.ac.il/en/collecting/smnhtau-mo-59720).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Israel, Palestine.

References for identification: Pilsbry (1948).

Remarks: The systematics of succineids is poorly understood and the distinctness and delimitation of *Novisuccinea* is questionable. The introduction of the North American *Novisuccinea ovalis* to Israel and Palestine is not well-documented. It should be checked whether the introduced species reported from Israel and Palestine (Roll et al. 2009; Vaisman and Mienis 2017) as *Novisuccinea ovalis* might, in fact, be the species reported as *Succinea* (*Calcisuccinea*) *luteola* Gould, 1848 from the United Arab Emirates (Feulner and Green 2003) and/or the species reported as *Succinea* (*Calcisuccinea*) sp. from the Iberian Peninsula (Holyoak et al. 2013). *Novisuccinea ovalis* (if that is what it is) is the only alien species that occurs in the western Palearctic south of its native latitudinal range (Fig. 4).

Roll et al. (2009) and Vaisman and Mienis (2016) reported another invasive succineid species from Israel and Palestine as *Novisuccinea horticola* (Reinhardt, 1877) from East Asia. In the Gaza Strip, the species was found in a hothouse. It is not known whether it also occurs outdoors in Israel or Palestine. *Novisuccinea horticola* (Reinhardt, 1877) is a synonym of *Novisuccinea lyrata* (Gould, 1859) (Ueshima 1995).

Succinea (*Calcisuccinea*) sp. (Succineidae; Fig. 3B)

Origin: North and Central America (Pilsbry 1948; Hubricht 1985).

First record for the Western Palaearctic Region: Spain, 2011 (Holyoak et al. 2013).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Portugal, Spain.

References for identification: Holyoak et al. (2013).

Remarks: It has not yet been possible to clarify the specific identity of the succineid species introduced to the Iberian Peninsula (Holyoak et al. 2013). Feulner and Green (2003) recorded an introduced population of *Succinea* (*Calcisuccinea*) *luteola* Gould, 1848 from the United Arab Emirates. *Succinea luteola* is widespread in southern USA and in Mexico. It is not unlikely that the species introduced in the Iberian Peninsula is the same as the one reported from the Arabian Peninsula.

Naesiotus quitensis (Pfeiffer, 1848) (Bulimulidae; Fig. 3C)

Origin: Ecuador (Parodiz 1979; Breure et al. 2022).

First record for the Western Palaearctic Region: Spain, 2018 (Ramos Sánchez et al. 2018).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Spain.

References for identification: Parodiz (1979); Ramos Sánchez et al. (2018).

Remarks: *Naesiotus quitensis* is endemic to Ecuador. It lives in humid temperate climates at 1700–2400 m a.s.l. in the Andes (Breure et al. 2022). In some areas of Ecuador, it is used as food (Gutiérrez Cantuña and Guainilla Maldonado 2018). It is, therefore, possible that it was intentionally introduced into Spain.

Gastrocopta pellucida (Pfeiffer, 1841) (Gastrocoptidae; Fig. 3D)

Origin: Southern North America (Pilsbry 1948; Hubricht 1985; Nekola and Coles 2010).

First record for the Western Palaearctic Region: Israel, 1993 (https://smnh.tau.ac.il/en/collecting/smnhtau-mo-40901/).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Israel.

References for identification: Pilsbry (1948); Nekola and Coles (2010).

Remarks: *Gastrocopta pellucida* is a widespread species originally from Central America and southern North America, but it is apparently spreading northwards in North America (compare Hubricht (1985); Nekola and Coles (2010); GBIF.org (2022)).

Gastrocopta procera (Gould, 1840) (Gastrocoptidae; Fig. 3E)

Origin: Eastern North America (Pilsbry 1948; Hubricht 1985; Nekola and Coles 2010).

First record for the Western Palaearctic Region: Turkey, 2015 (Frank 2016).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Turkey.

References for identification: Pilsbry (1948); Nekola and Coles (2010).

Remarks: Frank´s (2016: fig. 4) figure of *G. procera* from an irrigated hotel park on the south coast of Turkey shows the deeply inserted lower palatal fold lying parallel to the aperture as characteristic for *G. procera*. The identification was confirmed by J. Nekola (pers. comm.). For the *Gastrocopta* population from En Gedi in Israel, which was initially identified as *G. procera*, see *Gastrocopta sterkiana*.

Gastrocopta rupicola (Say, 1821) (Gastrocoptidae; Fig. 3F)

Origin: South-eastern North America, Caribbean, northern South America (Pilsbry 1948; Haas 1960; Hubricht 1985; Nekola and Coles 2010; GBIF.org 2022).

First record for the Western Palaearctic Region: Israel, 2004 (https://smnh.tau.ac.il/en/collecting/smnhtau-mo-72414/).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Israel.

References for identification: Pilsbry (1948); Nekola and Coles (2010).

Remarks: *Gastrocopta rupicola* is the third American *Gastrocopta* species that has been introduced to Israel (Vaisman and Mienis 2011).

Gastrocopta sterkiana Pilsbry, 1917 (Gastrocoptidae; Fig. 3G)

Origin: Southwest of the USA (Pilsbry 1948; Hubricht 1985; Nekola and Coles 2010).

First record for the Western Palaearctic Region: Israel, 1972 (Mienis 1977).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Israel.

References for identification: Pilsbry (1948); Nekola and Coles (2010).

Remarks: The introduced *Gastrocopta* population from En Gedi in Israel was initially identified as *G. procera* (Mienis 1977). Later, the *G. procera* complex was split into *G. procera* sensu stricto, *G. riparia* Pilsbry, 1916 and *G. sterkiana* Pilsbry, 1917 (Hubricht 1978; Nekola and Coles 2010). Based on the criteria given by Hubricht (1978) and Nekola and Coles (2010), the specimens from En Gedi can be identified as *G. sterkiana* because their lower palatal fold inserts moderately deep, lying at a 45° angle to the aperture axis rather than parallel to the aperture and many of them are higher than 2.4 mm. This identification was confirmed by J. Nekola (pers. comm.). The identifications of other *Gastrocopta* population from Israel that were identified as *G. procera* have to be checked.

Zonitoides arboreus (Say, 1817) (Gastrodontidae; Fig. 3H)

Origin: North and Central America (Pilsbry 1946; Hubricht 1985).

First record for the Western Palaearctic Region: Russia, 1907 (Lindholm 1911; as *Hyalina roseni* Lindholm, 1911).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Albania, Austria, Azores, Bosnia and Herzegovina, Canary Islands, Czech Republic, France, Germany, Greece, Hungary, Israel, Italy, Madeira, Morocco, Portugal, Russia, Spain, Sweden, Switzerland.

References for identification: Pilsbry (1946); Kerney et al. (1983).

Remarks: This species is common in greenhouses and nurseries (Kerney et al. 1983; Hausdorf 2019) and increasingly spreads from these into the wild. The first

report of an outdoor population of *Zonitoides arboreus* in the Western Palaearctic was from a park in Moscow (Lindholm 1911). Although the species was observed in the park from 1907 to 1918 (Boettger 1929), there are doubts as to whether this was really a self-sustaining outdoor population. The animals came from greenhouses in the park (Boettger 1929) and it is possible that the outdoor population was only maintained by the continuous supply of live animals from the greenhouses. This hypothesis is supported by the fact that neither this population nor any other population of *Zonitoides arboreus* appears to still exist in Moscow (Tappert 2009). If we neglect the population in Moscow, the first established populations of the species in the Western Palaearctic were found in the Azores. From Egypt, only a record from a nursery is known (Ali and Robinson 2020), but it is likely that *Zonitoides arboreus* also occurs in agricultural land and gardens there.

Hawaiia minuscula (Binney, 1841) (Pristilomatidae; Fig. 3I)

Origin: North and Central America (Pilsbry 1946; Hubricht 1985).

First record for the Western Palaearctic Region: Madeira, 1938 (http://id.luomus.fi/MY.2183079).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Austria, Azores, Canary Islands, France, Germany, Greece, Israel, Italy, Madeira, Morocco, Portugal, Spain.

References for identification: Pilsbry (1946); Kerney et al. (1983).

Guppya gundlachii (Pfeiffer, 1840) (Euconulidae; Fig. 3J)

Origin: Southern North America and northern South America (Pilsbry 1946; Hubricht 1985).

First record for the Western Palaearctic Region: Israel, 2015 (Mienis et al. 2016; as *Euconulus praticola* (Reinhardt, 1883)).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Israel.

References for identification: Pilsbry (1946).

Remarks: The occurrence of *Guppya gundlachii* in Israel is a new record for the Western Palaearctic Region. Mienis et al. (2016) misidentified specimens from Israel as *Euconulus praticola* (Reinhardt, 1883), a synonym of *Euconulus alderi* (Gray, 1840) (Horsáková et al. 2020). *Guppya gundlachii* differs from *Euconulus alderi* in the, on average, smaller, more depressed shell, with more distinct incised spiral lines at the bottom side. *Guppya gundlachii* is a globally expanding species. It has been introduced to New Guinea and adjacent islands (van Benthem Jutting 1964) and Java (Nurinsiyah and Hausdorf 2019). It is probably also established in mainland Southeast Asia, as Robinson (1999) reported regular interceptions of this species in shipments from Thailand. In South America, *Guppya gundlachii* has recently been reported for the first time from Peru (Wendebourg and Hausdorf 2019) and mainland Ecuador (Ramirez Perez and Hausdorf 2022). It is unclear whether the South American occurrences are also the result of introductions or whether they are part of the native range of the species. Robinson (1999) even considered the occurrences of *Guppya gundlachii* in North America as introduced.

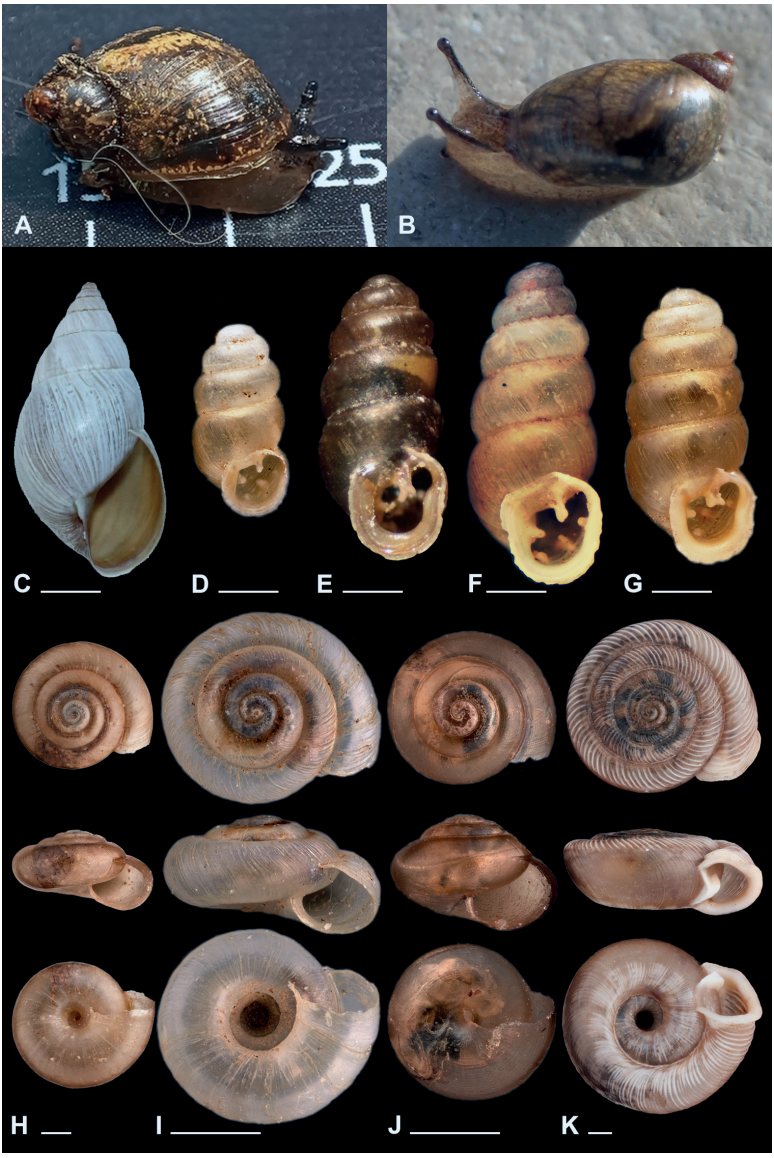

Figure 3. Alien land snail species in the Western Palaearctic Region **A** *Novisuccinea ovalis* (Say, 1817), Israel, Haifa (iNaturalist observation 118548596, courtesy of O. Shabbiel Lebber-Shabbat) **B** *Succinea* (*Calcisuccinea*) sp., Portugal, Seixal (iNaturalist observation 92683866, courtesy of N. Veríssimo P.) **C** *Naesiotus quitensis* (Pfeiffer, 1848), Spain, Madrid, Casa de Campo Park (reproduced from Ramos Sánchez et al. (2018), courtesy of J. López-Soriano) **D** *Gastrocopta pellucida* (Pfeiffer, 1841), Dominican Republic, Guaraguo (ZMH 51838) **E** *Gastrocopta procera* (Gould, 1840), Turkey, Evrenseki (reproduced from Frank (2016), courtesy of C. Frank) **F** *Gastrocopta rupicola* (Say, 1821), USA, Texas, San Marcos, Spring Lake Hills (iNaturalist observation 17346779, courtesy of B. Hutchins) **G** *Gastrocopta sterkiana* Pilsbry, 1917, Israel, En Gedi (ZMH 69886) **H** *Zonitoides arboreus* (Say, 1817), Canary Islands, Tenerife, Bajamar (ZMH 145645) **I** *Hawaiia minuscula* (Binney, 1841), Canary Islands, Tenerife, Puerto de la Cruz (ZMH 99003) **J** *Guppya gundlachii* (Pfeiffer, 1840), Peru, Huánuco, reserva Panguana (ZMH 143639) **K** *Polygyra cereolus* (Megerle von Mühlfeld, 1816), Egypt, Cairo, El Zamalek (ZMH 75229). Scale bars: 5 mm (**C**); 0.5 mm (**D–G**); 1 mm (**H–K**).

***Polygyra cereolus* (Megerle von Mühlfeld, 1816) (Polygyridae; Fig. 3K)**

Origin: Southern North America (Pilsbry 1940; Hubricht 1985).

First record for the Western Palaearctic Region: Spain, 2011 (Navarro Barrachina et al. 2012).

Western Palaearctic distribution (Suppl. material 1, Fig. 2): Cyprus, Egypt, Greece, Iraq, Italy, Kuwait, Libya, Spain, Tunisia, Turkey.

References for identification: Pilsbry (1940).

Remarks: *Polygyra cereolus* has been spread from southern North America into other continents only in the past decades: into Hawaii (Cowie 1996), Saudi Arabia (Neubert 1995, 1998), the United Arab Emirates (Feulner and Green 2003), Qatar (Al-Khayat 2010), the Lesser Antilles (Charles 2014) and the Greater Antilles (Charles and Lenoble 2020). It is also spreading northwards in the USA (compare Hubricht (1985) and GBIF.org (2022)). It has been intercepted on cargoes imported into the USA from Spain and Italy, as well as from Puerto Rico and the Dominican Republic long before introduced populations were recorded in these countries (Robinson 1999).

Timing of the introductions

Twenty-two land snail species have been introduced to the Western Palearctic Region and established outdoor populations there. There has been a continuous increase in the number of established alien species since the beginning of the 19th century (Fig. 5). The increase was slow in the 19th century and the first half of the 20th century and became exponential in the 1970s.

Latitudinal ranges of the established alien land snail species in the Western Palearctic and in their native region

The latitudinal mid-points of the Western Palaearctic ranges of established alien land snail species and of their native ranges are not significantly correlated. However, if *Naesiotus quitensis* is omitted, there is a significant correlation (Fig. 4, Table 1). The native range of this species at low latitudes in Ecuador implies that it is a tropical species. However, it lives at high altitudes in the Andes (1700–2400 m a.s.l.; Breure et al. (2022)), where the climate corresponds to the oceanic climate in Western Europe (Beck et al. 2018). The higher limit of the latitudinal ranges of 11 of the established alien species is higher in the Western Palaearctic than in their native region, whereas only a single species occurs in the Western Palaearctic at a latitude that is lower than the lower limit of its natural range. The ranges of ten alien species in the Western Palaearctic are entirely positioned within their native latitudinal limits. As upward shifts of the higher limits of the non-native ranges prevail, the latitudinal mid-points of the Western Palaearctic ranges also tended to be higher on average than those of the native ranges. The highest latitudinal limits of the ranges of the alien snails in the Western Palaearctic and of their native regions are significantly correlated, but their lowest limits and their latitudinal extents are

not (Table 1). The latitudinal ranges of the alien species in the Western Palearctic significantly increased with increasing time since the first record of introduction (Pearson, $r^2 = 0.621$, $p < 10^{-4}$, Fig. 4).

Discussion

Number and timing of introductions

The present compilation lists 22 land snail species that were introduced into the Western Palearctic Region from elsewhere and established outdoor populations there. As in many other taxa (Roques et al. 2009; Seebens et al. 2017), the number of established alien land snail species increased exponentially (Fig. 5). The dynamics of the introduction of alien species into the Western Palearctic Region is also demonstrated by the fact that only nine of the 22 established alien species were listed in the last comprehensive list of introduced species in Europe (DAISIE 2009). Ten species were only introduced after the publication of this list (three previously introduced species were not listed).

Origin and spread of alien species

Land snails, like most invertebrates (Roques et al. 2009), are usually introduced unintentionally as contaminants of commodities, often agricultural products or ornamental plants (Cowie and Robinson 2003). Thus, the number of introduced invertebrate species is usually correlated with trade volume (Kobelt and Nentwig 2008; Roques et al. 2009). The largest share of imports into the Western Palaearctic comes from East Asia, followed by North America (Kobelt and Nentwig 2008). This is reflected in the highest number of introduced invertebrate species also coming from East Asia, followed by North America (Kobelt and Nentwig 2008; Roques et al. 2009). In contrast, no land snail species from temperate East Asia has yet become established in the Western Palaearctic until now. The reason for the lack of successful immigrants from East Asia is unclear. Given that the largest share of established alien plants in Europe is from temperate Asia (van Kleunen et al. 2015), there were obviously many opportunities for the introduction of East Asian land snails. Thirteen of the 22 established alien land snail species came from North America or adjacent areas. Two were from the Australian region or neighbouring island groups. Only recently did six species from tropical Sub-Saharan Africa or the Oriental Region establish populations in human-modified habitats in North Africa and the Middle East. One species from high altitudes of the Andes of South America was also only recently recorded.

The establishment of outdoor populations of most of these introduced land snail species began at the western or southern rims of the Western Palearctic (Figs 1, 3). The first populations of five of the introduced species, three from North America (*Helicodiscus parallelus*, *Lucilla scintilla* and *Hawaiia minuscula*), but also the two from the Australian region (*Paralaoma servilis* and *Discocharopa aperta*), were reported from the Macaronesian Islands. Perhaps some of these introductions date back to the time

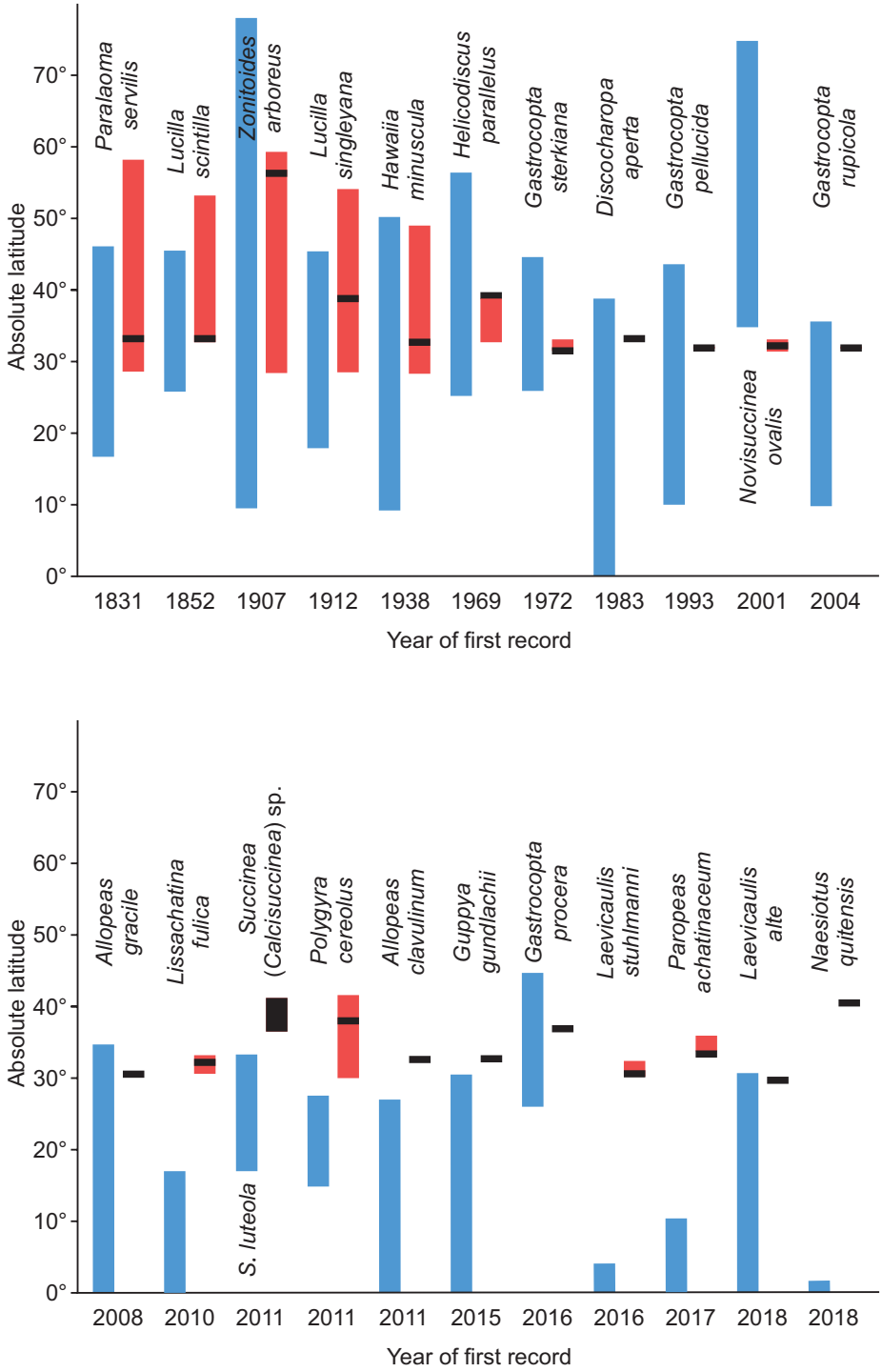

Figure 4. Comparison of the latitudinal distribution of established alien land snail species in their native range (blue) and in the Western Palaearctic Region (red), also showing the latitude at which a species was first recorded in the Western Palaearctic Region (black bar) and the year of the first record.

when the Macaronesian Islands were an important stop-over for sailing ships on their way to Europe. However, this may also be related to the higher susceptibility of island ecosystems to establishment of introduced species than mainland ecosystems (van Kleunen et al. 2015). The pattern of establishment changed in the second half of the 20th century. The first outdoor populations of 12 of the introduced species established during this period were found in North Africa and the Middle East, in Israel, Palestine, Egypt, Libya or Iraq. Israel become a hotspot of introduction. The reason may be the extensive economic trade between Israel and the USA and the transformation of large parts of the landscape of Israel into anthropogenic habitats and irrigated agricultural areas. The importance of Israel as a hotspot of introductions may be slightly exaggerated by the fact that there are malacologists in Israel who are able to record and recognise introduced species, whereas such expertise is lacking in many other countries in the Middle East and North Africa. Another recent pathway for the invasion of North American species into the Western Palearctic appears to be via Arabia. The North American species *Succinea* (*Calcisuccinea*) *luteola* and *Polygyra cereolus* were first recorded from the Arabian Peninsula (Neubert 1995, 1998; Feulner and Green 2003; Al-Khayat 2010) before *Succinea* (*Calcisuccinea*) sp. and *Polygyra cereolus* were found in the Mediterranean Region. The presumably Oriental *Allopeas gracile*, which is also widespread in southern North America, may also have been introduced into Iraq via Arabia. The introduction of these species could be due to the increased military and economic involvement of the USA in the region. In fact, Neubert (1995) supposed that *Polygyra cereolus* was introduced with military equipment from the USA for Operation Desert Storm at the beginning of the 1990s.

The change of the establishment patterns is correlated with the different ecology and origin of the naturalised species. Whereas most of the species introduced in the 19th century and the first half of the 20th century were temperate, mesophilic species, later more thermophilic species from southern North America arrived. These taxa established populations especially in warm, but often irrigated habitats in the Mediterranean. The newest arrivals are tropical species from Sub-Saharan Africa and the Oriental Region that can survive in the Mediterranean and Middle East outside greenhouses only in irrigated, anthropogenic habitats. This trend is probably favoured by climate change.

After their establishment at the periphery of the Western Palaearctic, many of the alien land snail species spread across Europe, usually from south to north and from west to east (Figs 1 and 3; with regard to the apparently exceptional *Zonitoides arboreus*, see remarks under the entry for this species). The continental climate in Eastern Europe is apparently challenging for alien land snail species, although large parts of North America, the main source area of the alien species, are also characterised by a continental climate. The lower levels of imports to Eastern European countries may also have contributed to the observed gradient, but can hardly explain that the gradient remained despite increasing trade between Western and Eastern Europe. A decreasing gradient of alien species towards Eastern Europe was also found in other invertebrate taxa (Roques et al. 2009: fig. 5.3).

Table 1. Correlations between mid-latitudes, highest and lowest latitudinal limits and latitudinal extents of the Western Palaearctic ranges of established alien land snail species and of their native ranges (considering absolute latitudes).

Correlations	r^2	p
Mid-latitudes	0.130	0.108
Mid-latitudes (without *N. quitensis*)	0.246	0.026
Highest latitudinal limits	0.197	0.044
Lowest latitudinal limits	0.003	0.810
Latitudinal extents	0.164	0.069

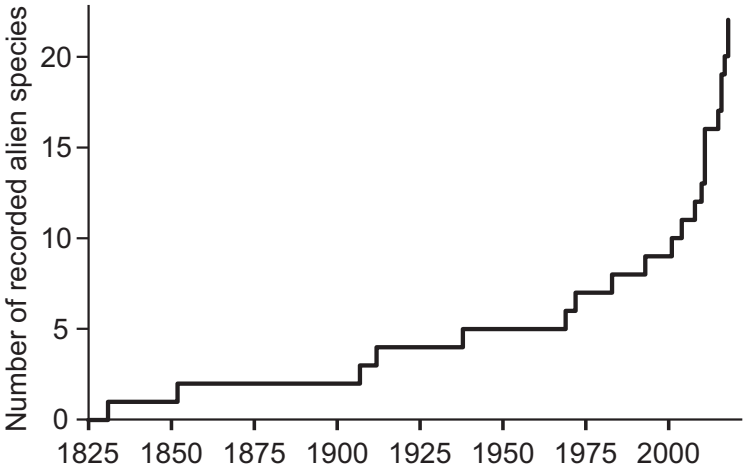

Figure 5. Cumulative number of recorded established alien land snail species in the Western Palaearctic Region.

The latitudinal ranges of the established alien land snail species in the Western Palearctic significantly increased with increasing time since the first record of introduction (Fig. 4). The latitudinal extent of their native ranges, a proxy for the ecological flexibility of the species, did not explain a significant part of the variation of the latitudinal extent of their ranges in the Western Palearctic (Table 1). This may indicate that many of the alien species have not yet colonised all the area that is potentially suitable for them rather than that their ecological requirements are irrelevant for invasion success.

The latitudinal mid-points of the Western Palaearctic ranges of established alien land snail species and of their native ranges are significantly correlated if *Naesiotus quitensis* is omitted (Fig. 4, Table 1) as in many other taxa (Guo et al. 2012). However, the latitudinal mid-points of the ranges in the Western Palaearctic tended to be higher than those of the native ranges on average. Eleven of the 22 alien species expanded into higher latitudes in the Western Palearctic than in their native region (Fig. 4). Such poleward shifts of ranges in the non-native region were found by Guo et al. (2012) for

several taxa on a global scale. Guo et al. (2012) discussed several possible mechanisms that may have contributed to such shifts. The main reason for the poleward shifts of the ranges of alien species in the Western Palaearctic is probably the arrangement of climate zones in the region, especially in comparison with eastern North America, the main source of the alien land snail species. Whereas subtropical and continental climate zones are latitudinally ordered in eastern North America, the arrangement of climate zones in Europe is more complicated (Beck et al. 2018). The oceanic climate of Western Europe allows species originating from the south to expand a long way north. On the other hand, species adapted to humid subtropical climates of south-eastern North America can hardly colonise similar latitudes in the Western Palaearctic where a much drier Mediterranean climate or even a desert climate prevails. Based on the observation that, on average, alien species have become naturalised at significantly lower latitudes on islands than on continents, Sax (2001) hypothesised that low latitude boundaries are usually set by biotic pressures. However, this is not the case in the Western Palaearctic where abiotic conditions, namely the aridity of the Mediterranean and the desert belt at the southern rim of the Western Palaearctic, are the main cause of the low latitude boundaries of the majority of alien as well as native species. Although the temperatures in the Mediterranean and the desert climate zones may be suitable for snails from the subtropical or even tropical climate zones, they can only colonise localities that are characterised by unusual high humidity. For example, *Guppya gundlachii* from Florida and Central America colonised artificially irrigated anthropogenic habitats in Israel. Similar habitats could also be colonised by tropical species like the *Laevicaulis* species and the giant African snail *Lissachatina fulica* from Sub-Saharan Africa. Thus, there are three reasons for the average poleward shifts of the ranges of alien land snail species in the Western Palaearctic compared to their native ranges (Fig. 4): (1) the northward expansion of some species in Western Europe facilitated by the oceanic climate, (2) the impediment to the colonisation of southern latitudes occupied in North and Central America due to the aridity in the southern Western Palaearctic and (3) the establishment of tropical species in artificially irrigated anthropogenic habitats in the Mediterranean and the Middle East north of their native ranges.

Potential impacts of established alien species

The land snail species that have been introduced to the Western Palearctic Region from elsewhere are generally restricted to anthropogenic habitats like most other introduced invertebrates (Roques et al. 2009). None of them is carnivorous. None of them is known to cause ecological damage or to be a pest in the field. *Zonitoides arboreus* is reportedly a pest of potted ornamental plants, which it damages especially by feeding on the roots (Godan 1983; Hollingsworth and Armstrong 2003). In the same way, it may cause root rot of sugar cane (Rands 1924). This may become a problem in greenhouses and plant nurseries where *Zonitoides arboreus* may become abundant. However, field populations of this species are rare and there are no reports of damage caused by it in the Western Palaearctic. Most of the alien snail species in the Western

Palaearctic are minute or small and are unlikely to cause serious economic damage. In contrast, the African *Laevicaulis* slugs, which were recently introduced to Egypt and Libya (Ali 2017a, b; Ali and Robinson 2020; Liberto et al. 2021) and the giant African snail *Lissachatina fulica*, may become pests in greenhouses and irrigated agricultural areas in the Mediterranean and the Middle East and should be extirpated or a least controlled. This is especially true for *Laevicaulis alte* and *Lissachatina fulica*, which have been spread globally in the tropics by humans (Robinson 1999). *Laevicaulis alte* and *Lissachatina fulica* were amongst the species with the highest negative total impacts in an assessment of alien land snails and slugs in Indonesia (Nurinsiyah and Hausdorf 2019) and also ranked high in an assessment of quarantine significance, based on the potential to damage natural ecosystems, agriculture or human health or commerce in the USA (Cowie et al. 2009).

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Supplementary material 1

Supplementary file

Author: Bernhard Hausdorf

Data type: Occurrences (Excel document).

Explanation note: Distribution of established alien land snail species in the Western Palaearctic Region. For each country to which a species has been introduced, the year of first record of outdoor populations (if not known, the year of first reference) and the reference are given. The author has no funding to report. The author has declared that no competing interests exist.

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RESEARCH ARTICLE

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Advancing research on alien species and biological invasions

Evidence of plant-soil feedback in South Texas grasslands associated with invasive Guinea grass

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Abstract

Plant-soil feedback (PSF) processes play an integral role in structuring plant communities. In native grasslands, PSF has a largely negative or stabilizing effect on plant growth contributing to species coexistence and succession, but perturbations to a system can alter PSF, leading to long-term changes. Through changes to soil abiotic and biotic properties, invasion by non-native plants has a strong impact on belowground processes with broad shifts in historical PSFs. Guinea grass, *Megathyrsus maximus*, an emerging invasive in South Texas, can efficiently exclude native plants in part due to its fast growth rate and high biomass accumulation, but its impacts on belowground processes are unknown. Here, we provide a first look at PSF processes in South Texas savannas currently undergoing invasion by Guinea grass. In this pilot study, we addressed the question of how the presence of the invasive *M. maximus* may alter PSF compared to uninvaded grasslands. Under greenhouse conditions, we assessed germination and growth of Guinea grass and the seed bank in soil collected from grasslands invaded and uninvaded by Guinea grass. We found that Guinea grass grown in soil from invaded grasslands grew taller and accumulated higher biomass than in soil from uninvaded grasslands. Plants grown from the seed bank were more species rich and abundant in soil from uninvaded grasslands but had higher biomass in soil from invaded grasslands. In South Texas savannas, we found evidence to support shifts in the direction of PSF processes in the presence of Guinea grass with positive feedback processes appearing to reinforce invasion and negative feedback processes possibly contributing to species coexistence in uninvaded grasslands. Future work is needed to determine the mechanisms behind the observed shifts in PSF and further explore the role PSF has in Guinea grass invasion.

Keywords

bulk soil, grassland, Guinea grass, invasive species, *Megathyrsus maximus*, *Panicum maximum*, plant-soil feedback, South Texas

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Introduction

Invasive species are an increasingly widespread concern due to their negative impacts on ecosystems and difficulty in controlling their spread (Assessment 2005; Pyšek and Richardson 2010). Invasion by non-natives reduces plant diversity and extreme cases can result in monodominant plant stands and subsequent declines of wider biodiversity (Assessment 2005; Dogra et al. 2010). At the ecosystem level, invasion disrupts nutrient cycling, disturbance regimes, and microbial communities above- and belowground with some changes persisting for decades (Hawkes et al. 2005; D'Antonio and Flory 2017). A difficulty we face in predicting and preventing invasions is that the outcome of an introduction is largely context dependent, varying with initial plant density, life history, and dispersal traits of the invasive plant (Suding et al. 2013). To address this variability, more examples of invasion need to be studied to discern overarching patterns and to inform management opportunities for distinct invasive species and geographical locations.

By modifying the abiotic and biotic qualities of their soil environment, plants can influence the establishment and growth of subsequent generations of plants within that same soil environment in a process termed plant-soil feedback (PSF) (Bever 1994; Bennett and Klironomos 2019). PSF effects both conspecific and heterospecific plants with three possible outcomes: a) positive feedback through increasing establishment, growth, and/or fitness; b) negative feedback by inhibiting establishment, growth, and/or fitness; or c) neutral in which plant function is not impacted by modifications to the soil environment (Bennett and Klironomos 2019). Additionally, the response of individual species within the plant community is species-specific with both positive and negative PSFs present simultaneously. In native grasslands, PSF has a largely negative or stabilizing effect on plant growth which contributes to species coexistence and succession through negative-density dependent processes (e.g. competition, pathogens, herbivory) (Kulmatiski et al. 2008; Hawkes et al. 2013; Lekberg et al. 2018). Changes to plant community composition as those seen during invasion (Reinhart and Callaway 2006; Hawkes et al. 2013; Zhang et al. 2019; Fehmi et al. 2021) can impact subsequent plant growth, reducing native plant establishment and disrupting historical PSF processes in native communities (see Belnap et al. 2005; Hawkes et al. 2005; Wolfe and Klironomos 2005; Batten et al. 2006; Levine et al. 2006). PSF studies are increasing in frequency, but only about 46% (32 of 69) of studies have looked at non-native species; of these, 65% (21 of 32) focused on grasses with only 23 genera and 34 species within Poaceae represented (Crawford et al. 2019). Although some species of Poaceae become effective and widespread invaders, others fail to establish or only establish locally, but are unsuccessful at expanding their range. Non-native grasses weaken the negative PSF processes that dominate native grasslands, indicating that this could be a contributing factor in invasion success (Crawford et al. 2019), but studies on a wider range of non-native grasses, including both noxious invaders and naturalized species, need to be conducted to understand this pattern and what drives this shift.

In South Texas, Guinea grass, *Megathyrsus maximus* (Jacq.) B.L. Simon and Jacobs, is emerging as a problematic invasive (CABI 2021). A perennial bunchgrass native to Africa, Guinea grass has been introduced in tropical areas globally as a pasture grass due to its fast growth, high biomass accumulation, and stress tolerance, but these same traits also make it a successful invader (Rhodes et al. 2021a). For instance, the fast growth rates and high biomass accumulation of Guinea grass results in displacement of many native species through direct competition for space and resources (Ho et al. 2016). After senescence, native seedling germination is restricted directly by a thick layer of Guinea grass litter (Rhodes et al. 2021a), but native plant regeneration is also reduced in areas without a litter layer or where Guinea grass has been removed previously (pers. obs). This could indicate factors other than direct shading are inhibiting native plant germination and growth. A study conducted in Hawaii comparing establishment of natives from seeds versus transplants after removal of Guinea grass found that transplants had higher rates of establishment than seeds (Ammondt et al. 2013). When compared to rates of germination under greenhouse conditions, rates in the field were approximately 30 times lower (Ammondt et al. 2013). Research into methods to control Guinea grass invasion have focused on removal of Guinea grass with herbicides, burn treatments, and grazing followed by reintroduction of natives from seeds or out-plantings, but results have been mixed (Ramirez-Yanez et al. 2007; Ammondt and Litton 2012; Ammondt et al. 2013; Ellsworth et al. 2015). If Guinea grass does alter PSF processes toward a positive feedback for conspecifics, the reestablishment of native plants could be hindered even when Guinea grass is removed prior to plantings (Reinhart and Callaway 2006). Although soil microbes are known to impact seed germination and survival which could slow the recovery of native communities (Zalamea et al. 2015; Sarmiento et al. 2017), the effect of PSF on germination from the seed bank has received little attention.

Our goal was to assess the study system in South Texas for evidence of PSF in grasslands invaded and uninvaded by Guinea grass specifically addressing the question: how does the presence of invasive Guinea grass alter PSF compared to uninvaded grasslands? Overall, aboveground contributions to the high competitive ability of Guinea grass are well documented (Ammondt and Litton 2012; Ho et al. 2016; D'Antonio and Flory 2017; Rhodes et al. 2021a, b), but little is known about how Guinea grass impacts belowground processes (but see Chou and Young 1975) and what role this may have in facilitating invasion. Conducting a greenhouse study using whole soil from invaded and uninvaded grasslands, we hypothesized that germination and growth of Guinea grass would be higher in soil from invaded grasslands than soil from uninvaded grasslands. In contrast, plants from the seedbank would not experience a similar increase in germination and growth in soil from invaded grasslands possibly due to inhibition by Guinea grass (Chou and Young 1975). In uninvaded grassland soils, growth and germination of the seedbank and Guinea grass will be lower than in soils from invaded areas, but species richness of plants from the seedbank would be higher than in soils from invaded sites possibly indicating the presence of negative PSF processes in uninvaded grasslands (Kulmatiski et al. 2008; Hawkes et al. 2013; Lekberg et al. 2018). This is

the first study to assess PSF processes in South Texas savannas and to address whether PSF may be playing a role in Guinea grass invasion. Our research provides a baseline for understanding the role of PSF in Guinea grass invasion into native ecosystems.

Methods

To test our hypotheses, we conducted a greenhouse experiment that used soil collected in August 2020 from grasslands invaded by Guinea grass, *Megathyrsus maximus*, and uninvaded grasslands in Kleberg County, Texas (27.433, -97.67). Here in its unmanipulated state, grasses form the matrix of a savanna punctuated by clumps or mottes of diverse shrubs and low trees dominated by mesquite (*Prosopis glandulosa*). The area receives on average 73.6 cm of rain per year (Weather Service). Sampled grasslands were located between 4 to 8 km apart, spanning an area of approximately 5.5 km^2. Soil from the three sites sampled in this study was composed predominantly of sand (mean 92% ± 1.8%) with minor amounts of silt and clay (mean 5.7% ± 0.8% and 2.3% ± 1.5%, respectively). Two of the sample sites were in grasslands that had remained intact at least since the 1980's, while the third site had been mechanically treated in 2000 to partially remove encroaching mesquite (Suppl. material 1). These grasslands are grazed annually with occasional prescribed burns.

Sampling and experimental design

Within each of three sites, we sampled soil from plots invaded by Guinea grass and uninvaded plots (i.e., predominantly native with no Guinea grass present) (n = 6) that were located within 10 m of each other to minimize the confounding effects of distance on soil microbial communities or soil traits (Suppl. material 1). We collected two sets of soil from invaded and uninvaded sites: a) bulk live soil for use as the growth medium from each site and b) soil for use as a supplemental inoculum. For both sets of soil, we removed the litter layer and excavated the soil using a hand trowel to a depth of 15 cm. Bulk soil was collected from two locations in each plot and pooled. For the inoculum, we collected five soil cores from each plot with individual cores located approximately 1 m apart. The inoculum soil was collected individually in plastic bags and stored in a 4 °C fridge. Bulk soil was stored at room temperature in a climate-controlled building (~20–22 °C). Within one week of collection, we sieved all the soil (i.e., bulk soil and inoculum) using a 2 mm soil sieve to remove leaf litter and plant roots. Between each use, the sieve was sterilized with 0.5% NaOCl for five minutes, washed with tap water, and allowed to air dry.

For our experiment, we chose to use bulk soil due to concerns that autoclaving impacts soil nutrient availability and composition/abundance of microbial communities. To confirm the effect autoclaving has on soil nutrient availability, we conducted a small assessment on soil nutrients in the bulk soil pre-autoclaving and after two autoclave times (30 minutes and 60 minutes). We found that autoclaving increased levels of phosphorus, sulfur, sodium, and electrical conductivity with autoclave time (ANOVA results in Suppl.

material 4, also see Skipper and Westermann 1973; Tuominen et al. 1994). Studies on the effect of autoclaving on microbial communities demonstrate that sterilization is incomplete with a subset of the fungal and bacterial communities persisting (Skipper and Westermann 1973; Tuominen et al. 1994; Bárcenas-Moreno et al. 2011). Therefore, we did not autoclave the soil to limit the influence of these confounding factors (see Discussion).

Since we were unable to refrigerate the bulk soil due to its large quantity, we added inoculum that was kept at 4 °C to counter any changes in the microbial community in the bulk soil. For this, we created two sets of inoculums: a pooled inoculum referred to hereafter as a mixed soil sample (MSS) and an unpooled inoculum referred to as an individual soil sample (ISS). To create the MSS inoculum, we pooled inoculum at a 1:1 ratio based on soil origin (invaded or uninvaded grasslands) for each of the three sites to create a common inoculum that was applied to replicates (n = 6 inoculum pools used for MSS treatments). For ISS inoculum, we used distinct (i.e., unpooled) soil cores for each replicate.

For the experiment, treatments included soil origin (invaded grassland, uninvaded grassland) and soil handling method (ISS, MSS). Each cross was replicated five times with soil from three separate sites (20 samples per site, 60 samples total). We filled black plastic pots (2.4 L) with the same amount of unautoclaved bulk soil (2640 g) and then added the additional soil inoculum (3% mass: mass; 79.2 g) to each pot (Van Der Putten et al. 2007b). Pots were randomized in the greenhouse to account for potential variation in temperature and lighting. We matched the bulk soil and the inoculum by soil origin (site and invasion status), i.e. MSS and ISS inoculum treatments from invaded sites were added to bulk soil also from the same invaded site. A soil sample from each of the treatments were submitted for nutrient analysis at the Texas A&M AgriLife Extension Service Soil, Water, and Forage Testing Laboratory. Soils were analyzed for pH, nitrate, phosphorus, potassium, electrical conductivity, calcium, magnesium, sodium, and sulfur (Schofield and Taylor 1955; Mehlich 1984; Rhoades 1984).

In each pot, we sowed approximately 0.015 g of Guinea grass seed collected from the same area and time in South Texas. Although we were unable to quantify the seed bank, we used the same amount of soil in each pot to normalize the seed bank. During the sieving process, we homogenized the bulk soil based on site and soil origin as described above, then placed the same amount of bulk soil and inoculum as stated above into each pot. We visually assessed the sieved litter for seeds to ascertain whether larger seeds were removed during soil sieving (i.e. size sorting of seeds), but noted only plant leaves and roots in the material were removed during sieving.

Germination and growth of Guinea grass

After three weeks, we counted the total number of Guinea grass seedlings and thinned them to a single seedling per pot. At this stage the seedlings were approximately 5 cm tall and could be identified as Guinea grass. After this point, any new Guinea grass that emerged was counted and then removed from the pot. We monitored growth of these seedlings over the course of the experiment (14 weeks), after which plants were carefully removed from pots to keep as much of the root intact as possible. We measured the

plant height at the end of the experiment, then separated the aboveground tissue from roots at the root collar and placed both in a drying oven at 65 °C for 3–5 days in labeled paper bags. We measured the dry weight of both above- and below-ground tissue.

Germination and growth of seed bank

We monitored the total number of plant seedlings sprouting from the seed bank weekly. At the end of the experiment, we counted the number of plants present within each pot noting how many were monocots and dicots. We were unable to identify seedlings to species as the plants were juveniles and did not have flowering structures. Therefore, to quantify species richness, we used phenotypic differences to distinguish morphospecies within each pot (hereafter, referred to as species richness) (Benítez-Malvido and Martínez-Ramos 2003; Martini et al. 2021). We acknowledge that using phenotype to delimit species has limitations due to underestimating (Derraik et al. 2002, 2010) or overestimating (Arnold et al. 2007) species richness. To control for this, a single person familiar with plant identification assessed all pots. To measure dry weight (total biomass) of the seedbank community, we placed above- and belowground tissue in drying ovens at 65 °C for five days before weighing. Plants germinating from the seed bank were monitored in the same pots as Guinea grass. We chose this experimental design (germination in same pot as planted Guinea grass) as this more closely mimics field conditions by hopefully overcoming some of the limitations seen in greenhouse studies of PSF (see Heinze et al. 2016; Forero et al. 2019), although a side-by-side comparison of same pot and separate pot studies would be informative.

Statistical analyses

All statistical analyses were conducted in R and code is available for reproducibility. All data and scripts used for analyses are available on GitHub (eabowman/Bowmanetal-STexasGuineaGrass-PlantSoilFeedback) or at https://doi.org/10.5281/zenodo.7487382. To assess the effect of soil origin (invaded or uninvaded grasslands) and soil handling method on Guinea grass growth and germination, we used a mixed effect model to analyze germination, height, root length, and dry biomass. We treated soil origin and soil handling method as fixed variables and site as a random variable. We considered Guinea grass germination rate as the total number of seedlings and did not normalize this number as we used the same mass of seeds (0.015 g) per pot. We evaluated all data for normality and homogeneity of variance prior to analysis. Germination, height, and biomass data were log-transformed prior to analysis. Three pots had no Guinea grass growth and were removed from analyses.

The effect of soil origin and soil handling method on germination and growth of the seedbank plant community was also assessed using mixed-effects models as above. Here we also treated germination as the total number of seedlings that germinated as the amount of bulk soil and inoculum used was the same across all treatments and replicates. As above, all data were assessed to see if they met the assumptions for parametric analysis. Germination counts and plant abundance were log-transformed prior to analysis, whereas species richness and biomass were transformed using the formula log (x + 1).

To assess for differences in soil characteristics as a function of invasion, we used a t-test and included only data from unautoclaved soil (n = 6 samples; 3 from invaded sites and 3 uninvaded sites). Electrical conductivity, phosphorus, and sulfur were log transformed prior to analysis.

Results

Effect of soil origin (invaded and uninvaded grasslands)

We found a significant difference in Guinea grass growth between invaded and uninvaded sites (Fig. 1; Table 1). Height, root length, and biomass of Guinea grass were higher when grown in soil from invaded sites (height: 46.6 cm ± 17.4; root length: 14.1 cm ± 4.2; biomass: 0.8 g ± 0.7) versus uninvaded sites (height: 22.1 cm ± 8.3;

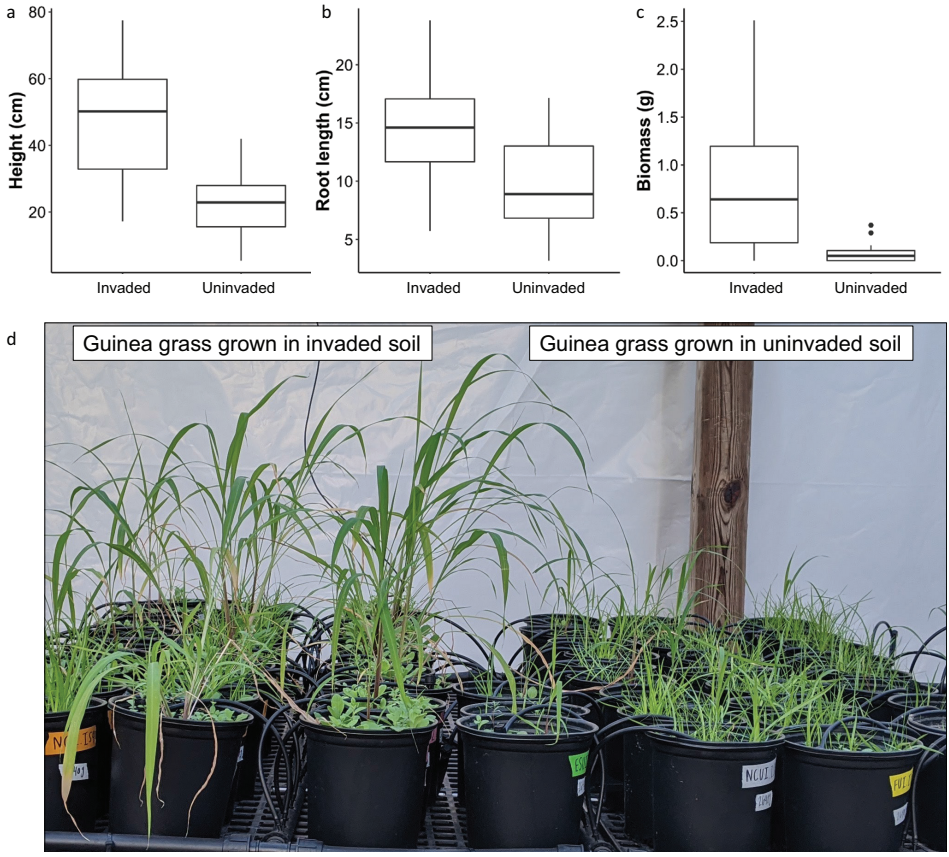

Figure 1. Guinea grass height (**a**), root length (**b**), and biomass (**c**) when grown in soil collected from i) grassland invaded by conspecifics and ii) uninvaded grasslands dominated by native species. Experimental pots (**d**) after 14 weeks with larger Guinea grass in soil from invaded grasslands (left). All data shown are non-transformed.

root length: 9.8 cm ± 4.2; biomass: 0.01 g ± 0.1). Germination of Guinea grass did not differ in invaded or uninvaded soil (Table 1), but germination within the first week was higher in soil from invaded sites ($F_{1,54}$ = 6.86, p = 0.0114; Suppl. material 2: fig. S2a). Within the first week, average germination of Guinea grass in invaded soil was 4.1 ± 4.4 seedlings compared to 1.9 ± 2.3 in soil from uninvaded sites.

Plant abundance and species richness of plants from the seed bank were significantly higher in soil from uninvaded sites than invaded sites (Fig. 2; Table 2). Average plant abundance was 54 ± 21 in uninvaded soil and 41 ± 17 in invaded soil, and average species richness was 8 ± 2 species versus 6 ± 2, respectively. Seedling germination overall was higher in uninvaded sites (Fig. 2; Table 2), but when we looked at seedling germination within the first week, we found that seedling germination was initially higher in soil from invaded sites ($F_{1,54}$ = 32.74, p < 0.0001; Suppl. material 2: fig. S2b). The seedbank community had higher total biomass (mean 1.3 g ± 0.4) in soil from invaded sites than uninvaded sites (mean 0.6 g ± 0.3) (Fig. 2; Table 2). When we broadly separated plants from the seedbank into dicots and monocots, we found that monocots had significantly higher species richness and abundance in soil from uninvaded sites than invaded sites (species richness: Kruskal-Wallis X^2_1 = 13.4 , p = 0.0002; plant abundance: Kruskal-Wallis X^2_1 = 18.1, p < 0.0001; Fig. 3). Dicots showed no difference.

Effect of soil handling method

Guinea grass germination, seedbank plant abundance, and total biomass of the seedbank plant community showed significant differences between the two soil handling methods we tested. Soil handling method significantly influenced Guinea grass

Table 1. Results of ANOVA mixed effect model to assess the effect of soil origin (invasion status) and soil handling method on Guinea grass germination and growth. Seedling count is the total seedling number of seedlings in the first three weeks.

	Soil origin		Soil handling method		Interaction	
	$F_{1,51}$	p	$F_{1,51}$	p	$F_{1,51}$	p
Seedling count	0.71	0.4057	7.20	0.0098	2.44	0.1245
Height	38.60	< 0.0001	0.98	0.3278	0.00	0.9789
Root length	14.55	0.0004	0.20	0.6601	0.39	0.5350
Biomass	31.22	< 0.0001	0.08	0.7852	0.03	0.8740

Table 2. Results of ANOVA mixed effect model to assess the effect of soil origin (invasion status) and soil handling method on germination and growth of plants from the seedbank. Seedling count here is the total seedling number of seedlings in the first three weeks.

	Soil origin		Soil handling method		Interaction	
	$F_{1,51}$	p	$F_{1,51}$	p	$F_{1,51}$	p
Seedling count	49.31	< 0.0001	0.14	0.7116	4.52	0.0382
Plant abundance	9.05	0.004	5.57	0.0219	3.09	0.0843
Total biomass	51.65	< 0.0001	4.26	0.0439	0.10	0.7539
Species richness	4.52	0.0382	0.02	0.8877	0.08	0.7850

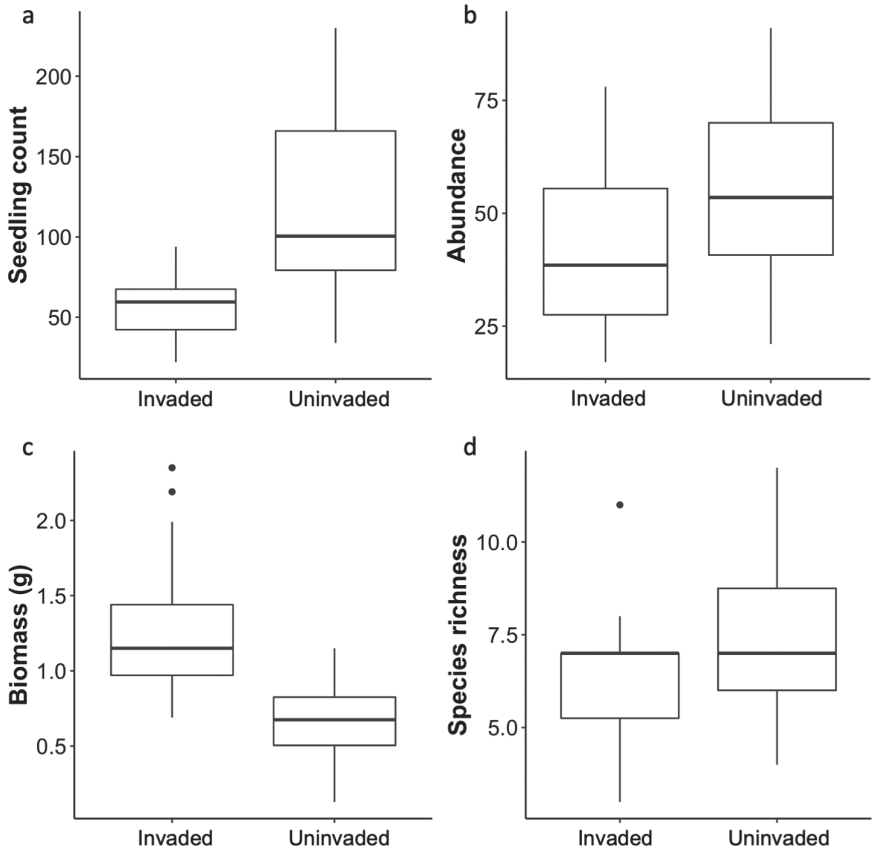

Figure 2. Seedling count (**a**), abundance (**b**), biomass (**c**), and species richness (**d**) of plants which emerged from the seedbank in soil from Guinea grass invaded and uninvaded grasslands. All data shown are non-transformed.

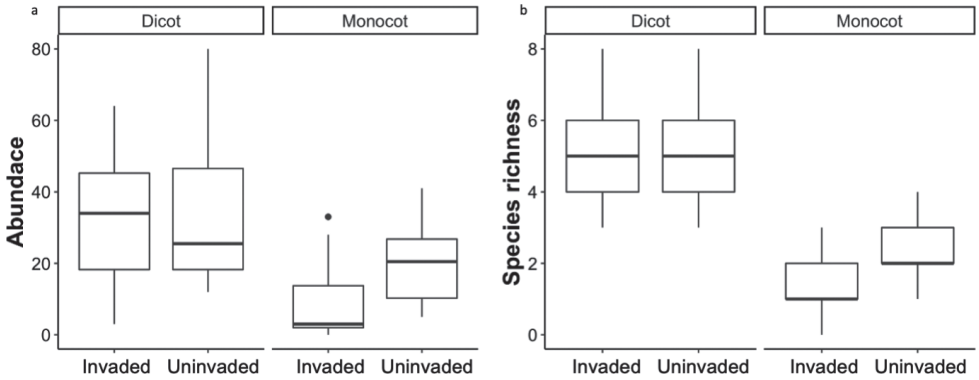

Figure 3. Plant abundance (**a**) and species richness (**b**) as a function of invasion and plant group. Monocot species richness and plant abundance were significantly higher in soil from uninvaded sites than invaded sites (species richness: Kruskal-Wallis $X_1^2 = 13.4$, $p = 0.0002$; plant abundance: Kruskal-Wallis $X_1^2 = 18.1$, $p < 0.0001$), whereas species richness and abundance of dicots showed no difference. All data shown here are non-transformed.

germination with MSS treatments having higher germination (mean 21 ± 15) than ISS treatments (mean 12 ± 11) (Suppl. material 3; Table 1). Within the seedbank plant community, plant abundance and total biomass were higher in ISS treatments (plant abundance: mean 53 ± 21; total biomass: mean 1.04 ± 0.5) than MSS (plant abundance: mean 43 ± 17; total biomass 0.85 ± 0.5) (Fig. 2; Table 2).

Soil nutrients

We found no significant difference between soil nutrients in invaded and uninvaded sites, although some nutrients trended higher in invaded sites (Fig. 4; Suppl. material 5).

Discussion

Our experiment presents initial and novel data on PSF processes in the mesquite savannas in South Texas, the impact of Guinea grass invasion on PSF in uninvaded grasslands, and the response of seedbanks to shifts in PSF. In line with our hypothesis, Guinea grass grew taller and accumulated more biomass when grown in soil from invaded grasslands than soil from uninvaded grasslands consistent with a positive PSF on conspecific plants post-invasion (Fig. 1, Table 1). In contrast, plants germinating from the seed bank had

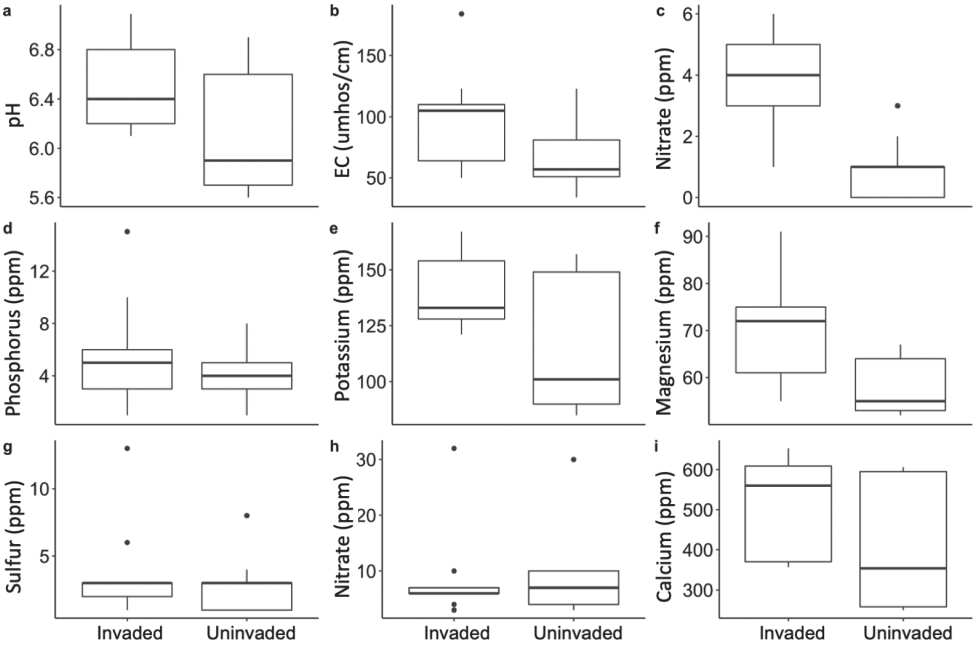

Figure 4. Soil characteristics as a function of invasion. None of the soil characteristics were significantly different based on soil origin although in general soil nutrients and characteristics were higher in soil from invaded sites. All data shown here are non-transformed. EC is electrical conductivity.

higher species richness (delimited based on plant morphology) and abundance in soil from uninvaded grasslands consistent with negative feedback processes (Kulmatiski et al. 2008; Hawkes et al. 2013; Lekberg et al. 2018). If negative PSF is present in uninvaded grasslands then the observed decrease in species richness and increase in biomass accumulation of plants from the seedbank in invaded grasslands indicates a possible release from negative feedback processes (Fig. 2, Table 2). Interestingly, we found evidence of a broad phylogenetic signal in the response of monocots and dicots to invaded and uninvaded soil (Fig. 3) indicating that Guinea grass may have a stronger inhibitory effect on more closely related plant species. These results suggest the presence of distinct patterns of PSF in invaded and uninvaded grasslands in South Texas with evidence of positive PSF on Guinea grass in invaded grasslands that reinforces invasion and an overall negative PSF in uninvaded grasslands that could slow invasion.

For a non-native to be a successful invader, it needs to be able to colonize, establish, and disseminate to new environments (Theoharides and Dukes 2007). During colonization, seed germination requires both an appropriate climate and soil conditions, such as texture, nutrients, and microbial community (Theoharides and Dukes 2007; Sarmiento et al. 2017). Despite no difference in climate or soil texture and no statistical difference in soil nutrients, we observed faster initial germination of Guinea grass and the seed bank (Suppl. material 2) in invaded soil, possibly indicating an effect of the soil microbial community on germination. For instance, a low abundance of seed pathogens in the invaded soil can release seeds from negative density dependence processes found in native grasslands (Gilbert and Parker 2006; Halbritter et al. 2012). Ultimately, germination of Guinea grass was not different between the two soil types but was higher overall than we would have expected as, in our observations, Guinea grass has a low germination rate in grasslands (Rhodes et al. 2022). In contrast, germination from the seedbank was higher in uninvaded grasslands which could indicate a low abundance of seed pathogens or conversely higher propagule pressure in these sites. It would be expected that with increasing invasion time, there would be a decrease in native seeds in the seedbank (Robertson and Hickman 2012), but we expect this difference to be small as our invaded and uninvaded plots bordered each other (within 10 m) indicating a relatively short time since invasion and allowing for the introduction of seeds from nearby uninvaded areas.

After germination, the successful establishment of non-native plants is reliant on their fast growth rate, competitive ability with native plants, and efficient resource usage (Theoharides and Dukes 2007). The fast growth rate of Guinea grass has been noted (Rhodes et al. 2021a), but here we show that the presence of Guinea grass in invaded areas further increased its growth and biomass accumulation. This result, in combination with the observed higher biomass of all plants from the seedbank in soil from invaded grasslands, suggests that either the microbial community or soil nutrients play a role in re-enforcing invasion. Although soil nutrients were marginally higher in invaded soil than in uninvaded soil (Fig. 4, Suppl. material 5), these differences were not statistically significant. Invasion is generally found to be associated with shifts in nutrient availability and cycling (reviewed in Ehrenfeld 2003; Sardans et al. 2017). Since our samples number was quite small (n = 6, 1 sample per treatment

combination), we think a deeper exploration of soil is warranted to fully rule out soil nutrients as a contributing factor.

Invasion has been shown to impact multiple functional guilds within soil microbial communities through several pathways (e.g. phytochemicals, litter inputs) thus altering community processes (reviewed in Wolfe and Klironomos 2005; Reinhart and Callaway 2006; Van Der Putten et al. 2007a). Shifts in soil communities by invasive species can indirectly cause alterations in nutrient cycling by supporting decomposers and rhizosphere mutualists (Zhang et al. 2019). Plant-associated microbes can directly influence the ability of non-natives to invade native ecosystems (Rudgers et al. 2005). Additionally, the enemy release hypothesis posits that movement of plants to novel environments causes a decrease in negative pressures from pathogens, herbivores, and parasites found in their home range (Keane and Crawley 2002). Although we did not sterilize our bulk soil and added only 3% of the supplemental inoculum, we were able to see differences based on our handling of the supplemental inoculum. The observed effect of our soil handling methods supports a possible difference in the microbial communities in invaded and uninvaded grasslands. Guinea grass germination was higher in treatments where soils were pooled and homogenized (MSS) than treatments that were kept distinct (ISS), but abundance and biomass of plants from the seedbank was higher in ISS than MSS (Suppl. material 3). These results could indicate that the plant community is influenced strongly by localized soil microbial communities that are overwhelmed by the wider community upon pooling (e.g. due to rareness or competitive ability) (Batten et al. 2006; Mummey and Rillig 2006; Rúa et al. 2016). Although we did not assess microbial community composition in this study, differences between the soil handling methods could be influenced by shifts in the relative abundance of particular community members after pooling inocula or specificity of PSF effects on native versus non-native plant species (Brinkman et al. 2010; van de Voorde et al. 2012). As part of ongoing research, we are evaluating soil microbial communities, litter decomposition rates, and levels of soil nutrients across invasion and disturbance types to assess changes in the soil environment more fully.

Another possible contributing factor, not considered in this study, is allelopathy. Invasion of non-native plants may cause cascading effects on conspecific native species through allelopathy as examples of the novel weapons hypothesis (Callaway and Ridenour 2004). Allelochemicals can directly impact fitness of native species or indirectly through conditioning of the soil microbial community, such as has been shown with *Centaurea diffusa* (Callaway et al. 2004; Wolfe and Klironomos 2005). Allelopathic effects have been found to decrease with increasing phylogenetic distance (Zhang et al. 2021), such that species of monocots should be more negatively impacted than dicots in grasslands invaded by Guinea grass. When we assessed differences in the effect of PSF on monocots and dicots, monocot species richness and plant abundance were higher in soil from uninvaded sites than invaded sites, whereas dicots showed no difference (Fig. 3). These results indicate that in invaded grasslands monocot species that are more closely related to Guinea grass phylogenetically do experience a negative feedback. These results raise interesting questions such as whether negative PSF is driving species coexistence in uninvaded communities, whether the switch to an overall positive feedback mechanism in invaded grasslands is due to nutrient availability, and whether allelopathy or patho-

gen accumulation is suppressing other monocot species post-invasion. In our ongoing research, we aim to parse out the effect of Guinea grass invasion on soil nutrients, allelopathy, and soil microbial communities to better understand how Guinea grass impacts PSF processes and how this varies across the heterogeneous landscapes of South Texas.

Conclusions and future directions

In this initial study, we found evidence that the presence of Guinea grass alters PSF for con- and heterospecific plant species indicating that Guinea grass could reinforce through positive feedback processes. Negative PSFs in uninvaded grasslands were associated with higher species richness and abundance of the plants in the seedbank possibly contributing to species coexistence in native grasslands. We found evidence to suggest that positive PSFs observed in invaded grasslands could be reinforcing establishment of Guinea grass, although the mechanism needs to be explored further. Our results represent the first time PSF processes have been studied in South Texas savannas and show how Guinea grass, an emerging invasive within the southern United States, influences these processes reinforcing its own invasion.

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Supplementary material 1

Soil sampling sites showing extent of Guinea grass patch (white boundary, I) and adjacent uninvaded grassland (N) with nearby mesquite tree mottes. Google Earth Imagery date 1/13/2014. Scale bar 70m.

Authors: Elizabeth A. Bowman, Robert M. Plowes, Lawrence E. Gilbert

Data type: figure

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Link: https://doi.org/10.3897/neobiota.81.86672.suppl1

Supplementary material 2

Initial germination of Guinea grass seed (a) and the seedbank (b) during week 1 was higher in soil from invaded sites than uninvaded sites. All data shown here are non-transformed.

Authors: Elizabeth A. Bowman, Robert M. Plowes, Lawrence E. Gilbert

Data type: figure

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Supplementary material 3

Effect of soil handling method on Guinea grass seedling count (a), native community plant abundance (b), and native community biomass (c). MSS: mixed soil sampling; ISS: individual soil sampling. All data shown are non-transformed.

Authors: Elizabeth A. Bowman, Robert M. Plowes, Lawrence E. Gilbert

Data type: figure

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Supplementary material 4

Results of one-way ANOVA examining the effect of autoclave time on soil characteristics. Electrical conductivity, phosphorus, and sulfur were log-transformed prior to analysis.

Authors: Elizabeth A. Bowman, Robert M. Plowes, Lawrence E. Gilbert

Data type: table

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Supplementary material 5

Results of t-test examining differences in soil characteristics between invaded and uninvaded sites. Electrical conductivity, phosphorus, and sulfur were log-transformed prior to analysis.

Authors: Elizabeth A. Bowman, Robert M. Plowes, Lawrence E. Gilbert

Data type: table

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BOOK REVIEW

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Book Review: On ecological networks and biological invasions

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Invading Ecological Networks by Cang Hui and David M. Richardson, Cambridge University Press, 2022. 423 pp. hbk.: US$115.00, ISBN 9781108478618; pbk.: US$ 49.99, ISBN 9781108745963

There are several remarkably active research areas in contemporary ecology. Biological invasions and study of ecological networks are two of them. Since the SCOPE international programs, initiated in the final decades of the last century, the number of publications on biological invasions has been increasing exponentially. Besides NeoBiota, at least five other current journals are completely dedicated to this topic. The number of publications on ecological networks has been also increasing and recent years have seen a burst in the study of this subject (e.g., Polis and Winemiller 1996; Pascual and Dunnde 2006; Dáttilo and Rico-Gray 2018; Losapio et al. 2019; Guimaraes 2020; Kéfi 2020; Benadi et al. 2022). Twenty-three volumes of the journal "Food Webs" have been published since 2014. More than 1300 ecological networks are included in Mangal – a database for species interaction networks (Poisot et al. 2021). Therefore, combining these two areas into one treatment was a good idea. True, the attempt by Hui and Richardson is not the first one (e.g., Romanuk et al. 2009; Galiana et al. 2014; Lurgi et al. 2014; Kinlock and Munch 2021). Nevertheless, building on their previous journal articles, mathematician Cang Hui and plant ecologist David Richardson provide, in 423 pages, the most ambitious attempt to synthesize the two research areas so far.

The book is divided into seven chapters. The first chapter summarizes what authors call invader-centric "Invasion Science 1.0" and sets a stage for a more complex new world of "Invasion Science 2.0" that is developed in the following chapters. The sum-

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mary provided in the first chapter, while sketchy, is mostly accurate. The authors' multiple complaints about context dependence and low predictability of existing invasion hypotheses is certainly justified. One important aspect that has been for some time already part of "1.0" and is omitted from this summary is the accent on phylogenetic relatedness in many recent studies of biological invasions (e,g., Strauss et al. 2006; Diez et al. 2008; Cadotte et al. 2009; Schaefer et al. 2011; Cadotte and Davies 2016; Park et al. 2020; Schmidt et al. 2021). This research is, however, touched at the end of the second chapter.

It is not completely clear to whom the book ("a hitchhiker's guide" as it is characterized by the authors) is addressed. However, if biologists are among them, they may be, unfortunately, discouraged by the very first equation in this chapter. The equation (1.1) describes spreading dynamics of biological populations: $\partial n/\partial t = rn(1 - n) + D(\partial^2 n/\partial x^2)$. We learn in the text that n represents the population density and is a function of time t and location x; the left of this equation describes the time derivative of population density; the first term on the right depicts a simple logistic growth, with the intrinsic rate of growth r. In ecological literature, population density is usually measured in terms of number of individuals, and a biologically trained ecologist will therefore probably be puzzled by the expression $rn(1 - n)$ ("a simple logistic growth" according to the authors) predicting that in equilibrium (when the density of logistically growing population reaches what is called "carrying capacity"), the population would consist of only one individual ($n = 1 \Rightarrow 1 - n = 0$). Therefore, unless n means something else than number of individuals, using $rn(1 - n/K)$ where K is a scaling constant, i.e. carrying capacity (Murray 2004, p. 400; Cosner 2012, p. 607), instead $rn(1 - n)$, would be preferable. Nevertheless, readers should not be deterred by this confusion. The book provides a large collection of potentially applicable mathematical procedures for dealing with multispecies systems, mainly for theoretical ecologists, as well as references to many empirical studies that may be interesting for biologists.

The second chapter ("Relentless Evolution") is dedicated to species interactions, their coexistence, and co-evolution of traits. Here we learn about some conceptually useful approaches to quantification of interaction strength in the realm of Hessian interaction matrices. After that, we explore different kinds of equilibria and the Lyapunov stability of such systems. In this context, conditions for invasion and coexistence can be determined as inequalities in values of particular parameters (including competition coefficients and carrying capacities), their ratios, fitness differences, and niche separations. A call for studies of the impacts of higher-order interactions is certainly justified. Some basic concepts of evolutionary biology are recalled here and the importance of adaptive interaction switching is inevitably stressed because it is important in the context of dynamic ecological networks. Interaction strength is then expressed as a niche-based interaction kernel that is a function of the relevant traits of interacting species. Because co-evolution of traits could explain structures of many ecological networks, the rest of the chapter is dedicated to this topic. This is done mostly via references to rather demanding theoretical concepts (canonical equation of adaptive dynamics, convergence stable singularity, evolutionary stable strategy, continuously

stable strategy, Price equation, etc.). The evolution of competitive ability of invasive species (EICA) is mentioned in this context.

Chapter 3 ("Network Assembly") is the core of the presented network-invasion synergy. It explores how structures of ecological networks emerge from interactions among species. First, a history of ideas about mechanisms of ecological succession and community assembly processes is extensively reviewed. Almost all relevant concepts and ongoing debates in contemporary ecology are packed into the introduction to this chapter. To summarize current knowledge, the authors proposed sorting non-random patterns in invaded biotic communities along three types of dispersion: temporal, spatial, and ecological. The first one is reflected in time series of abundance, species richness or other relevant variables that may or may not reflect shifts due to invasions or some other environmental changes. Such changes may be associated with dynamics and instability of invaded ecological networks – the topic covered in chapters 4 and 5. Spatial dispersion amounts of spatial patterns of species under interest – their positive or negative associations and aggregations. In this context alpha, beta and zeta (developed by Hui and McGeoch 2014) indices of diversity are introduced. Ecological dispersion is a measure of the functional similarity or dissimilarity between resident species. Basic concepts of network topology and architecture are introduced (connectance, linkage density, node degree, centrality, modularity, nestedness, etc.). Then, three types of networks are distinguished: competitive, antagonistic and mutualistic.

The results of several recent studies of plant communities and food webs are reviewed. A multivariate plant community analysis of *Clidemia hirta* invasion in Sabah (Fig. 3.14) is a nice example. Decline of connectance with network size (for the first time documented by Rejmánek and Starý 1979) is discussed and some results showing increase of invasion resistance with increasing connectance are presented. However, whether there is a general causal connection remains an open question. The enemy release hypothesis, as well as the evolution of increased competitive ability is mentioned here again. Whether there is some fundamental difference in the structure of antagonistic and mutualistic networks remains to be properly analyzed with respect to network-area relationships. Examples of invasions into mutualistic networks are listed and a conceptual framework for inferring establishment success and invasion performance of introduced legumes is provided (Fig. 3.20). Several examples illustrate changes in network structure due to invasions (e.g., an increase of nestedness in pollination networks). Inevitably, a special research challenge is posed by ecological networks with multiple (trophic and non-trophic) interaction types. The rest of the chapter is dedicated to the role of co-evolution in the emergence of dynamic and adaptive networks. Several original contributions of Cang Hui are utilized in this context. Finally, Daniel Janzen's concept of ecological fitting (the formation of biotic interactions without co-evolution) is utilized to explain the novel interactions between species that had shared little evolutionary history. A list of more than 300 references concludes this chapter.

Chapter 4 ("Regimes and Panarchy") explores how invasion performance and invasibility are related to the loss of network stability or instability. To do that, the authors first define a complex adaptive system (CAS) as "a dynamic system comprising

multiple interacting parts that respond, adaptively and collectively, to perturbations, often reactively but sometimes actively or proactively." Then, several different concepts and definitions of stability applicable on a CAS are presented. Inevitably, such a topic has to start with Robert May's stability criterion and its extensions. (There is an incorrect reference to May 1973; it should be a reference to his book, not the article in The American Naturalist.) As the authors correctly reproduce, stability of May's random community matrices decreases with their complexity. However, stability of matrices representing competition communities may increase with connectance (Rejmánek et al. 1983; Rozdilsky and Stone 2001; Fowler 2009). From a theoretical point of view, this is an extremely interesting research area. However, sooner or later we have to realize that there are serious problems with the application of stability criteria based on eigenvalue analyses of real systems defined by their size, connectance, nestedness and interaction strengths. Reliable estimates of these parameters are obtained only very rarely from real laboratory or natural biotic communities (Seifert and Seifert 1976; Roxburgh and Wilson 2000; Fox and McGrady-Steed 2002; Carrara et al. 2015).

Nevertheless, the discussion about how these parameters may be changed via propagule pressure, niche occupation, fluctuating resources, etc. (p. 224) may lead to some new research directions. Also, some theoretical studies are supported by empirical data. For example, modeling studies show that a highly connected and nested architecture promotes stability in mutualistic networks, while the stability of trophic networks is enhanced in compartmented and weakly connected communities. A meta-analysis of the architecture of 57 real networks supports this prediction (Thébault and Fontaine 2010).

The rest of the chapter is dedicated to the formal descriptions and examples of regime changes, adaptive cycles (panarchy), collapses and meltdowns in invaded networks. To illustrate a possibility of the construction of interaction matrices, the authors used available data on the well-studied biocontrol agent, ladybird *Harmonia axylaris* that is predicted to be a major threat to other species within the aphidophaguous guild. Based on the literature and expert opinions, the authors compiled the semi-quantitative interaction matrices of agricultural and forest systems that are currently invaded by this species (Fig. 4.15 and Hui et al. 2016). Based on the eigenvalue analysis, both systems are asymptotically stable before the invasion. After invasion, both systems become ecologically unstable, with the forest more than the agricultural system, suggesting stronger impact of the invader on the forest from the perspective of the aphidophagous guild stability. This is a nice example of how even rather tentative data can be used to make interesting inferences.

Finally, the potentially useful concept of marginal instability (self-organized criticality, Solé et al. 1999) is introduced in this chapter. Driven by constant input of propagules and successful invasions, open adaptive networks operate close to instability. Because of that, the stability-complexity relations discussed earlier in this chapter are either weak or lacking in such networks. Surfing in gentle waves is used as a metaphor illustrating systems under persistent transition at marginal instability (criticality).

Chapter 5 ("Network Transitions") explores the dynamics of ecological networks resulting from invasion-induced instabilities. Of course, this is a domain where pre-

dictability is very low and forecasting inherently unreliable. However, to outline some options, the authors introduce (1) "early warning signals" of bifurcation/regime shifts in ecological systems (inevitably, such signals are highly system specific); (2) "temporal turnover" of residing species and network interactions (theory of island biogeography is a starting point for actual monitoring and generalizations); (3) "weather vane" as an indicator of the transient dynamics of network turnover (such short-term indicators would certainly be helpful if required Hessian and Jacobian matrices were available). Finally, the role of rare species in maintaining system stability, functionality and invasibility is discussed. Conclusion: ". . . rare species hold the key to network instability and invasibility, while the commonness-rarity gradient, captured by the weather vane, gives us the direction and magnitude of temporal turnover."

Chapter 6 ("Network Scaling") deals with the fact that ecological networks are not isolated, but embedded in larger systems (meta-webs, meta-communities). Assembly of any open ecological networks depends on constant influx of alien or regionally native species and extinction of species that were present earlier. Therefore, fitting a particular network into a broader landscape context is one topic covered in this chapter. Another topic is spatial scaling. The structure and functioning of ecological networks change with spatial scales at which they are analyzed. As the authors correctly point out, such scale dependence creates both problems and opportunities for our understanding of real nature. Several relevant questions, including scale dependent correlation of native and exotic species are discussed here. Meta-network dynamics, stability criteria of meta-networks and the role of dispersal in meta-network transitions are covered in the rest of the chapter. This is an area of active research and some new, mostly theoretical, results emerged since the book was written (e.g., Erös et al. 2020; Clark et al. 2021; Galiana et al. 2022; Liu et al. 2022; Saravia et al. 2022; Yang and Bao 2022). I would expect that more attention will be paid to quantification of environmental spatial heterogeneity and its effects on the pattern and processes discussed in this chapter.

The final chapter ("Rethinking Invasibility") attempts to provide a fresh look at the classic problem of invasion biology: how trait-mediated interactions can cause invasions and impacts in the recipient biotic communities. First, the major points in the previous chapters are reiterated. Then, apparently as a backbone of the "Invasion Science 2.0", a model of the eco-evolutionary dynamics of an open adaptive network (Hui et al. 2021) is presented. Conceptually and mathematically, this is a beautiful model. It certainly stimulates nontraditional and multidimensional thinking about biological invasions. Eventual parametrization of the four equations in this section is left to the readers. Nevertheless, some intuitively expected generalizations emerge from this model: ". . . to be successful, invaders need to position their traits relative to the trait distributions of resident species from different functional guilds. They must also mitigate negative interactions by occupying peripheral trait positions and increase positive interactions by seeking central trait positions." Perhaps some generalizations based on field and laboratory studies of invasions (e.g., Kimball et al. 2013; Fridley et al. 2022) will find their place within this framework. It seems that at the end of this final chapter, the authors felt an obligation to say something about management. This resulted in

many correct but rather trivial statements with only a very loose connection to the rest of the book. There are several management related topics that are not covered, but will be important in the near future. For example, with ongoing climate change, maintenance of demographic/taxonomic composition will be less important than the functional stability – persistence of biomass production, carbon sequestration and climate regulation (e.g., Loreau et al 2001; Mathes et al. 2021). Also, interactive effects of invasions, habitat loss and global warming are a highly timely research area. The extensive Glossary (14 pages) after the last chapter, will be very helpful for all readers.

At the end of the preface, the readers are warned: "It is not a recipe book. . .". Still, many ecologists would be interested to learn more of a real world where the data on ecological networks could be collected and analyzed. For example, problems with different kinds of sampling bias (Costa et al 2016; Fründ et al. 2016; Brimacombe et al. 2022) and taxon resolution (Hemprich-Bennett et al. 2021), are not trivial. Obviously, there is an open niche for a different book showing how to do it in the field. Of course, this does not diminish the value of the book under review. It will provide a lot of inspiration for theoretical ecologists and mathematicians. Biologists, if they are not discouraged by mathematical concepts and expressions, will find many interesting references and ideas. Very likely, they will conclude that what is presented here is not really completely new to them. The novelty stressed by the authors is not really so new. Ecologists working on biological invasions are well aware of the multispecies and multidimensional complexity of their subject. Therefore, there is no need to break through an open door.

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RESEARCH ARTICLE

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Advancing research on alien species and biological invasions

Linear scaling – negative effects of invasive *Spiraea tomentosa* (Rosaceae) on wetland plants and pollinator communities

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Abstract

Invasive plants directly and indirectly disrupt the ecosystem functioning, of which indirect effects, for example, through trophic cascades, are particularly difficult to predict. It is frequently assumed that the impact of an invading species on the ecosystem is proportional (linearly related) to its density or abundance in a habitat, but this assumption has rarely been tested. We hypothesised that abundance and richness of plants and potentially pollinators of wet meadows change as a result of invasion of steeplebush *Spiraea tomentosa* and that these changes are proportional to the density of the shrub. We selected 27 sites amongst wet meadows habitats invaded by *S. tomentosa* with coverage ranging from 0% to 100% and examined the diversity of plants, as well as the abundance and diversity of flower visitors (bees, butterflies with moths and flies). Our results showed that the richness of plants, as well as the richness and number of individuals of flower visitors, decrease significantly and linearly with an increase of the *S. tomentosa* cover. This finding supports the hypothesis that the impact of an invasive species can be proportional to their population density, especially if this species is limiting the available resources without supplying others. Our study is the first to show such an unequivocal negative, linear effect of an invasive shrub on the abundance

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and richness of potential pollinators. It proves that the negative impact of *S. tomentosa* on the wetland ecosystem appears even with a minor coverage of the invader, which should be taken into account when planning activities aimed at controlling the population of this transformer species. The simultaneously detected linear dependence allows us to assume that the benefits of controlling secondary populations of the shrub can be proportional to the incurred effort.

Keywords
bees, biodiversity, biological conservation, butterflies, flies, flower visitors, invasive plants, non-native species, wetlands

Introduction

Freshwater wetlands are important refuges for hygrophilous and hygrobiont plants and animals and, as such, they support diverse and unique species assemblages (Burke and Gibbons 1995). Nevertheless, in spite of the ecosystem services they provide, these types of ecosystems have been lost, degraded or strongly modified by human activities worldwide (Moroń et al. 2008; Davidson 2014; Reis et al. 2017). One of the most important reasons for their degradation are biological invasions, to which these ecosystems seem to be especially vulnerable (Zedler and Kercher 2004) due to frequent, large-scale disturbances, influx of nutrients, runoff of propagules flowing down the ground and accumulating in land depressions, as well as their limited connection over the network of corridors (Zedler and Kercher 2004; Fletcher et. al. 2019). Invasive plants disrupt the functioning of wetland ecosystems at different levels of their organisation both directly, for example, through competition for resources or changes in habitat conditions and indirectly, for example, through the trophic levels (Dibble et al. 2013; Mazurczyk and Brooks 2021). By initiating food chains, these plants can affect trophic interactions (Pearson 2009), which may initiate a trophic cascade (López-Núñez et al. 2017) manifested in population changes of consumers caused by direct and indirect relationships between them.

Amongst animals, insects are a group particularly sensitive to disturbances resulting from plant invasions (Van Hengstum et al. 2014; Schirmel et al. 2016), because they are highly dependent on plants as sources of food (Ehrlich and Raven 1964; Coley et al. 2006), shelter and breeding ground (Spafford et al. 2013). Therefore, the magnitude of response to changes in native flora composition caused by invasive plants varies extremely in different guilds of insects (Moragues and Traveset 2005; Fenesi et al. 2015). One of the crucial functions insects play in the ecosystem is pollination (Klein et al. 2007), which is the key in maintaining plant species diversity (Potts et al. 2010). However, data on the impact of invasive plants on pollinator populations are still scarce, whereas the effect of invasive plants on a pollinator community is equivocal (Bjerknes et al. 2007). Invasive plant species often compete with native ones for ecosystem services, such as pollination (Moragues and Traveset 2005; Larson et al. 2006; Bjerknes et al. 2007; Dietzsch et al. 2011; Williams et al. 2011). There are also known cases of pistil stigmas of native species being blocked by deposited foreign pollen,

which may limit the reproductive success of native plants (Brown et al. 2002; Larson et al. 2006). Nevertheless, invasive plants, due to their higher level of generalisation with regard to pollinators when compared to native plants, may also play new, important topological roles. For example, they attract pollinators to visit invaded ecosystems (Albrecht et al. 2014), increase the frequency of visits of pollinators on flowers of plants found in the same habitat (Bartomeus et al. 2008), increase pollinator populations, flight frequency and range (Moragues and Traveset 2005) and fill the seasonal resource gap in the native flora (Tepedino et al. 2008).

The direction of the impact of invasive plants on pollinators is strongly dependent on the scale of the invasion (Powell et al. 2013; Rejmánek and Stohlgren 2015). It is often assumed that the impact of invasive plants is proportional to their population density (Yokomizo et al. 2009; Elgersma and Ehrenfeld 2011; Panetta and Gooden 2017), but, as noted by Elgersma and Ehrenfeld (2011), this assumption has been rarely tested and there is ample evidence that the effects of plant invasions on native pollinators are not linear (Moroń et al. 2019). Thus, the question arises whether the scenario of the non-linear effect of invaders on native plants and pollinators is a more general pattern. Therefore, in this study we assessed the impact of steeplebush on the species diversity of vascular plants, as well as the species number and diversity of pollinators in wet meadows.

The North American steeplebush (*Spiraea tomentosa* L., Rosaceae) is a highly invasive shrub found in central and northern Europe (Dajdok et al. 2011), with high potential for further spread (Wiatrowska et al. 2020). In the area of its natural occurrence, in the southern United States (USDA – The Plants Database 2022), *S. tomentosa* grows especially in wetland habitats and enters transitional and raised bogs (Reschke 1990; Schafale and Weakley 1990; Faber-Langendoen 2001). According to LaRosa et al. (2004), in its natural range, the shrub offers pollen and nectar as a reward for pollinators and, depending on the population density, it may have different (opposing) impacts on pollinators, such as bees (bumblebees) included in this study.

In Europe, *S. tomentosa* has been cultivated as an ornamental plant since the 18th century (Symes 1983). Currently this shrub is found in nine countries: Sweden, Germany, Poland, Belgium, Denmark, Norway, Croatia, Romania and Great Britain (Dajdok et al. 2011; GBIF 2022), while it is considered as an invasive species in five countries: Belgium (Invasive species of Belgium 2022), Denmark (Bruus et al. 2007), Germany (Balkenhol et al. 2018), Sweden (Tyler et al. 2015) and Poland (Dajdok et al. 2011; Tokarska-Guzik et al. 2012). In the area of its secondary occurrence, this shrub forms monodominant plant stands completely changing the structure and plant species composition of wetland communities – wet grasslands, lowland peat bogs or marsh forests (Dajdok et al. 2011; Wiatrowska and Danielewicz 2016) (Fig. 1).

However, still very little information is available on its effects on pollinators – flower visitors and the plant species composition. These data are urgently needed to communicate management priorities in times when invasions are a threat and challenge in nature conservation (Pyšek et al. 2020; Ricciardi et al. 2021; Moodley et al. 2022).

Spiraea tomentosa interacts with pollinators (LaRosa et al. 2004) and meets all four conditions (flower attraction, taxonomic affinity to native plants, formation of

dense populations and generalised pollination strategy) that, according to Bjerknes et al. (2007), make alien plants strong interactors for pollination in the area of their secondary range. The shrub was brought to Europe (Symes 1983; Hardtke and Ihl 2000) because it has stately inflorescences (Dajdok et al. 2011) that can be attractive to pollinators (Chittka and Schürkens 2001; Brown et al. 2002). The plant has a taxonomic affinity to *S. salicifolia* L. (Mirek et al. 2002) native to Central Europe, as well as many other *Spiraea* spp. common in cultivation (e.g. *S. douglasii* Hook. or *S.* ×*pseudosalicifolia* Silverside), which may facilitate attracting pollinators. Moreover, *S. tomentosa* develops denser and larger populations (Wiatrowska and Danielewicz 2016) than other species known as particularly attractive to pollinators (Ågren 1996; Mustajarvi et al. 2001; Thompson 2001). Probably, due to the relatively simple structure of flowers (*S. tomentosa* flowers are bisexual, 0.5–1.5 mm in diameter, with five free sepals, five petals orbiculate, free, usually light pink, five carpels and 15–20 stamens (Flora of North America 2022)), it also has a generalised pollination strategy, which means that it can attract many groups of pollinators.

Based on these premises, our main goal was to assess whether there was a relationship between the abundance of *S. tomentosa* and the diversity of plants, as well as the abundance and diversity of potential pollinators in wet meadow communities. We considered what influence the invader – non-linear or linear – has on plants and potential pollinators of indigenous communities. In the case of a non-linear relationship, the question arises whether there is a certain minimum point (tipping point), at which a pollinator population changes as the invasive plant becomes dominant.

We tested the hypotheses that: (1) the richness of plants and the abundance and richness of visiting pollinators change as a result of *Spiraea tomentosa* invasion and (2) changes are proportional (linearly) to the density of the shrub. The implementation of these studies was essential to provide insight into the density-dependent impact of the invasive alien species *S. tomentosa* on biodiversity, focusing on plants and pollinator species.

Figure 1. *Spiraea tomentosa* in wet meadows located in the Lower Silesian Forests (photo by B. Wiatrowska).

Methods

Study area

The research was carried out in a wet meadow complex located in the Lower Silesian Forests, in south-western Poland, where one of the first documented observations of *S. tomentosa* naturalisation in Europe was made (Fiek 1881; Schube 1903). Based on the water table (Bieroński et al. 2000a, b) and the present vegetation maps (Forest Data Bank 2022), we prepared distribution maps for wet meadows, where the soil is periodically saturated with water. The meadows are located in the same physical and geographic division (the Lower Silesian Forests mesoregion) (Solon et al. 2018) and have a similar geological history (Rzechowski 1994), climate (Woś 1999), soil properties and moisture conditions – the groundwater table is located just below the soil surface (Forest Data Bank 2022).

In the Lower Silesian Forests from the 1890s, large-scale drainage works were carried out, but after the Second World War, the maintenance of hydrotechnical structures was abandoned, which resulted in secondary bogging of the area (Bieroński et al. 2000a, b). Nowadays wet meadows are mainly maintained by regular management schemes, but *S. tomentosa* is spreading in many places (Wiatrowska and Danielewicz 2016). All studied meadows are dominated by *Molinia caerulea* (L.) Moench and *Juncus effusus* L. with numerous other native plants (Rutkowski 2011) suitable for pollinators (e.g. *Lythrum salicaria* L., *Lotus uliginosus* Schkuhr, *Cirsium palustre* (L.) Scop., *Filpendula ulmaria* (L.) Maxim., *Galium palustre* L., *Potentilla erecta* (L.) Raeusch, *P. reptans* L. or *Linaria vulgaris* Mill.) (Bělìn 1999; Buszko and Masłowski 2008).

In 2021, amongst six wet meadow complexes, 27 study sites were randomly selected for further analyses, each characterised with different *S. tomentosa* coverage. Wet meadows were at least 5000 ± 620 m apart, while the study sites located in the same meadow, but differing in *S. tomentosa* density, were at least 60 ± 42 m apart. To control the disruptive effects of the potential spatial gradients (distance from forests, human settlements, farmlands and meadows), we applied the Spearman test to make sure that these features did not correlate with steeplebush cover. We ensured that the selected study sites do not correlate with the distance of places to the closest forest areas (woodlands) ($r_S = -0.08$, $p = 0.703$), human settlements ($r_S = 0.36$, $p = 0.069$), farmland ($r_S = 0.04$, $p = 0.844$) and meadows ($r_S = 0.14$, $p = 0.461$). The distances were measured with QGIS 3.16 (QGIS Development Team 2022).

Surveys

In each of the study sites (n = 27), permanent circular plots of 100 m^2 were established. On each of these sites, the *S. tomentosa* cover was determined, a list of vascular plants was made and flower visitors were caught using a pan-trap placed in their centre. Data were collected during the period of full flowering of the shrub (Wiatrowska et al. 2018a) – in the second half of July and in August 2021.

The estimation of *S. tomentosa* coverage in the study sites was performed between 18 and 20 July 2021. Shrub cover was estimated visually using a cover class method (a modified Braun-Blanquet method) (Kercher et al. 2003), which provided reliable estimates for the dominant shrubs (Floyd and Anderson 1987). The coverage was estimated in classes with an accuracy of 10%, or less (every 0.5%), in the case of very low shrub densities (< 10%). The estimation consisted in an evaluation of what part of the study site is covered by all above-ground steeplebush organs jointly (e.g. shoots, leaves, flowers, fruits) by projecting them vertically on to the plane surface of the tested site. On all of the study sites, *S. tomentosa* cover ranged from 0% to 100% (47.6 ± 36.2%; mean ± SD) (see Appendix 1), where meadows completely free of the invasive shrub were taken as controls (0% invader coverage).

The plants species composition was surveyed twice (18–20 July and 27–29 August 2021) at each study site (n = 27) located in wet meadows at permanent circular plots (100 m^2). The vast majority of plant communities consisted of native species (74). However, in addition to *S. tomentosa*, the presence of single seedlings or juveniles of five other alien species was found (seedlings of *Prunus cerasifera*, *P. serotina*, *Quercus rubra* and juvenile of *Solidago canadensis* and *Juncus tenuis*). All the identified plant species, including *S. tomentosa*, were included in the analysis. Due to the fact that alien species other than *S. tomentosa* did not bloom during the field study, their presence was found on single sites and all had a negligible coverage (< 1%), thus it was assumed that they had no effect on flower visitors. Additionally, there was no relationship between *S. tomentosa* cover and the number of non-native species (generalised linear mixed-effects models; $t = -0.513$, $R^2 = 0.01$, $p = 0.618$). All plants were identified according to Rutkowski (2011).

Pan traps to catch insects (n = 27) were set up in the central part of each of the 27 study sites. This type of trap was used because they are an effective method of trapping insects in semi-natural habitats, including open areas with a wider field of vision (Mazon and Bordera 2008; Westphal et al. 2008; Acharya et al. 2021). Despite the limitations of the pan-trap method (Westphal et al. 2008; O'Connor et al. 2019), caused amongst others by their varying effectiveness in catching different groups of insects (Vrdoljak and Samways 2012), widely discussed perception of colour by insects (Briscoe and Chittka 2001; Song and Lee 2018; Van Der Kooi et al. 2021), including the colour of traps (Campbell and Hanula 2007; Vrdoljak and Samways 2012; Acharya et al. 2021), this method shows relevant effectiveness (O'Connor et al. 2019). Pan traps are useful for species that are active at night, trapping also rare or scarcely represented species. Their permanent presence in the field regardless of the temperature changes during daytime is of particular importance to obtain data on the complete species community, including specific weather conditions, during which, for example, bee flights take place (Borański 2015). According to premises presented above, one type of unicoloured, white traps were used to catch insects spontaneously attracted by the flowers of *S. tomentosa.* White pan traps are also commonly used in research on flower-visiting insects (Disney and Erzinclioglu 1982; Banaszak et al. 1994; Duelli et al. 1999; Campbell and Hanula 2007; Westphal et al. 2008; Vrdoljak and Samways 2012).

The traps were positioned in sunny places, on poles at the height of *S. tomentosa* inflorescences (ca. 70 cm above the ground and approx. 10 cm from the inflorescences of the shrub). The traps were 15 cm in diameter and filled to 2/3 volume with a mixture of water (95%), ethylene glycol (4.8%) and detergent (0.2%). Traps were first installed on 21 July 2021 and inspected three times at 14-day intervals during the peak of flowering and the peak of pollen season of this species. The samples were collected 03, 17 and 31 of August (exposure 21 July-03 August, 04 August-17 August, 18 August-31 August 2021), which made a total of 81 samples (pan traps). The caught insects were poured through a strainer and preserved in test tubes with 75% ethyl alcohol. Each selected group of flower visitors was identified according to Dathe (1980); Schmid-Egger and Scheuchl (1997); Pesenko et al. (2000); Pawlikowski and Celary (2003); Celary (2005); Scheuchl (2006); Bogusch and Straka (2012) – bees Apoidea Hymenoptera, Karsholt and Razowski (1996) – butterflies and moths Lepidoptera, Speight (2017) – flies Diptera.

Statistical analysis

All data analyses and visualisations were performed using the R ver. 4.2.1 software (R Development Core Team 2022). To verify the number of individuals and the species richness of potential pollinators, as well as plant species richness depending on *S. tomentosa* cover, we used the generalised linear mixed-effects models (GLMM) with a negative binomial distribution (bee abundance and species richness; butterfly and moth abundance and species richness, fly abundance) or Gaussian distribution (fly species richness, plant species richness) with the study meadow and site identities as the nested random factors. The models' assumptions were verified using the DHARMA ver. 0.4.6 package (Hartig and Lohse 2022). Additionally, models and results were provided applying GGEFFECTS ver. 1.1.4 (Lüdecke 2022), LME4 ver. 1.1-31 (Bates et al. 2022), LMERTEST ver. 3.3 (Kuznetsova et al. 2022) and MUMIN ver. 1.47.1 (Bartoń 2022) packages. The visualisations were performed using GGPLOT2 ver. 3.4.0 package (Wickham et al. 2022).

In addition, to understand if possible differences in the composition of potential pollinator communities depending on *S. tomentosa* cover are caused by pollinator species replacement or loss, we calculated the mean rank of the samples in a maximally packed matrix for overall pollinators: nestedness means that species-poor sites (i.e. those with a high rank in the nested matrix) are subsets of species-rich sites (those with a low rank). Data analyses and visualisation were performed using BIPARTITE ver. 2.18 (Dormann et al. 2022) and VEGAN ver.2.6-4 (Oksanen et al. 2022) packages.

We compared the rank of samples in the maximally packed matrix with GLMM (Gaussian distribution with the meadow and site identities as the nested random factors). The models' assumptions were verified using the DHARMA ver. 0.4.6 package (Hartig and Lohse 2022). Additionally, to obtain the models and results, we used GGEFFECTS ver. 1.1.4 (Lüdecke 2022), LME4 ver. 1.1-31 (Bates et al. 2022), LMERTEST ver. 3.3 (Kuznetsova et al. 2022) and MUMIN ver. 1.47.1 (Bartoń 2022) packages. The visualisations were performed using GGPLOT2 ver. 3.4.0 package (Wickham et al. 2022).

Results

During overall 27 216 hours of the pan-trap deployment, we collected 3649 individuals of 191 potential pollinator species or families (in the case of flies). Flies (Diptera) formed the most abundant pollinator group, accounting for 75% of all trapped insects. Butterflies and moths (Lepidoptera) comprised 15% of the collected insects. Bees (Apoidea, Hymenoptera) were only a minor fraction of flower visitors (10% of the specimens). A total of 80 vascular plant species were recorded in the investigated study sites (Table 1).

A negative relationship was found between steeplebush cover and plant species richness (t = –7.15; Fig. 2), with a 60% decrease of plant species richness.

An increase in *S. tomentosa* cover correlated also with a decline in the number of bee, butterfly and moth and fly individuals by about 70%, 80% and 45% (Fig. 3A–C), respectively (bees: Z = –4.77; butterflies and moths: Z = –7.54; flies: Z = –2.81). Similarly, bee, butterfly (and moth) and fly species richness decreased across the range of *S. tomentosa* cover by approx. 70%, 70% and 30% (Fig. 3D–E), respectively (bees: Z = –4.35; butterflies and moths: Z = –6.22; flies: t = –2.46).

The potential pollinator community in the habitats studied was significantly nested, indicating that species-poor samples (pan traps with a high rank) constituted subsets of species-rich samples (pan traps with a low rank) and that this pattern was not random. The nestedness rank significantly increased in proportion to *S. tomentosa* cover (t = 6.40; Fig. 4; see Appendix 2).

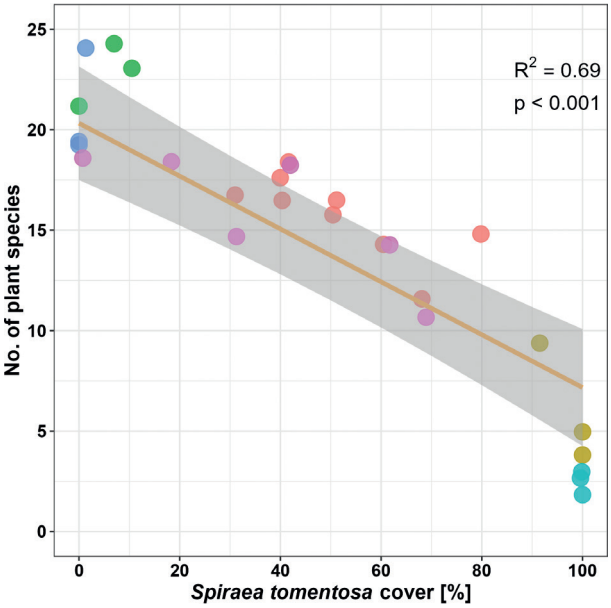

Figure 2. The relationship between species richness of plants and site cover by *Spiraea tomentosa*. Points represent each of 27 sites. Point colours correspond to a meadow. The 95% CI are marked with polygons. Jittering was added to aid visualisation.

Table 1. List of vascular plants and flower visitors found at study sites with their numbers.

Plants	Bees	No.	Butterflies and moths	No.	Flies	No.
Achillea millefolium L.	*Ammophila sabulosa* (Linnaeus, 1758)	2	*Abrostola tripartita* (Hufnagel, 1766)	5	*Chalcosyrphus nemorum* (Fabricius, 1805)	2
Achillea ptarmica L.	*Andrena bimaculata* (Kirby, 1802)	1	*Abrostola triplasia* (Linnaeus, 1758)	1	*Cheilosia longula* (Zetterstedt, 1838)	1
Agrostis capilaris L.	*Andrena dorsata* (Kirby, 1802)	3	*Actinotia polyodon* (Clerck, 1759)	2	*Chloromyia formosa* Scopoli, 1763	1
Agrostis gigantea Roth	*Andrena flavipes* Panzer, 1799	3	*Agrotis segetum* (Denis & Schiffermüller, 1775)	4	*Chrysotoxum bicinctum* (Linnaeus, 1758)	3
Agrostis stolonifera L.	*Andrena minutula* (Kirby, 1802)	1	*Amphipoea oculea* (Linnaeus, 1761)	22	*Chrysotoxum festivum* (Linnaeus, 1758)	1
Alnus glutinosa (L.) Gaertn.	*Apis mellifera* Linnaeus, 1758	25	*Apamea monoglypha* (Hufnagel, 1766)	7	*Chrysotoxum verralli* Collin, 1940	3
Alopecurus pratensis L.	*Astata boops* (Schrank, 1781)	9	*Aphantopus hyperantus* (Linnaeus, 1758)	8	*Dasysyrphus tricinctus* (Fallen, 1817)	1
Angelica sylvestris L.	*Bombus bohemicus* Seidl, 1837	3	*Aporia crataegi* (Linnaeus, 1758)	1	*Episyrphus balteatus* (De Geer, 1776)	21
Athyrium filix-femina (L.) Roth	*Bombus jonellus* (Kirby, 1802)	2	*Araschnia levana* (Linnaeus, 1758)	8	*Eristalinus sepulhralis* (Linnaeus, 1758)	1
Betula pendula Roth	*Bombus lapidarius* (Linnaeus, 1758)	2	*Argynnis adippe* (Denis & Schiffermüller, 1775)	3	*Eristalis arbustorum* (Linnaeus, 1758)	11
Calamagrostis canescens (Weber) Roth	*Bombus lucorum* (Linnaeus, 1761)	17	*Argynnis aglaja* (Linnaeus, 1758)	3	*Eristalis lineata* (Harris, 1776)	3
Calamagrostis epigejos (L.) Roth	*Bombus pascuorum* (Scopoli, 1763)	24	*Argynnis paphia* (Linnaeus, 1758)	17	*Eristalis obscura* Loew, 1866	1
Campanula patula L.	*Bombus terrestris* (Linnaeus, 1758)	22	*Autographa gamma* Linnaeus, 1758	16	*Eristalis pertinax* (Scopoli, 1763)	3
Cardamine pratensis L.	*Colletes fodiens* (Geoffroy, 1785)	1	*Boloria selene* (Denis & Schiffermüller, 1775)	5	*Eristalis tenax* (Linnaeus, 1758)	14
Carex hirta L.	*Crabro cribrarius* (Linnaeus, 1758)	29	*Calophasia lunula* (Hufnagel, 1766)	1	*Helophilus hybridus* Loew, 1846	11
Carex ovalis Gooden.	*Crossocerus nigritus* (Lepeletier & Brülle, 1834)	1	*Carterocephalus palaemon* (Pallas, 1771)	1	*Helophilus pendulus* (Linnaeus, 1758)	6
Carex praecox Schreb.	*Dasypoda hirtipes* (Fabricius, 1793)	2	*Celaena leucostigma* (Hübner, 1808)	1	*Helophilus trivittatus* (Fabricius, 1805)	12
Cirsium arvense (L.) Scop.	*Ectemnius cephalotes* (Olivier, 1791)	1	*Cerapteryx graminis* (Linnaeus, 1758)	1	*Myathropa florea* (Linnaeus, 1758)	3
Cirsium palustre (L.) Scop.	*Ectemnius confinis* (Walker, 1871)	3	*Chiasmia clathrata* (Linnaeus, 1758)	2	*Oxycera leonina* (Panzer, 1798)	1
Deschampsia caespitosa (L.) P.B.	*Ectemnius continuus* (Fabricius, 1804)	44	*Coenonympha arcania* (Linnaeus, 1761)	1	*Parhelophilus versicolor* (Fabricius, 1794)	6
Dryopteris cartchusiana (Vill.) H.P.Fuchs	*Ectemnius lapidarius* (Panzer, 1804)	5	*Coenonympha glycerion* (Borkhausen, 1788)	1	*Scaeva pyrastri* (Linnaeus, 1758)	2
Epilobium palustre L.	*Ectemnius ruficornis* (Zetterstedt, 1838)	1	*Coenonympha pamphilus* (Linnaeus, 1758)	20	*Sericomyia silentis* (Harris, 1776)	1
Equisetum arvense L.	*Evylaeus albipes* (Fabricius, 1781)	3	*Cyclophora albipunctata* (Hufnagel, 1767)	1	*Sicus ferrugineus* (Linnaeus, 1761)	27
Festuca rubra L.	*Evylaeus calceatus* (Scopoli, 1763)	1	*Diachrysia chrysitis* (Linnaeus, 1758)	2	*Sphaerophoria scripta* (Linnaeus, 1758)	7
Filipendula ulmaria (L.) Maxim.	*Evylaeus laticeps* (Schenck, 1869)	1	*Diarsia brunnea* (Denis & Schiffermüller, 1775)	10	*Syritta pipiens* (Linnaeus, 1758)	9
Frangula alnus Mill.	*Evylaeus malachurus* (Kirby, 1802)	1	*Diarsia mendica* (Fabricius, 1775)	10	*Syrphus ribesii* (Linnaeus, 1758)	1
Galeopsis tetrachit L.	*Gorytes albidulus* (Lepeletier, 1832)	1	*Diarsia rubi* (Vieweg, 1790)	1	*Syrphus torvus* (Osten-Sacken, 1875)	3
Galeopsis bifida Boenn.	*Gorytes laticinctus* (Lepeletier, 1832)	2	*Dioryctria simplicella* Heinemann, 1863	1	*Tropidia scita* (Harris, 1780)	1
Galium aparine L.	*Gorytes quinquecinctus* (Fabricius, 1793)	2	*Endotricha flammealis* (Denis & Schiffermüller, 1775)	3	*Xylota segnis* (Linnaeus, 1758)	30
Galium palustre L.	*Halictus maculatus* Smith, 1848	1	*Epirrhoe alternata* (Müller, 1764)	8	*Xylota tarda* Meigen, 1822	15
Galium saxatile L.	*Halictus sexcinctus* (Fabricius, 1775)	3	*Euclidia glyphica* (Linnaeus, 1758)	2	Anthomyiidae	482
Galium uliginosum L.	*Hylaeus brevicornis* Nylander, 1852	1	*Eupithecia virgaureata* Doubleday, 1861	1	Calliphoridae	800
Glechoma hederacea L.	*Hylaeus cardioscapus* Cockerell, 1924	1	*Euxoa tritici* (Linnaeus, 1761)	1	Fanniidae, Muscidae, Scathophagidae	400
Holcus lanatus L.	*Hylaeus communis* Nylander, 1852	18	*Gonepteryx rhamni* (Linnaeus, 1758)	1	Rhinophoridae	156

Plants	Bees	No.	Butterflies and moths	No.	Flies	No.
Holcus mollis L.	*Hylaeus confusus* Nylander, 1852	1	*Heliothis viriplaca* (Hufnagel, 1766)	1	Sarcophagidae	184
Hydrocotyle vulgaris L.	*Hylaeus difformis* (Eversmann, 1852)	2	*Hemaris fuciformis* (Linnaeus, 1758)	1	Tachinidae	530
Hypericum maculatum Crantz	*Hylaeus dilatatus* (Kirby, 1802)	1	*Hesperia comma* (Linnaeus, 1758)	33		
Juncus articulatus L.	*Hylaeus leptocephalus* (Morawitz, 1870)	1	*Hipparchia semele* (Linnaeus, 1758)	1		
Juncus effusus L.	*Hylaeus moricei luteifrons* (Strand, 1909)	1	*Hyloicus pinastri* (Linnaeus, 1758)	2		
Juncus tenuis Willd.	*Hylaeus pectoralis* Förster, 1871	5	*Hypena proboscidalis* (Linnaeus, 1758)	9		
Linaria vulgaris Mill.	*Lasioglossum leucozonium* (Schrank, 1781)	2	*Idaea aversata* (Linnaeus, 1758)	3		
Lotus uliginosus Schkuhr	*Lasioglossum zonulum* (Smith, 1848)	29	*Idaea emarginata* (Linnaeus, 1758)	1		
Lychnis flos-cuculi (L.) Greuter & Burdet	*Lestica clypeata* (Schreber, 1759)	1	*Inachis io* (Linnaeus, 1758)	1		
Lycopus europaeus L.	*Lindenius pygmaeus* (Van der Linden, 1829)	1	*Issoria lathonia* (Linnaeus, 1758)	1		
Lysimachia thyrsiflora L.	*Macropis europaea* Warncke, 1973	6	*Lacanobia oleracea* (Linnaeus, 1758)	2		
Lysimachia vulgaris L.	*Megachile centuncularis* (Linnaeus, 1758)	2	*Lacanobia suasa* (Denis & Schiffermuller, 1775)	1		
Lythrum salicaria L.	*Megachile ligniseca* (Kirby, 1802)	2	*Lycaena alciphron* (Rottemburg, 1775)	3		
Mentha arvensis L.	*Megachile versicolor* Smith, 1844	2	*Lycaena phlaeas* (Linnaeus, 1761)	4		
Molinia caerulea (L.) Moench	*Megachile willughbiella* (Kirby, 1802)	1	*Lycaena tityrus* (Poda, 1761)	2		
Peucedanum palustre (L.) Moench	*Melitta haemorrhoidalis* (Fabricius, 1775)	2	*Lycaena virgaureae* (Linnaeus, 1758)	43		
Phalaris arundinacea L.	*Nomada zonata* Panzer, 1798	1	*Lycophotia porphyrea* (Denis & Schiffermüller, 1775)	2		
Plantago lanceolata L.	*Oxybelus trispinosus* (Fabricius, 1787)	6	*Macaria alternata* (Denis & Schiffermüller, 1775)	3		
Poa pratensis L.	*Oxybelus uniglumis* (Linnaeus, 1758)	1	*Macaria liturata* (Clerck, 1759)	2		
Poa trivialis L.	*Pemphredon inornata* Say, 1824	1	*Mamestra brassicae* (Linnaeus, 1758)	2		
Polygonum hydropiper (L.) Delarbre	*Pemphredon lethifer* (Schuckard, 1837)	2	*Maniola jurtina* (Linnaeus, 1758)	64		
Populus tremula L.	*Pemphredon rugifer* (Dahlbom, 1845)	1	*Manuela complana* (Linnaeus, 1758)	3		
Potentilla anserina L.	*Philanthus triangulum* (Fabricius, 1775)	1	*Mecyna flavalis* (Denis & Schiffermüller, 1775)	3		
Potentilla erecta (L.) Raeusch	*Podalonia affinis* (Kirby, 1798)	1	*Melanargia galathea* (Linnaeus, 1758)	8		
Prunus cerasifera Ehrh.	*Seladonia tumulorum* (Linnaeus, 1758)	2	*Melanchra pisi* (Linnaeus, 1758)	2		
Prunus serotina Ehrh.	*Sphecodes hyalinatus* Hagens, 1882	1	*Mesapamea secalis* (Linnaeus, 1758)	2		
Quercus robur L.	*Sphecodes pellucidus* Smith, 1845	1	*Miltochrista miniata* (Forster, 1771)	3		
Quercus rubra L.	*Tachytes panzeri* Dufour, 1841	5	*Mythimna albipuncta* (Denis & Schiffermuller, 1775)	43		
Ranunculus repens L.	*Trypoxylon attenuatum* Smith, *1851*	3	*Mythimna ferrago* (Fabricius, 1787)	8		
Ranunculus acris L.	*Trypoxylon deceptorum* Antropov, 1991	2	*Mythimna pallens* (Linnaeus, 1758)	34		
Rubus idaeus L.	*Trypoxylon figulus* (Linnaeus, 1758)	9	*Noctua interjecta* Hübner, 1803	1		
Rubus plicatus Weihe & Nees			*Noctua pronuba* Linnaeus, 1758	3		
Rumex acetosa L.			*Nymphalis antiopa* (Linnaeus, 1758)	1		
Rumex acetosella L.			*Ochlodes venata* (Bremer & Grey, 1853)	1		
Salix aurita L.			*Oligia versicolor* (Borkhausen, 1792)	1		

Plants	Bees	No.	Butterflies and moths	No.	Flies	No.
Scirpus sylvaticus L.			*Pandemis heparana* (Denis & Schiffermüller, 1775)	1		
Scutelaria galericulata L.			*Pelosia obtusa* (Herrich-Schäffer, 1847)	2		
Solanum dulcamara L.			*Perizoma alchemillata* (Linnaeus, 1758)	1		
Solidago canadensis L.			*Pieris brassicae* (Linnaeus, 1758)	5		
Sorbus aucuparia L.			*Pieris napi* (Linnaeus, 1758)	1		
Spiraea tomentosa L.			*Platyptilia nemoralis* Zeller, 1841	1		
Stellaria graminea L.			*Plusia festucae* (Linnaeus, 1758)	1		
Stellaria palustris Retz.			*Rusina ferruginea* (Esper, 1785)	1		
Urtica dioica L.			*Scopula immutata* (Linnaeus, 1758)	2		
Veronica chamaedrys L.			*Scotopteryx chenopodiata* (Linnaeus, 1758)	3		
Viola palustris L.			*Synaphe punctalis* (Fabricius, 1775)	1		
			Thalpophila matura (Hufnagel, 1766)	1		
			Thyatira batis (Linnaeus, 1758)	1		
			Timandra comae A. Schmidt, 1931	2		
			Tineola bisselliella (Hummel, 1823)	1		
			Vanessa atalanta (Linnaeus, 1758)	1		
			Xestia baja (Denis & Schiffermüller, 1775)	19		
			Xestia c-nigrum (Linnaeus, 1758)	13		
			Xestia ditrapezium (Denis & Schiffermüller, 1775)	25		
			Xestia stigmatica (Hübner 1813)	1		
			Xestia xanthographa (Denis & Schiffermüller, 1775)	16		

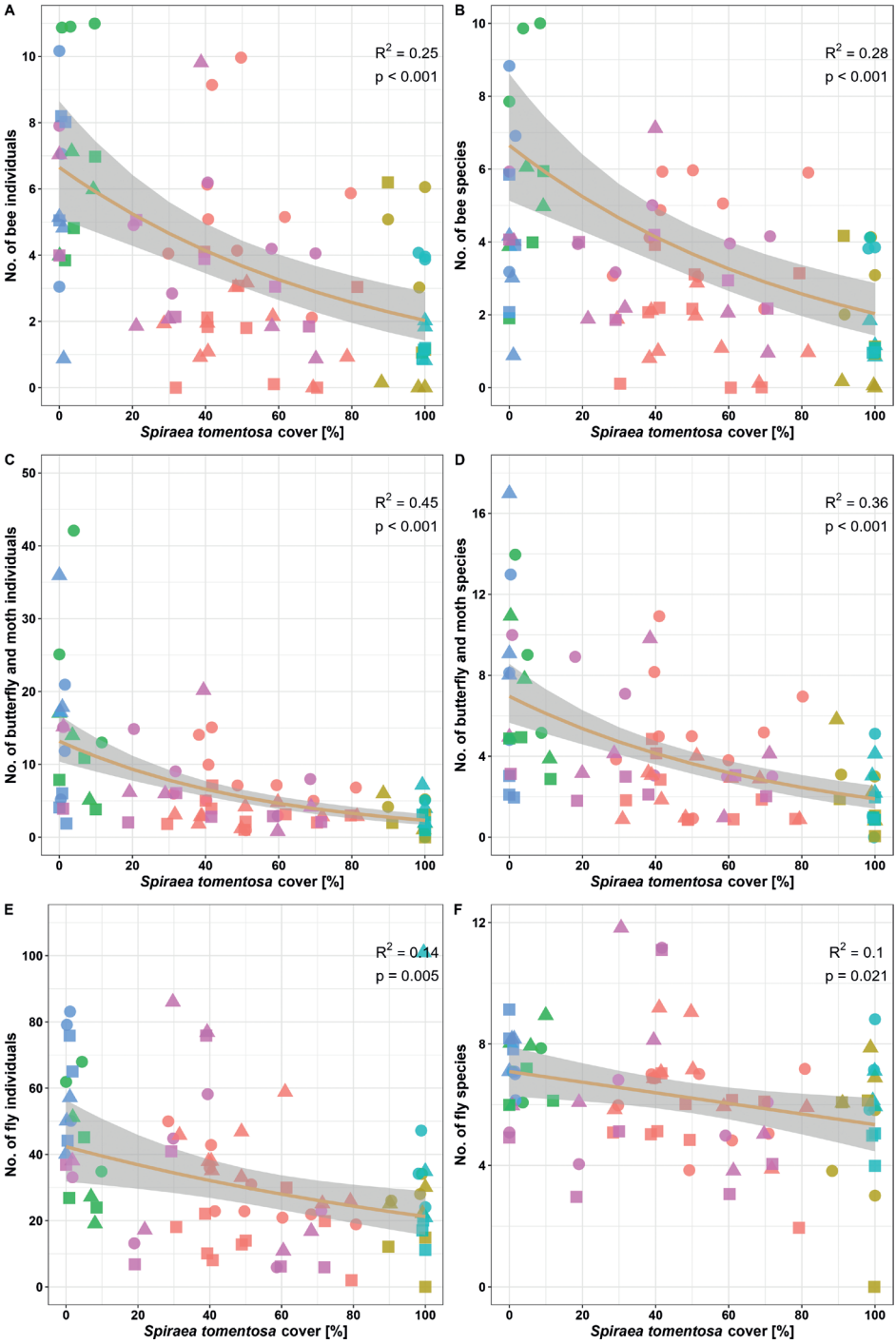

Figure 3. The relationship between abundance of **A** bees **C** butterflies and moths and **E** flies, as well as species richness of **B** bees **D** butterflies and moths **F** flies and site cover by *Spiraea tomentosa*. Points represent each of 81 surveys. Point colours correspond to a meadow and point shapes correspond to a survey number. Legend as in Fig. 2.

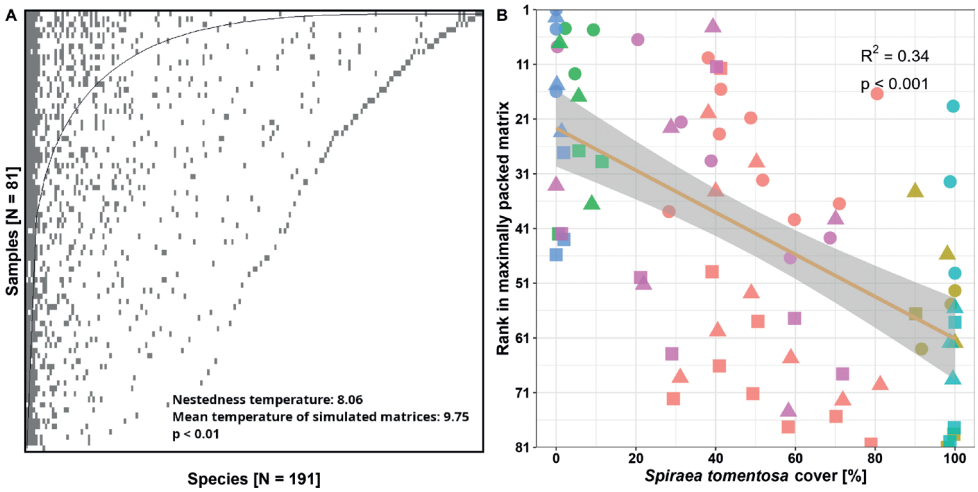

Figure 4. Nestedness structure of pollinator communities in the study sites **A** maximally packed matrix and **B** single ranks (points) for each pan trap depending on *Spiraea tomentosa* cover. Legend as in Fig. 2 and Fig. 3.

Discussion

The direction (negative vs. positive), the shape (linear vs. non-linear) and the strength of the relationship between the abundance of the invasive species and the diversity of native species determine which invaders pose the greatest threat to ecosystems (Bradley et al. 2019). It is often indicated that the impact of some invading species is proportional (linearly related) to its density or abundance in a habitat (Yokomizo et al. 2009; Elgersma and Ehrenfeld 2011; Panetta and Gooden 2017; Sofaer et al. 2018), but there is also much evidence that the impact of other invaders may elicit a non-linear response from native species (Elgersma and Ehrenfeld 2011; Panetta and Gooden 2017; Moroń et al. 2019).

In our research, we found a strong, negative, linear impact of the *Spiraea tomentosa* cover on vascular plant species richness, so this result positively validates the hypothesis. Our results showed that the diversity of plants decreased due to the increased invasive shrub coverage. These results correspond with a global meta-analysis that assessed the direction, shape and strength of the response of native communities to the increasing abundance of invasive species (Bradley et al. 2019). It was found that most often the impacts of invasive plants on native plant communities (at the same trophic level) are significantly negative and linear. However, the average impact of invasive plants on the diversity of native plants, estimated at 28% (Bradley et al. 2019), is much smaller than that shown for *S. tomentosa* in our research (60%).

In other studies on the impact of alien species on plant species richness, it was found that, amongst alien species entering wetlands in Central Europe, the invasion of *Mimulus guttatus* DC and *Impatiens glandulifera* Royle does not reduce the species richness of native plants. The invasion of *Solidago gigantea* Aiton and *Rudbeckia laciniata* L. decreases species richness by about 26% and 30%, while the invasion of *Fallopia sachalinensis* (F. Schmidt) Ronse Decraene, *F. japonica* (Houtt.) Ronse

Decraene and *F.* ×*bohemica* (Chrtek & Chrtková) JP Bailey contributes to the reduction of species richness by 86%, 73% and 66%, respectively (Hejda et al. 2009). Amongst the species entering wetlands, the impact of *S. tomentosa* on plants is, therefore, comparable to the impact of alien *Fallopia* sp. considered as an example of transformer species (Sukopp and Sukopp 1988; Cronk and Fuller 1995; Sukopp and Starfinger 1995), which changes the nature, condition and form or character of ecosystems (Richardson et al. 2000).

The direction, shape (linear vs. non-linear) and strength of the impact of an invasive plant species on insects, including potential pollinators, is more difficult to predict (Stout and Morales 2009; Lenda et al. 2010). When invasive species are at a lower trophic level, no consistent trend of impacts on native species or communities has been demonstrated (Bradley et al. 2019). This is due to the properties of environments that have different buffering potentials, for example, due to the condition of the recipient's native ecosystem (e.g. Mason and French (2007); Pyšek et al. (2012)), different redundancy of the food web (Gilbert and Levine 2013), as well as properties of the invasive species themselves. The role of the invasive species impact on pollinator assemblages is ambivalent – some of them increase the base for pollinators (Moragues and Traveset 2005; Bartomeus et al. 2008; Hejda et al. 2009; Stout and Morales 2009), while others may limit it (Vanbergen et al. 2018). Reducing plant diversity is considered to be a factor that is directly manifested in reduced food resources for pollinating insects (Potts et al. 2003; Moroń et al. 2008; Senapathi et al. 2015, 2017), but, as noted by Vanbergen et al. (2018), surprisingly little research unequivocally indicates the negative impact of invasive species on the diversity or abundance of pollinators.

In our research, we found a strong, negative, linear influence of *S. tomentosa* on the abundance and diversity of flower visitors, which allows us to positively verify our hypothesis regarding the negative effect of the shrub cover on potential pollinators.

Butterflies and moths seem to be least resistant to *S. tomentosa* infestation, as in dense populations of this shrub, the number of individuals decreased by 80% and species richness was reduced by 70%. The strong response of this group of insects is understandable, because Lepidoptera species strongly depend on plants throughout their life cycle – they use them for breeding and as a source of food for larvae and adults (Altermatt and Pearse 2011), resulting in their limited resistance to disturbance. Butterflies and moths have been shown to suffer from invasion, because alien plant species can replace beneficial native partners (Lenda et al. 2013; Trigos-Peral et al. 2018) and many butterfly species are recognised as food specialists, functionally constrained to exploiting a limited group of plants (Tallamy and Shropshire 2009), for which food source redundancy is relatively low (Moroń et al. 2019). Moreover, invasive plants due to their low nutritional value or toxicity may reduce their reproductive success and consequently lead to genetic bottlenecking (Davis and Cipollini 2014). Some of these plants can also affect the herbivores to become more attractive to predators (Bezemer et al. 2014). Although shoots and leaves of *S. tomentosa* can be used as a food source by a native moth species – *Earias clorana* larvae (Wiatrowska et al. 2018b), our results indicate that the buffering mechanism is not observed and butterflies, as well as moths, react quickly and very negatively to *S. tomentosa* invasion.

Other insects that have strong, often reciprocal, relationships with native species of flowering plants include bees. Pollinator bees are very sensitive to a particular diet source and combination of nutrients (Harmon-Threatt and Kremen 2015), such as the ratio of various essential amino acids (EAA) to carbohydrates and show poor growth and survival when reared on monotype or non-optimal nutrition diets (Vanbergen et al. 2018). It was found that the protein content of pollen varies with the plant species (Roulston et al. 2000), which influences the pollen-feeding behaviour of bees (Cook et al. 2003; Keller et al. 2005). The reduction or elimination of specialised partner plant populations is particularly important for certain solitary bee species that have specialised relationships with flowering plants (Mueller and Kuhlmann 2008). It is also known that even generalist bee species (which often benefit from abundant resources of mass-flowering invasive plants; Stout and Morales (2009)) require diverse sources of floral pollen, because pollen from different plant species varies in digestibility and nutrient content (Roulston et al. 2000). In our research, we found that bees are almost as sensitive to *S. tomentosa* invasion as butterflies. In dense populations of the shrub, a reduction in the number of bees by 60% was recorded and bee species richness decreased by 70%, which indicates that *S. tomentosa*, despite the large supply of pollen, which constitutes the majority of bee nutrition (Stout and Morales 2009), seems not to be attractive for this group of insects. It is worth noting that the response of bee populations to the presence of *S. tomentosa* in the ecosystem seems to be different in the area of the natural occurrence of the shrub and outside it. In North America, *S. tomentosa* offers both pollen and nectar as pollinator rewards and it is recognised as a species that attracts bumblebees (LaRosa et al. 2004). In Europe, the shrub provides only pollen, which may reduce its attraction to flower visitors looking for nectar. The differences between resources provided by *S. tomentosa* flowers in its native range and in invaded areas may be a result of the pollinator density differences between these areas (Muñoz and Cavieres 2008) or the lack of adaptation to obtaining flower reward (e.g. Liu and Pemberton 2009). However, the latter is unlikely in the case of *S. tomentosa* flowers, which are morphologically similar to flowers of other *Spiraea* species that naturally occur in Central Europe (Mirek et al. 2002).

Another important order amongst insects pollinating flowers around the world are flies from the Syrphidae, Bombyliidae and Muscoidea families (Larson et al. 2001), but also other erroneously overlooked Diptera pollinators (Ssymank et al. 2008; Orford et al. 2015). Amongst all the studied groups of pollinators, flies are the least specialised in flowers, because even though they use pollen and nectar, they also use other food sources (Brock 2015). Additionally, for this group of potential pollinators, a negative effect of *S. tomentosa* coverage on their number and diversity was revealed, but with the lowest impact. In dense populations of this shrub, a reduction in the number of individuals by 45% and reduction in species richness by 30% were found, which may result from the lowest dependence on a specific food source, but also from their greatest mobility amongst the studied groups of insects (Van Veen 2004). Unlike bees, whose females build nests for their offspring and are associated with them because they procure larval cells in the nest, expand it and sleep in it (Batra 1984), many flies have great power of dispersal spread and they are found far from their site of development (Ssymank 2001; Van Veen 2004).

For all the studied groups of potential pollinators, it was found that the influence of *S. tomentosa* is proportional to its density coverage. The number of individuals and richness of butterflies and moths, bees and flies significantly, linearly decreased with the increase in the steeplebush cover, which supports the thesis that the impact, at least of some invasive plants, is proportional to invader population density (Yokomizo et al. 2009; Elgersma and Ehrenfeld 2011; Panetta and Gooden 2017). Moreover, the potential pollinator community assemblages seem to be affected as *S. tomentosa* cover increases (Fig. 4). Changes in the community assemblages are a result of species loss rather than the constitution of new communities by species replacement. Thus, in areas highly impacted by invasive steeplebush, only a part of the original pool of species can persist. The next step should be to identify traits which make some species less vulnerable to biological invasions (Moroń et al. 2021).

Most studies indicate that the impact of invasive species on potential pollinators depends on whether the invasive species reduces resources, upon which the native species depends and also whether it acts as a novel resource for the native species (Bradley et al. 2019). In the case of the goldenrod (*Solidago canadensis*) invasion, it has been found that this plant reduces the resources, on which native pollinator species depend (it has a linear negative effect on plants). At the same time, it is also a food source for some butterflies and bees (Fenesi et al. 2015), which can cause a buffering effect and result in a non-linear plant impact on pollinators (Moroń et al. 2019). In the case of *S. tomentosa*, we found that this shrub is highly competitive with native plant species and displaces species of wet meadows, which reduces the resources available to native pollinators. Moreover, despite the large supply of pollen steeplebush is not attractive for most pollinators (Wiatrowska et al. 2018a), it does not have compensating properties that would buffer the displacement of native species, which is manifested in a strong, negative, linear response of potential pollinators to *S. tomentosa* invasion.

Conclusions

Effective nature conservation and management of invasive plant species should be based on a comprehensive understanding of the role they play in our ecosystems (Barney 2016). We found that *S. tomentosa* invasion in the wetland ecosystem has a very strong negative effect on the populations of plants and potential pollinators. In the areas invaded by this shrub, only a small part of the native species pool may persist, which implies that *S. tomentosa* should be considered as a transformer species.

The number and diversity of plants, butterflies and moths, bees and flies change at all points in the *S. tomentosa* invasion pathway (representing a linear response to invasion). Although it was assumed that invasive plant impacts are highly scale-dependent (Powell et al. 2013; Rejmánek and Stohlgren 2015), our study is the first to show such an unequivocal negative, linear effect of an invasive species impact on the abundance and diversity of potential pollinators.

Many studies showed that the management effort in the case of invasive species populations largely depends on the density–impact curve of the species and optimisation of management relies on minimising the sum of the costs of their impact and management (Yokomizo et al. 2009). For a linear effect of *S. tomentosa* on plants and potential pollinators, it can be expected that the benefits of controlling this plant will be proportional to the effort involved. As the strong negative impact of this shrub population is observed even at a small density of its population, the control of this plant population at the initial stage of invasion, before its indiscriminate spreading, seems to be the best and most promising approach.

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Appendix 1

Table A1. List of study sites.

Study sites	The nearest village	Geographical coordinates (DMS)	*S. tomentosa* cover (%)
1	Ruszów	51°23'39"N, 15°09'26"E	80
2	Ruszów	51°23'38"N, 15°09'28"E	40
3	Ruszów	51°23'36"N, 15°09'26"E	40
4	Ruszów	51°23'33"N, 15°09'30"E	50
5	Ruszów	51°23'31"N, 15°09'30"E	50
6	Ruszów	51°23'29"N, 15°09'31"E	30
7	Ruszów	51°23'26"N, 15°09'47"E	70
8	Ruszów	51°23'26"N, 15°09'44"E	60
9	Ruszów	51°23'26"N, 15°09'40"E	40
10	Poświętne	51°22'42"N, 15°14'03"E	90
11	Poświętne	51°22'41"N, 15°13'57"E	100
12	Poświętne	51°22'43"N, 15°13'49"E	100
13	Ołobok	51°18'32"N, 15°15'54"E	5
14	Ołobok	51°18'33"N, 15°15'51"E	10
15	Ołobok	51°18'35"N, 15°15'52"E	0,5
16	Gozdnica	51°24'45"N, 15°04'06"E	100
17	Gozdnica	51°24'44"N, 15°04'04"E	100
18	Gozdnica	51°24'45"N, 15°04'02"E	100
19	Iłowa	51°30'11"N, 15°11'11"E	0
20	Iłowa	51°30'12"N, 15°11'10"E	0
21	Iłowa	51°30'13"N, 15°11'11"E	0
22	Stary Węgliniec	51°17'55"N, 15°11'06"E	20
23	Stary Węgliniec	51°17'55"N, 15°11'03"E	60
24	Stary Węgliniec	51°17'57"N, 15°11'07"E	70
25	Stary Węgliniec	51°17'59"N, 15°11'20"E	40
26	Stary Węgliniec	51°17'59"N, 15°11'22"E	30
27	Stary Węgliniec	51°17'58"N, 15°11'18"E	0

Appendix 2

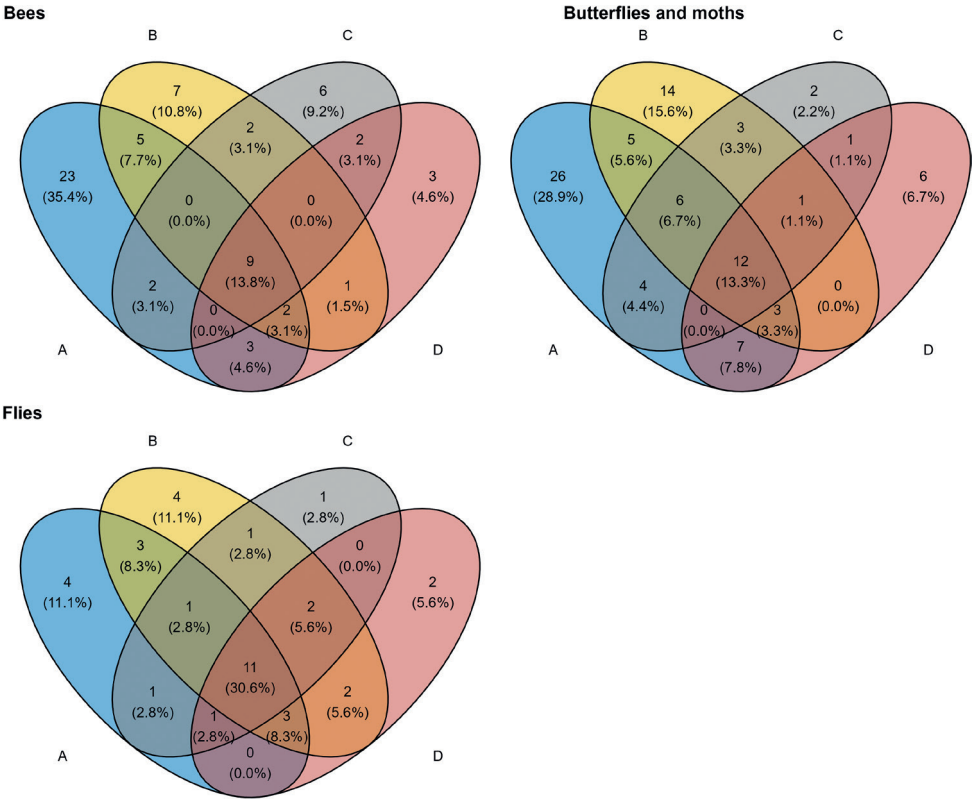

Figure A1. Venn diagrams showing the overlap between bee, butterfly (and moths) and fly species for four classes of *S. tomentosa* cover.

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RESEARCH ARTICLE

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Advancing research on alien species and biological invasions

Rarely naturalized, but widespread and even invasive: the paradox of a popular pet terrapin expansion in Eurasia

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Abstract

The North American terrapin, the red-eared slider, has globally recognized invasive status. We built a new extensive database using our own original and literature data on the ecology of this reptile, representing information on 1477 water bodies throughout Eurasia over the last 50 years. The analysis reveals regions of earliest introductions and long-term spatio-temporal dynamics of the expansion covering now 68 Eurasian countries, including eight countries reported here for the first time. We established also long-term trends in terms of numbers of terrapins per aquatic site, habitat occupation, and reproduction success. Our investigation has revealed differences in the ecology of the red-eared slider in different parts of Eurasia. The most prominent expression of diverse signs of invasion success (higher portion of inhabited natural water bodies, higher number of individuals per water body, successful overwintering, occurrence of juvenile individuals, successful reproduction, and establishment of populations) are typical for Europe, West Asia and East Asia and tend to be restricted to coastal regions and islands. Reproduction records coincide well with the predicted potential range based on climatic requirements but records of successful wintering have a wider distribution. This invader provides an excellent and possibly unique (among animals) example of wide alien distribution, without the establishment of reproducing populations, but through the recruitment of new individuals to rising pseudopopulations due to additional releases. Therefore, alongside the potential reproduction range, a cost-effective strategy for population control must take in account the geographical area of successful wintering.

Graphical abstract

Keywords
Alien species, biological invasions, global change, invasion ecology, nature conservation, wintering

Introduction

The growth of the global human population and the development of international transport networks has resulted in mass translocations of biological species outside of their native ranges, that have led to the homogenization of the Earth's biota within potential ecological niches (McKinney and Lockwood 1999; Seebens et al. 2020). Intentional and unintentional biological invasions represent considerable issues for native biodiversity, economic activities and even human health (Gilpin 1990; Vitousek et al. 1996; Mazza et al. 2014).

The invasion of alien amphibians and reptiles has significantly accelerated since the middle of 20th century (Kraus 2009; Capinha et al. 2017). Alongside the brahminy blindsnake *Indotyphlops braminus* and common house gecko *Hemidactylus frenatus*, the

pond slider *Trachemys scripta* (Schoepff, 1792) is one of the three most widespread alien reptiles globally (Capinha et al. 2017). The native range of the pond slider *Trachemys scripta* is restricted to central, southern and southeastern United States and the adjacent portion of Mexico (Rhodin et al. 2017). This species of terrapin consists of at least three subspecies. Subspecies *T. s. scripta* (yellow-bellied slider) and *T. s. troostii* (Cumberland slider) are kept and bred in captivity substantially less often compared with *T. s. elegans* (red-eared slider). The last taxon became very popular as a pet animal, sometimes also an ornamental pond animal, and has been one of the most-traded reptiles since the middle of the 20th century. Export from the United States to other countries reached millions of individuals per year (Telecky 2001; Reed and Gibbons 2003). Since the end of 20th century, large-scale commercial breeding of *T. s. elegans* also started in China and countries of Southeast Asia where it is used for human consumption (van Dijk et al. 2000). These active and mobile reptiles often escape captivity.

Young red-eared slider individuals are small and brightly colored, making them very attractive for aquarists. However, these animals grow rapidly, and large individuals require more space, are less visually appealing, aggressive and may bite. Releasing them into the nearest water body is a common way to get rid of an annoying pet. This terrapin easily adapts to outdoor conditions and can reproduce and establish stable populations in regions with an appropriate climate (Rödder et al. 2009; Heidy Kikillus et al. 2010). Once established, the slider may induce a negative impact on native macrophytes and hydrobionts (Ficetola et al. 2012). Amphibians are regarded to be especially vulnerable because this terrapin feeds on tadpoles, and the presence of chemical cues released by this predator can affect the development rate and size at metamorphosis of tadpoles (Polo-Cavia et al. 2010; Vodrážková et al. 2020). The red-eared slider is more aggressive and has higher reproductive characteristics and, hence, may successfully compete with native terrapin species for food, basking sites and, possibly, egg-laying places (Cadi and Joly 2003; Perez-Santigosa et al. 2008; Pérez-Santigosa et al. 2011; Polo-Cavia et al. 2011; Pearson et al. 2015). Experimental studies have confirmed a higher mortality of native European pond terrapin in the presence of the invasive red-eared slider (Cadi and Joly 2004). In addition, this alien terrapin can induce the genetic pollution of populations of native terrapins due to introgression (Parham et al. 2013) and is involved in the life cycles of native parasite species, while also acting as a vector for the invasion of alien parasites, which are capable of infecting native terrapins and increase the risk of epizootics, causing mass mortalities (Iglesias et al. 2015; Demkowska-Kutrzepa et al. 2018). Moreover, this alien reptile can carry the agents of salmonellosis, which is dangerous for human health (Nagano et al. 2006; Shen et al. 2011). For these reasons, the trade of small-sized (<10 cm) individuals of red-eared slider was banned in the 1970s in the United States and import of this reptile to Europe has been entirely banned since 1997 (Ficetola et al. 2012).

Despite biosecurity efforts in some countries, today the pond slider (mainly red-eared slider) occurs in outdoor water bodies on all continents except Antarctica

(Ramsay et al. 2007; Ficetola et al. 2012; Rhodin et al. 2017). The invasive ranges of the pond slider *T. scripta* and its subspecies *T. s. elegans* in some regions of Eurasia were recently reflected in several scientific reviews (Sillero et al. 2014; Rhodin et al. 2017). However, regions of Eurasia significantly differ in volumes of primary data. The best studied region is West Europe (Sillero et al. 2014) whereas huge areas of North Asia, South Asia, and Middle and Central Asia (marked below as Central Asia) are commonly depicted as a blank spot, reflecting the absence of appropriate studies (Rödder et al. 2009; Heidy Kikillus et al. 2010; Ma and Shi 2017; Rhodin et al. 2017). Detecting the alien terrapins is easy in park ponds during warm seasons but may be a difficult task when direct spotting is limited by seasonality, weather (especially in northern regions), large water body size, macrophyte densities, and landscape features. In those cases, indirect express methods of detection, such as detection dogs, e-DNA or parasitological analysis of co-inhabiting hydrobionts, may be applied (O'Keeffe 2009; Kakuda et al. 2019; Reshetnikov and Sokolov 2020).

Modelling of potential ranges of species is a popular direction of contemporary ecology; analyses have been performed for the red-eared slider, mainly at the species level using available datasets and on different geographic scales (e.g., Ficetola et al. 2009; Rödder et al. 2009; Heidy Kikillus et al. 2010; Masin et al. 2014; Banha et al. 2017). However, physiological differences of subspecies are debatable and individuals of other subspecies are less common in regions outside their native distribution. Importantly, additional primary data from extensive, previously unstudied, regions can alter knowledge about its niche and, hence, its potential distribution.

Different definitions of the term "invasive species" have been proposed based on ecological and/or practical approaches (e.g., Jeschke and Strayer 2005; Beck et al. 2008; Blackburn et al. 2011). We suggest that the main features of an invasive alien taxon are establishment of self-sustaining populations and their significant effect on native ecosystems. Due to assumed negative influences on freshwater ecosystems, the widely spread subspecies *T. s. elegans*, is regarded as an invasive taxon in Europe and North Asia (European Commission 2016; Reshetnikov et al. 2018). However, despite the large volume of scientific publications on this animal, to date, data on negative impact of the red-eared slider upon native species are scarce in most regions of Eurasia (but see: Cadi et al. 2004; Perez-Santigosa et al. 2008) and geographic limits of its invasive populations are still debatable because confirmation of its successful reproduction is a complex task (Cadi and Joly 2004). We hypothesized that the invasion ecology, including establishment of populations, of this reptile in different colonized areas may differ and thus the invasive status of red-eared slider needs to be reviewed. A distinguishing feature of our investigation is the use of an integrated comprehensive database, with primary data collected by professional herpetologists from previously non-studied regions. Here, we aimed to analyze the invasion ecology of this alien reptile in different parts of Eurasia, establishing foundations for the verification of its invasive status and for an update of current biosecurity approaches.

Materials and methods

Data collection

For assessing the current distribution, the verified original records of the red-eared slider from 236 geographic localities were collected by the authors of this paper during their field inspections of water bodies in different regions of Eurasia in 2002–2020. Additionally, 1241 relevant records from 1968–2020 were obtained from scientific papers (Suppl. material 1), however 99.4% of these literature records are from 1990 and later, and 96.1% are from 2000 and later. All original data were subjected to rigorous verification. In doubtful cases, i.e., without georeferenced location or exact identification of terrapins by authors of observations, we requested and analyzed the coordinates of the localities, and photos with details of head and neck coloration for correct identification. The identity of 167 inconclusive cases (not included in the above-mentioned numbers) was not confirmed and they were therefore not included in the analysis. We also used two datasets (for Europe and Asia) from the Global Biodiversity Information Facility (GBIF; www.gbif.org) with records from 1978–2020. Assuming red-eared slider is an invasive taxon with described remarkable impact on native species (Cadi et al. 2004; Perez-Santigosa et al. 2008), and keeping in mind the absence of data on its impacts for the majority of the georeferenced records, we analyzed all above-mentioned data regardless of impact. The data were structured into categories depending on the source of data (original/literature/GBIF) and identification level (species/subspecies). We did not include in the analysis the available data on the presence of red-eared sliders in open water bodies on territories of zoological parks (e.g., Rupperswil, Klagenfurt, Belgrade, Sofia, Odessa, Moscow, Rostov-on-Don, Barnaul, Singapore, Izmir, Istanbul, Mersin, Antalya) because of likely management and care by staff (i.e., artificial wintering of adult terrapins, special conditions for egg incubation), but we used data from other urban parks. The original and literature records of the red-eared slider were distributed as follows: 713 in Europe, 589 in East Asia, 21 in North Asia, 61 in West Asia, 4 in Central Asia, 50 in South Asia, 39 in Southeast Asia (see Suppl. material 2 for delineation of the continent). The database of original and literature records is available in Suppl. material 3. The data from GBIF represented 5967 records from Europe and 31 records from Asia. Altogether, 1477 original/literature records and 5998 records from GBIF of *T. s. elegans* were included in the analysis (Fig. 1a).

Terminology

We used earlier suggested terms (Reshetnikov 2013) for discussion of the invasion process: a. initial introduction; b. center (source) of the secondary distribution, i.e., the region invaded by the alien species around the point of initial introduction serving as a source for further expansion; c. invaded subrange, i.e., part of the invaded range assumed to have originated from a single or a limited number of initial introductions, geographically separated from other invaded subranges, which may be temporally separated and later merged. Commonly, these processes are identified through the spatio-temporal analysis of records but additional tools, such as molecular-genetic methods, are also important.

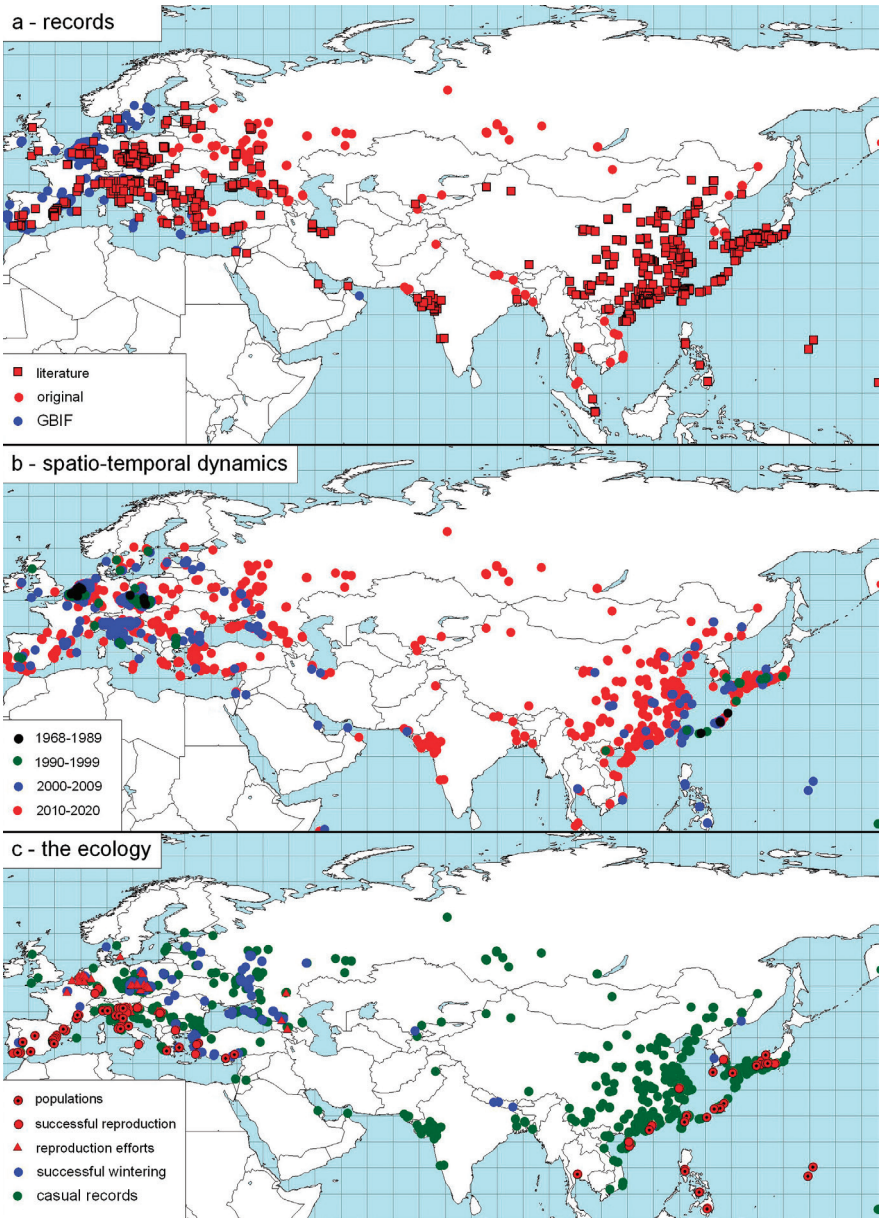

Figure 1. The geographical distribution of the red-eared slider *Trachemys scripta elegans* in Eurasia. **a** sources of data: 1 (red squares) – records from literature sources (see Suppl. material 1); 2 (red circles) – original records; 3 (blue circles) – records from GBIF.org (12 September 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.4qk7b3; https://doi.org/10.15468/dl.tppua3. The layers are located from 1 (above) to 3 (below) **b** spatio-temporal dynamics of records: 1 (black circles) – records of 1968–1989; 2 (green circles) – records of 1990–1999; 3 (blue circles) – records of 2000–2009; 4 (red circles) – records of 2010–2020. The layers are located from 1 (above) to 4 (below); **c** the ecology: 1 (red circles with dot) – records of established populations; 2 (red circles) – confirmed successful reproduction; 3 (red triangles) – unsuccessful reproduction attempts; 4 (blue circles) – confirmed successful overwintering; 5 (green circles) – records without information on ecology. The layers are located from 1 (above) to 5 (below).

Habitats, number of terrapins per water body, body sizes and ecology

We used all available georeferenced data (1968–2020) to understand the invasion ecology of this reptile in regions of Eurasia. Some original and literature records indicated habitat characteristics (N=1219), number of sliders per water body (N=963), measure of slider sizes (carapace length, CL, with accuracy ± 1cm) and/or distant assessing of sizes (with an interval of 5cm) (N=570), and information on ecology (N=270). The proportion of records with appropriate data are presented for each part of Eurasia separately in Table 1.

Table 1. Proportion of records (%) with appropriate data for each part of Eurasia.

	Europe	E Asia	N Asia	W Asia	S Asia	SE Asia	C Asia
Habitats	82.3	89.8	100	83.6	24.0	38.5	100
Numbers	75.3	54.5	95.2	93.4	22.0	33.3	100
Sizes	33.1	40.7	85.7	78.7	26.0	35.9	25
Ecology	26.2	6.1	4.8	50.8	6.0	28.2	100

We used data on latitude, longitude, date, habitat characteristics, number of individuals per water body, body sizes, and ecology to build correlation matrixes. Some parameters (habitat characteristics, body sizes, and ecology) were ranked as presented in Suppl. material 4. To assess the degree of synanthropy we used the above-mentioned data on habitats as continuing transition from habitats outside human settlements (lowest synanthropy) to recreational parks (highest synanthropization). When calculating relationships with sizes, we ignored scores "6" and "7" ("adults", "all sizes") as well as cases with several different sizes in the same water body. To build a histogram with body sizes, we included cases with several different sizes in the same water body (e.g., 1, 3 or 2, 3, 4); they were counted as separate cases of observations. Therefore, contrary to correlation analysis, the histogram with size classes represents analysis of cases of observations but not of water bodies. For assessment of the degree of reproduction success, we used data on ecology (see Suppl. material 4) after excluding score "1" ("casual records"). Therefore, the reproduction scale represents a continuum from just successful overwintering to established populations.

Species distribution models

We aimed to build two species distribution models (SDM) for red-eared slider: (a) the potential range of successful reproduction as an assessment of the probable area of population establishment (SDM1); (b) the potential range of successful overwintering as a probable area of long-term survival of released individuals (SDM2). The models were built using four sequential steps: (i) preparation of vector and raster layers; (ii) thinning of environmental variables and georeferenced records; (iii) selection of background areas for MaxEnt models; (iv) determination of MaxEnt model parameters; (v) building SDMs using MaxEnt.

i. Preparation of vector and raster layers. Vector layers of occurrence records were created in ArcGis 10.6.1 (Environmental Systems Research Institute 2020) using the full number of available records (9204 records: 1729 in the native and 7475 in Eurasian invasive parts of the slider range). Bioclimatic variables (all 19) were obtained from the WorldClim 2.1 dataset (Hijmans et al. 2005). In addition to this dataset, we also analyzed 16 predictor variables from the ENVIREM dataset (Title and Bemmels 2018), many of which are related to the ecology of the terrapin under study. Thus, we created raster layers for 35 environmental variables at a spatial resolution of 2.5 arc minutes (~5 km^2) for further analysis. This stage was common for both (SDM1 and SDM2) models.

ii. Thinning of environmental variables and georeferenced records. We tested for mulicollinearity amongst the potential predictor variables using two methods: the Pearson correlation coefficient, with a threshold value of > 0.75; and the variation inflation factor (VIF), with a threshold value of > 10 (Hair et al. 1995). The corSelect function in the fuzzySim package (Barbosa 2015) was used for these analyses. Based on these results, and the ecological requirements of the red-eared slider, we selected four predictor variables that were used in the SDMs. The selected four variables, their descriptions and links to slider ecology are as follows:

- BIO10 (defined as the mean temperature of the warmest quarter). This variable represents the availability of thermal energy, particularly for feeding activity, and was included because the northern distribution of red-eared sliders may be limited by low summer temperatures. This species requires water temperatures higher than 10 °C for the activation of feeding behavior, while the optimal soil temperature for embryonic development of eggs is 26–32 °C (Parmenter 1980).
- growingDegDays0 (defined as the sum of mean monthly temperature for months with mean temperature greater than 0 °C, multiplied by the number of days in that month). This variable reflects the duration of the ice-covered period, i.e., time without access to air oxygen. Red-eared sliders are assumed to have limited ability for long-term survival under anoxic conditions (Ultsch 2006).
- BIO18 (defined as levels of precipitation during the warmest quarter). This variable may be important for humidity-dependent embryonic development of skin-shelled eggs of red-eared sliders (Tucker et al. 1998).
- climaticMoistureIndex (defined as a metric of relative wetness and aridity). This variable is related to water availability and hence is a key factor for the stability of aquatic habitats (shallow water bodies), which may shrink during summer.

In our case, the maximum Pearson coefficient was PC=0.742 between the variables BIO10 and growingdegdays0, and the maximum VIF=6.8 for the variable BIO10.

We used a two-step procedure to identify and reduce the spatial autocorrelation of georeferenced records. We used the spThin package in R (Aiello-Lammens et al. 2015) to subsample the data ten times, using ten thinning parameters – the records were separated by distances of 10–100 km in intervals of 10 km. Then the ten datasets were subjected to a cluster analysis using the average nearest neighbor index (ANNI) in ArcGis 10.6.1 (Environmental Systems Research Institute 2020). After this

analysis, we chose the set of georeferenced records for which ANNI=1. As a result of this approach, we obtained a reduced dataset which was used for preparation of two datasets (DS1, DS2) for creating two bioclimatic models (SDM1, SDM2) accordingly (Suppl. material 6): the potential range of successful reproduction as an assessment of the probable area of population establishment (SDM1); the potential range of successful overwintering as a probable area of long-term survival of released individuals (SDM2). The first model was built based on georeferenced records (DS1) from the native range of the species in North America, taken from the International database GBIF (n=373 from GBIF.org (29 July 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.d88pay; we verified this dataset by comparing with the native range of *T. s. elegans* reported in Rhodin et al. 2017) and Eurasian original and literature records of successful reproduction and established populations (n=98). The second model, i.e., wintering range, was based on DS2 which included the above-mentioned datasets, with the addition of records of confirmed successful overwintering within Eurasia (n=124).

iii. Selection of background areas for MaxEnt models. We used the conventional choice of background localities from the presence region, here defined as the convex polygon, to build the two models (Rodda et al. 2011). However, the conventional choice of background localities in convex polygon may have some limitations as this minimizes the contrast between presence and absence, so we employed the recommendations presented in previous literature (Lobo et al. 2008; Lobo et al. 2010). These studies suggest selecting backgrounds from areas that are immediately adjacent to occupied habitats but are known to be unoccupied. For this reason, we combined convex polygons located in North America, southern Europe, East Asia, and Southeast Asia, which included appropriate georeferenced records. Background areas for the two models are presented in Suppl. material 6.

iv. Determination of MaxEnt model parameters. Although the SDMs built with MaxEnt (MaxEnt.jar; Dismo) (Phillips and Dudík 2008; Hijmans et al. 2017) using default parameters were based on extensive empirical material, some studies have shown that they can be inefficient (e.g., Muscarella et al. 2014). For this reason, we determined the optimal MaxEnt model parameters for each type of model using the AICc information criterion in the ENMeval R package (Muscarella et al. 2014). ENMeval applies three threshold-independent evaluation metrics: AUC_{Test}, AUC_{Diff}, and the size-corrected Akaike information criterion (AICc). AUC_{Test} is a metric that measures the discriminative ability of an SDM using georeferenced records that were not used when the model was built. AUC_{Diff} is the difference between the AUC calculated from the AUC_{Train} training sample and AUC_{Test}. This metric (AUC_{Diff}) is a measure of model overtraining. AICc, adjusted for small sample size, reflects the degree of fit and complexity (Muscarella et al. 2014; Guisan et al. 2017; Title and Bemmels 2018). The ENMeval package creates a number of MaxEnt models for each dataset using different regularization multiplier (RM) values and feature classes (FC), compares them using the AICc criterion and chooses the most appropriate model. This package typically selects a model that is less complex than the default model adopted by MaxEnt, with acceptable AUC_{Train} and AUC_{Diff} metrics (Halvorsen et al. 2016; Title and Bemmels 2018). Although we did not find any general trends in the selection of

FC, the FCs selected using the AICc models had higher RM values than the default value of 1.0 (Suppl. material 7). As a result, the following parameters were chosen for SDM1: feature classes (L = linear, Q = quadratic), and RM=4.0. For SDM2- feature classes (L = linear, Q = quadratic, H = hinge, P =product and T = threshold), and RM=4.0 (see Suppl. material 7)

v. Building SDMs using MaxEnt. Species distribution models were built using the maximum entropy method by MaxEnt 3.4.1 with optimal MaxEnt parameters (Hijmans et al. 2017). When training the models, we used occurrence records and background areas as presented in Suppl. material 6. We used a 'sre' strategy for the random generation of the background (pseudo-absence) (PA) points using the Biomod v.2.0 R package. The number of PA points generated (as recommended by Barbet-Massin et al. 2012) was according to the number (N) of georeferenced records (if N ≤ 1000 then 1000 points were selected, otherwise 10,000 points were selected). At the next stage, we projected the MaxEnt models with optimal parameters onto the territory of Eurasia. Final versions of these models were built as a result of 10 MaxEnt runs to randomly select test and training georeferenced records. In all MaxEnt runs, 80% of the records were used as training samples while 20% served as test samples. We used the Boyce index (Bind) to assess model performance (Boyce et al. 2002; Di Cola et al. 2017), with the help of the EcoSpat R package (Di Cola et al. 2017). The Boyce index lacks the drawbacks present in the AUC index (Lobo et al. 2008; Guisan et al. 2017; Petrosyan et al. 2020).

Analysis of niches

To analyze the features of environmental factors favorable for successful reproduction of the studied terrapin, a comparative analysis of the centroids (mean positions of species localities in relation to environmental factors) of niches for several predictor variables in three parts of the range (Europe, West Asia, and East Asia) was carried out. These parts of the range were selected because of sufficient records of four ecological characteristics: confirmed successful overwintering, unsuccessful reproduction attempts, confirmed successful reproduction, and established populations. Comparative analysis was performed using GLM ANOVA (see section Statistics) based on raw values of ecologically important predictor variables (BIO10, BIO18, growingDegDays0, climaticMoistureIndex the same as used for the SDMs – see the methodology above).

Statistics

Normalized histograms were used for visualization of data on invasion ecology; means and standard errors are shown in the text as descriptive statistics. Spearman R rank correlation coefficient was applied for assessing possible relationships between measures of invasion ecology, date, and latitude and longitude. Statistical hypotheses were tested at 0.05 *p*-level. Multiple comparisons of the proportion of key habitat use by the red-eared slider in the three parts of the invaded range (Europe, West Asia, East Asia) for which there were enough data for appropriate statistical analysis was performed using

the chi-square statistical test and then the Tukey Post hoc test (Zar 2010). In addition, we also used the Shannon's index to assess body size diversity in these parts of the range. A comparative analysis of Shannon's indices for size diversity was made using the test proposed by Hutcheson (Magurran 1988).

Comparative analysis of niche centroids was made using the Generalized Linear Model (GLM) procedure. In this model, one way analysis of variance (ANOVA) was used with equal and unequal numbers of replicates in the cells. In all cases, type I analysis of variance models was used, i.e., fixed factor models. In the first ANOVA model we used the factor "geographic region" and compared species niche centroids (means of predictor variables) in different geographic regions (Europe, West Asia, and East Asia), i.e. we used one-way ANOVA with three levels of region factors. For the second group of the models, the factor "establishment success" was used, consisting of four levels of reproductive/establishment status (see above). This analysis is important to identify the range of environmental parameters favorable for successful reproduction. If an analysis of variance with fixed effects showed a significant difference in the level of factors, a test of multiple comparison, the Post hoc Tukey HSD was used to determine which levels of the factor differed from each other. For multiple comparisons with unequal variances according to Leuven's test, the Tukey-Cramer test with Welch's modification was used (Zar 2010). Prior to the analysis, all data were Log-transformed to achieve normal distribution of the GLM ANOVA residuals. This additional analysis is important because it allows us to test the validity of GLM ANOVA results using non-transformed data with residuals that differ from the normal distribution, as recommended in the literature (Zar 2010).

Statistical analysis was performed using basic and special packages in the R language in RStudio Version 1.2.5033 (RStudio Team 2020). We used MaxEnt.jar and a set of R packages spThin (Aiello-Lammens et al. 2015), ENMeval (Muscarella et al. 2014), EcoSpat (Di Cola et al. 2017), Biomod2 (Thuiller et al. 2021), Raster (Hijmans et al. 2022), Dismo (Hijmans et al. 2017), fuzzySim (Barbosa 2015) in RStudio Version 1.2.5033 (RStudio Team 2020) to build SDM models. In addition, we also used ArcGis 10.6.1 (Environmental Systems Research Institute 2020) to prepare raster layers of predictor variables, analyze the average nearest neighbor index, and visualize SDMs.

Results

Spatio-temporal dynamics and current occurrence range in Eurasia

Records from 1968–1989 fall into countries in Europe, West Asia, and East Asia. The earliest records were reported from the Czech Republic from 1968, southern Japanese islands from 1972, Israel from 1975, the Netherlands from 1980, and Belgium from 1982. Records from 1990–1999 occurred in more regions of Europe, West Asia, East Asia and expanded to Southeast Asia (the Czech Republic, Spain, Italy, Sweden, England, Romania, Germany, Belgium, the Netherlands, Poland, Israel, Japan, Thailand, Vietnam, Republic of Korea and the Taiwan Island). By 2010

this reptile was already known in all parts of Eurasia, except Central Asia and North Asia, but today it occurs in all parts of Eurasia. Spatio-temporal dynamics of records are shown in Fig. 1b.

Synanthropy

In the most studied parts of the continent, i.e., Europe and East Asia, the proportion of records in parks and other urban environments reaches 83.8 and 82.6% respectively (Fig. 2a). In West Asia, with 51 appropriate observations, records in human settlements reach 86.3% (Fig. 2a). In Europe, synanthropy of the red-eared slider is more typical for eastern regions (see Suppl. material 5). Despite the general assessment that synanthropy did not correlate to latitude (see Suppl. material 5), records of the terrapin outside urban territories and rural settlements (score 1) highlighted a negative correlation with latitude values in Europe ($R = -0.10$; $t(n-2) = -2.41$; $N = 587$; $p<0.05$) and a positive correlation with reproduction success ($R = 0.20$; $t(n-2) = 2.36$; $N = 135$; $p<0.05$). In Europe, more synanthropic groups of terrapins are more abundant (higher number of individuals per water body), and portion of registered synanthropic groups has increased over the years. In East Asia, synanthropy is less common in southern regions and, similarly to Europe, has increased over the years. In West Asia, more synanthropic groups are more abundant (see Suppl. material 5).

Distribution of red-eared sliders among the three types of habitats does not differ between the European and East Asian parts of the range, but habitat distribution in both regions significantly differe from habitat distribution in West Asia (Fig. 3). Remarkably, in all parts of the studied range, the proportion of records in the second habitat, i.e., records located in water bodies within human settlements but outside recreational areas, is significantly greater than that of habitats 1 and 3, sites outside human settlements and public parks (Fig. 3). In West Asia, the studied terrapin is found significantly more often in parks and other recreational areas (Fig. 3) compared with Europe and East Asia. The proportion of records in habitat 2 (Fig. 3) in West Asia is significantly less than in Europe and East Asia. The proportion of records in nature environments (habitat 1), i.e., outside human settlements, does not differ in the three regions ($p = 0.06$): 16, 14 and 17.5% in Europe, West Asia and East Asia, respectively (Fig. 3).

Number of terrapins per water body

The three regions with the highest number of observations, Europe, West Asia, and East Asia (Fig. 1a), have a remarkably higher percentage of water bodies with more than one red-eared slider individual per aquatic site compared with other parts of Eurasia: ($\chi^2 = 100.6$, df = 6, $P << 0.001$) (Fig. 2b). The highest portion of such water bodies was observed in East Asia (72.9%); here, the proportion of these water bodies was significantly higher than in Europe, 43.0% ($Z = 8.5$, $P << 0.01$). The mean number of slider individuals per aquatic site was 23.2±9.6 (1–4288; n=490)

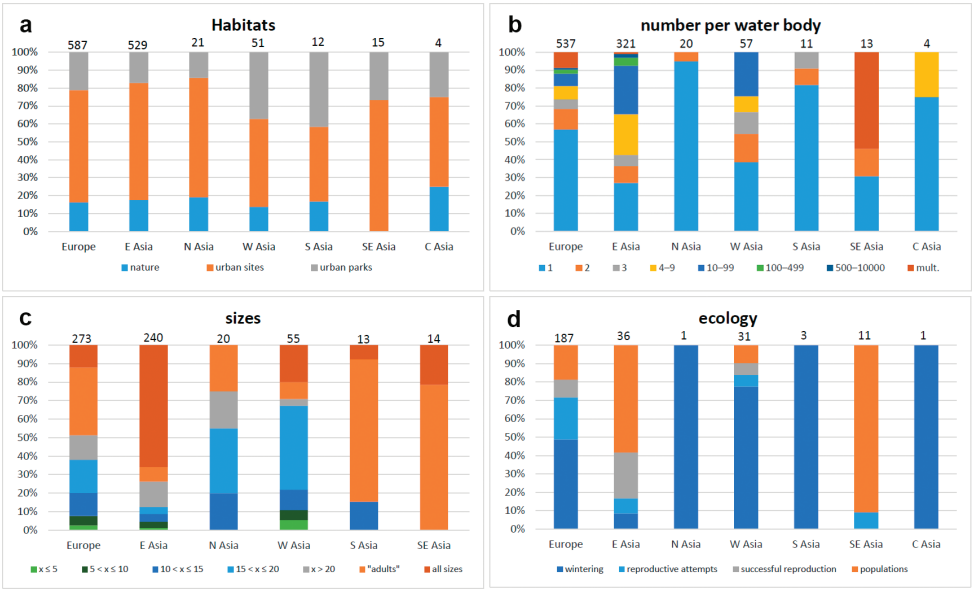

Figure 2. Ecological characteristics (left axis, %) and numbers of observations (at the tops of columns) of the red-eared slider *Trachemys scripta elegans* in different parts of Eurasia. **a** habitats: sites outside human settlements ("nature"); urban sites outside recreational zones ("urban sites"); public parks **b** number of individuals per water body (n) **c** body sizes (cm) **d** ecology: wintering; unsuccessful reproductive attempts; successful reproduction; establishment of populations. Colors are explained in the legends.

for Europe; 10.1±2.6 (1–98; n=57) for West Asia; 61.8±31.9 (1–10000; n=318) for East Asia (observations with an estimated number of "several individuals" were excluded from this calculation). Proportion of larger groups increased over the years in Europe (see Suppl. material 5). Here, the greatest numbers (>200 ind. per water body; 1186.4±537.1 (250–4288; n=7)) were reported in the 2000s in Spain (regions of Doñana National Park and Valencia (Perez-Santigosa et al. 2008; Sancho and Lacomba 2013). In East Asia, the greatest number (>200 ind.; 1425.4±860.6 (212–10000; n=11)) were noted in several regions of Japan and China (e.g., Taniguchi et al. 2017; Gong et al. 2018). We are not aware of such large groups of red-eared sliders in other parts of Eurasia. Ignoring these 18 extra-populated water bodies, the mean number of individuals in groups was 15.4±2.5 (2–191; n=485) for Europe, 15.8±4.0 (2–98; n=35) for West Asia and 17.6±1.9 (2–200; n=220) for East Asia. The number of individuals per water body in Europe correlated negatively with latitude in the original/literature dataset even after excluding seven extra-populated (>200 ind.) water bodies in southern regions ($R = -0.13$; $t(N-2) = -2.83$; $N = 485$; $p<0.01$). Such correlation is absent for water bodies in West Asia and East Asia ($R = -0.22$; $t(N-2) = -1.66$; $N = 57$; NS and $R = 0.02$; $t(N-2)=0.33$; $N = 305$; NS, respectively). However, the number of individuals correlates negatively with longitude in West Asia ($R = -0.29$; $t(N-2) = -2.22$; $N = 57$; $p<0.05$) and positively

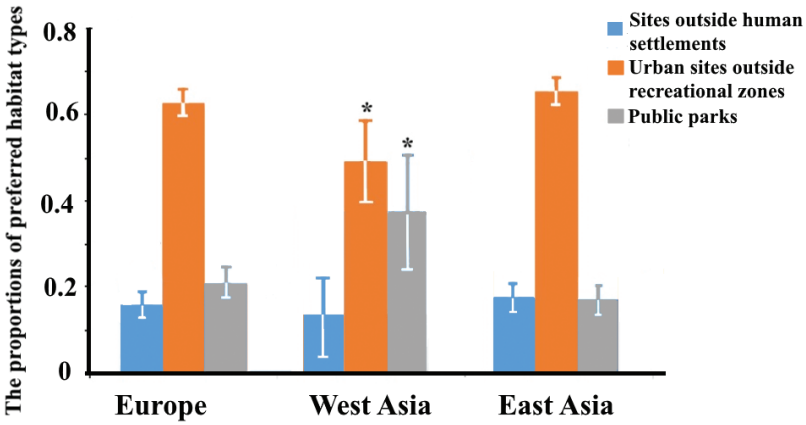

Figure 3. Comparison of the distribution of red-eared sliders among habitats in three different parts of the Eurasian invaded range. See details of habitat coding in Suppl. material 4. Whiskers show 95% Wald's confidence intervals. A multiple comparison of proportions of the same habitat types in different parts of the invaded range was performed using the Chi-square (Biotope 1: 12.5, df = 2, p = 0.001; Biotope 2: 1378.8; df = 2, p < 0.001; Biotope 3: 5.8, df = 2, p = 0.06) and Tukey's Post hoc tests. Significant differences between proportions of the same biotopes in different parts of the range are marked by *.

in East Asia (R = 0.19; t(N–2)=–3.36; N = 305; p<0.001) reflecting association with coastal regions, the Mediterranean coast in West Asia and the Pacific (seas of Pacific Ocean) coast in China.

Body sizes

Diversity and proportions of observations (not water bodies) of various size classes of red-eared slider in parts of Eurasia are presented at Fig. 2c. Below we discuss an assessment of the proportions of water bodies (%) inhabited by individuals of different size classes. Small individuals, with carapace length ≤ 10cm, are detected rarely: in 8.0, 12.5 and 4.6% of water bodies of Europe, West Asia, and East Asia, respectively. Including the category "all sizes", these percentages are 20.8, 33.3 and 70.4%, respectively. Big individuals with carapace length > 15cm were noted in aquatic sites of Europe, West Asia, and East Asia in 31.8, 52.1 and 17.5% or 88.1, 85.4 and 91.2% when including categories "adults" and "all sizes". Very big terrapins (> 20cm) were confirmed in 14.8, 4.2 and 13.7% of areas, respectively. In Europe, the occurrence of small individuals (≤ 10cm; scores 1, 2, 7) negatively correlated with latitude (R = –0.24; t(N–2)= –3.72; N = 236; p<0.001), longitude (R = –0.25; t(N–2)= –4.00; N = 236; p<0.001), positively correlates with number per water body (R = 0.57; t(N–2)= 10.27; N = 215; p<0.001) whereas occurrence of very big individuals (score 5) positively correlated with latitude (R = 0.17; t(N–2)=2.72; N = 236; p<0.01) and negatively correlates with longitude (R = –0.20;

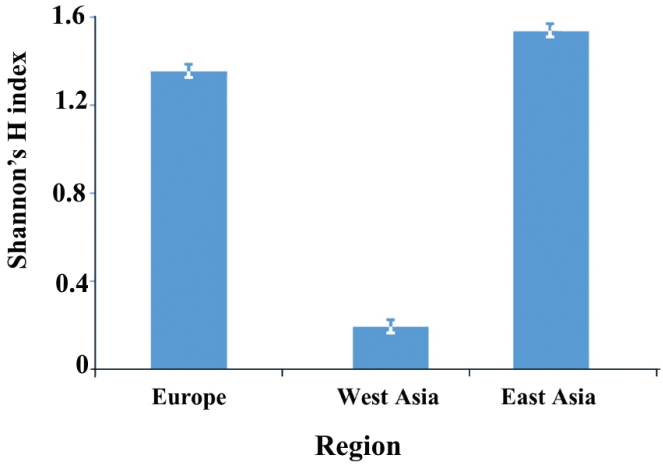

Figure 4. Shannon's index of body size diversity (H) for three different parts of the Eurasian invaded range. Whiskers show 95% Hutcheson's confidence interval.

t(N–2)= –3.09; N = 236; p<0.01). In West Asia, the occurrence of small individuals did not correlate with latitude or longitude (R = 0.16; t(N–2)=1.16; N = 48; NS and R = 0.16; t(N–2)=1.09; N = 48; NS); in East Asia, this size did not correlate with latitude (R = 0.06; t(N–2)=–0.20; N = 240; NS) but positively correlates with longitude R = 0.20; t(N–2)=3.18; N = 240; p<0.01). Therefore, occurrence of small-sized individuals positively correlates with coastal areas. Interestingly, in West Asia, registration of bigger individuals is more typical for water bodies with large groups of red-eared sliders and has increased over time (see Suppl. material 5).

Analysis of indices of the size diversity of terrapin individuals showed that in East Asia, Shannon's index (H = 1.53 ± 0.012) is higher than in Europe (H = 1.38 ± 0.015) and West Asia (H = 0.19 ± 0.032), i.e., body size diversity in East Asia is higher than in the other two parts of the range (Fig. 4). Hutcheson's test suggests the following ranked series for this index: H (East Asia) (t = 51.1; df = 220; p << 0.05) >> H (Europe) (t = 8.87; df = 114; p << 0.05) >> H (West Asia). Although data on the reproductive status in the studied parts of the range are limited, nevertheless, high H index values in East Asia and Europe suggest high size diversity with a sufficient number of both young and mature individuals in these parts of the range for the establishment of populations, if climatic conditions are appropriate.

Ecology

In all parts of Eurasia, except West Asia, the highest number of observations are casual records of red-eared sliders without additional information on ecology. For example, in the most studied regions, Europe and East Asia, the appropriate percentages of casual records are 73.8 and 93.9%, respectively. Multiple cases of unsuccessful reproduction attempts (e.g., egg laying) were registered in Europe and the Trans-Caucasus region,

whereas successful reproduction and even establishment of populations is reported from southern Europe, West Asia, East Asia, and Southeast Asia (Figs 1c, 2d). In European water bodies, successful wintering depended negatively on latitude (R = –0.23; t(N–2)=–6.22; N = 671; p<0.001; observations of successful reproduction and establishment of populations were also regarded as wintering points and included in the analysis here and below) and did not correlate with longitude (R = 0.03; t(N–2)=0.68; N = 671; NS) whereas successful wintering in West Asia and East Asia did not depend on latitude (R = 0.05; t(N–2)=0.42; N = 59; NS and R = 0.01; t(N–2)= 0.25; N = 586; NS, respectively). We found such a correlation with longitude for the water bodies of West Asia (R = –0.49; t(N–2)= –4.24; N = 59; p<0.0) and East Asia (R = 0.12; t(N–2)= 2.93; N = 586; p<0.01). We regarded the relationship between mortality during wintering and latitude using the example of the European part of Russia, a region with a remarkable climatic gradient of thermal conditions. Here, winter mortality was reported for 9.5% of water bodies. We did not find correlations between mortality events and latitude (R = 0.00; t(N–2) = 0.03; N = 73; NS) as dead individuals were registered in both northern (e.g., Saint-Petersburg, Moscow) and southern regions (e.g., Stavropol and Krasnodar territories, Voronezh province of Russia).

In Europe, reproduction is more effective in southwestern regions and positively correlates with terrapin abundance (see Suppl. material 5). In East Asia, reproduction is more successful in the eastern part. The registrations of reproduction have decreased over the years in both Europe and East Asia (see Suppl. material 5). The potential range of reproducing populations of the red-eared slider, as well as the potential range of successful wintering, are presented in Figs 5a, b.

Comparison of the mean values of the predictor variables shows that the niche centroids of the species in East Asia are characterized by relatively high values of mean air temperature in the warm season (T = 26.01 ± 0.46 °C, n = 35), precipitation (W = 676.4 ± 15.4, mm), climate moisture index (Mi = 0.4 ± 0.03), and total temperature above 0 °C (SigmaT = 7.78 * 10^4 ± 3207 °C) (Fig. 6). Some niche centroids in West Asia occupy an intermediate position (T = 23.4 ± 0.49 °C; n = 31; SigmaT = 5.868 * 10^4 ± 3408 °C; n = 31) compared to centroids in Europe and East Asia. The moisture index in the West Asian part of the range (Mi = -0.33 ± 0.03; n = 31) is significantly lower than in East Asia, but does not differ from Europe (Mi = -0.27 ± 0.02, n = 75). Concerning precipitation in the warm season, the niche of the red-eared slider in West Asia is characterized by the lowest precipitation (W = 82.3 ± 16.7 mm; n = 31). The centroids of temperature (T = 19.3 ± 0.32 °C, n = 75) and the sum of temperatures (SigmaT = 3.671 * 104 ± 2191 °C, n = 75) in Europe are characterized by the lowest values, do not differ in the humidity index from the West Asian part of the range, and occupy an intermediate position in terms of precipitation in the warm season of the year. The centroids of niches in East Asia differ significantly from two other analyzed parts of the range for all studied predictor variables (Fig. 6). Comparison of the mean values of the Log-transformed predictor variables using GLM ANOVA is presented in Suppl. material 8: fig. S4. It can be seen that Fig. 6 and Suppl. material 8: fig. S4 similarly display niche centroid positions across all predictor variables. The normal

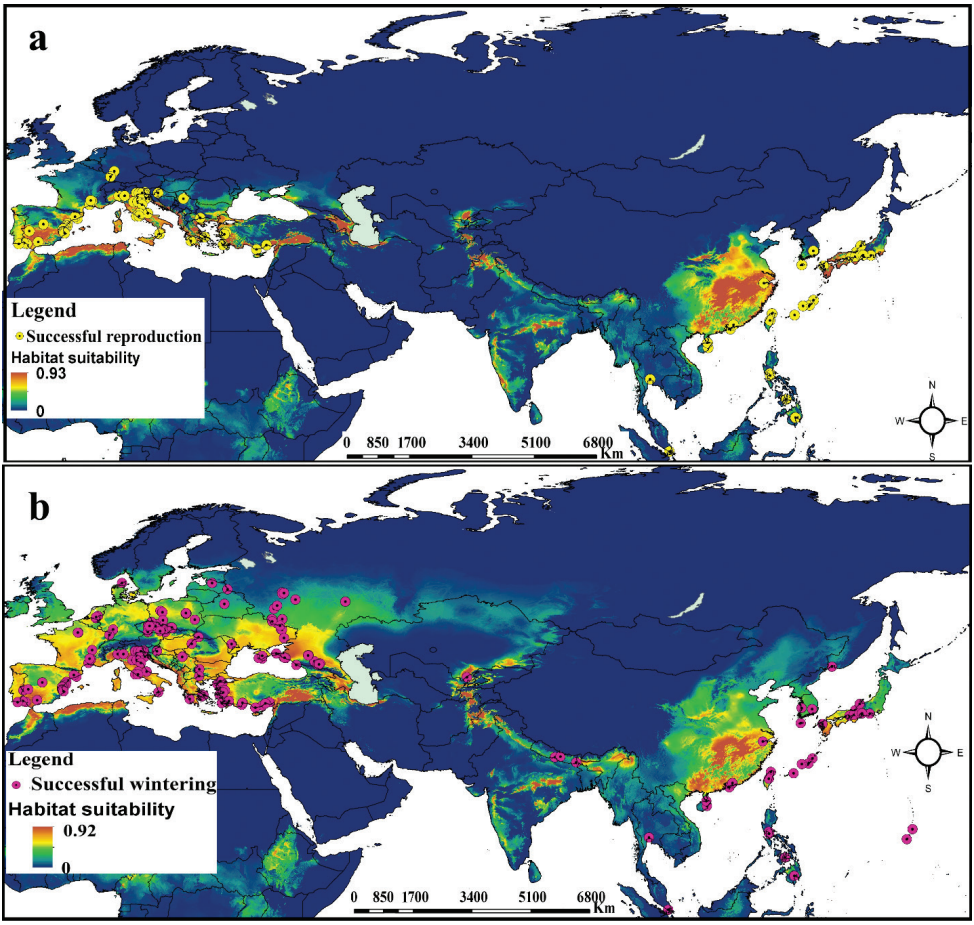

Figure 5. Potential distribution of the red-eared slider *Trachemys scripta elegans,* created with MaxEnt analysis of climatic requirements. **a** potential range of successful reproduction. Species Distribution Model has been built based on records of the native range of the red-eared slider within Northern America and records of successful reproduction and established populations within Eurasia (which are shown by yellow points) **b** potential range of successful wintering. Species Distribution Model has been built based on records used for Fig. 5a with the addition of records with confirmed successful wintering within Eurasia (which are shown by pink points).

distribution of GLM ANOVA residuals after Log-transformation for all variables suggests that conclusions regarding the significance of the centroid difference, established without data transformation, are correct.

A comparative analysis of the parameters of reproductive efforts in Eurasia showed that centroids 2 and 3 (wintering and egg laying) significantly differ from 4 and 5 (successful reproduction and establishment of populations) (Fig. 7). We combined centroids of 2 and 3 and presented them as level I and combined 4 and 5 as level II. The appropriate mean values and ranges of values for level I (n = 100) in Eurasia are as follows: T = 20.6 (range 19.1–21.21) °C; W = 298.5 (206.3–390.7) mm;

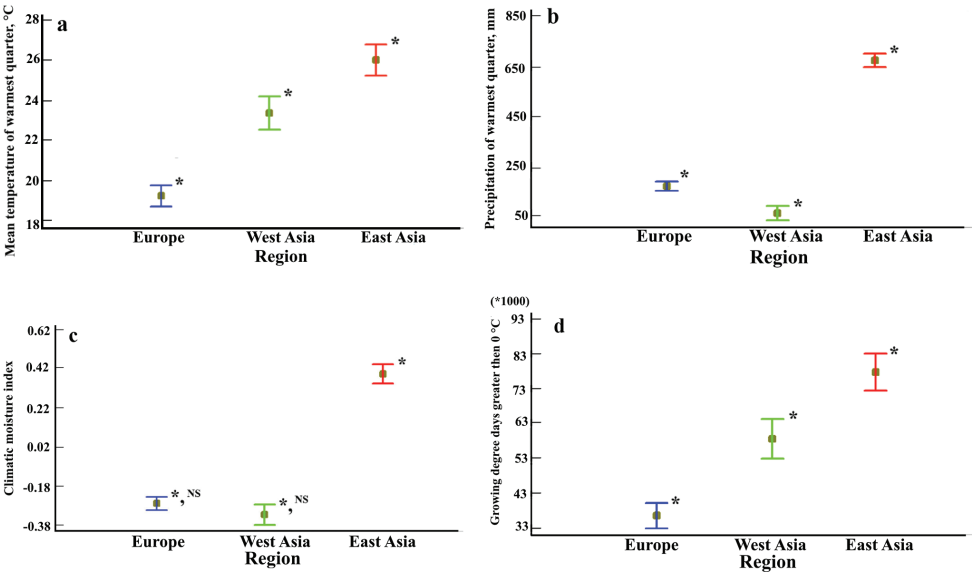

Figure 6. Comparison of mean values (± 95% Tukey HSD confidence intervals) of the main predictor variables of terrapin habitats in different parts of the invaded range. The results of one factor ANOVA based on General Linear Model are presented. The GLM ANOVA tested the main effects of regions: **a** $F = 78.31$, df = 2, $p < 0.01$ **b** $F = 424.21$, df = 2, $P < 0.01$ **c** $F = 196.42$, df = 2, $p < 0.01$ **d** $F = 58.62$, df = 2, $p < 0.01$ (F is Tukey HSD test; P-value is given for the factor effects). Significant differences of means according to Post hoc Tukey HSD test are marked by *. Absence of significant differences is marked as NS, i.e., values for Europe and West Asia do not differ from each other on Fig. 6c. Records with ecological characteristics 2–5 (see Methods) were used (so, we ignored casual records for this analysis).

Mi = -0.17 (-0.31 – -0.04); SigmaT = $4.152*10^4$ ($3.22*10^4$–$5.084*10^4$) °C and for level II (n = 41) are: T = 25.5 (24.4–26.7) °C; W=521.3 (410.2–631.0) mm; Mi = 0.15 (0.08–0.3); SigmaT = $7.294*10^4$ ($6.185*10^4$–$8.404*10^4$) °C. A comparative analysis of the parameters of reproductive efforts in Eurasia with Log-transformed data is presented in Suppl. material 8: fig. S4. Importantly, the results of comparing the niche centroids did not differ regardless of whether the original data are Log-transformed or not. Since the residuals of the GLM ANOVA models after Log-transformation of the predictor variables did not differ from the normal distribution, we therefore limited our comparison to mean values only.

Discussion

Spatio-temporal dynamics

The earliest reports of the red-eared slider in outdoor water bodies of Eurasia originate from the late 1960s – early 1970s in Europe (Rumburk, Czech Republic), where this animal was recorded in 1968 (Moravec and Široký 2006), and East Asia (Okinawa

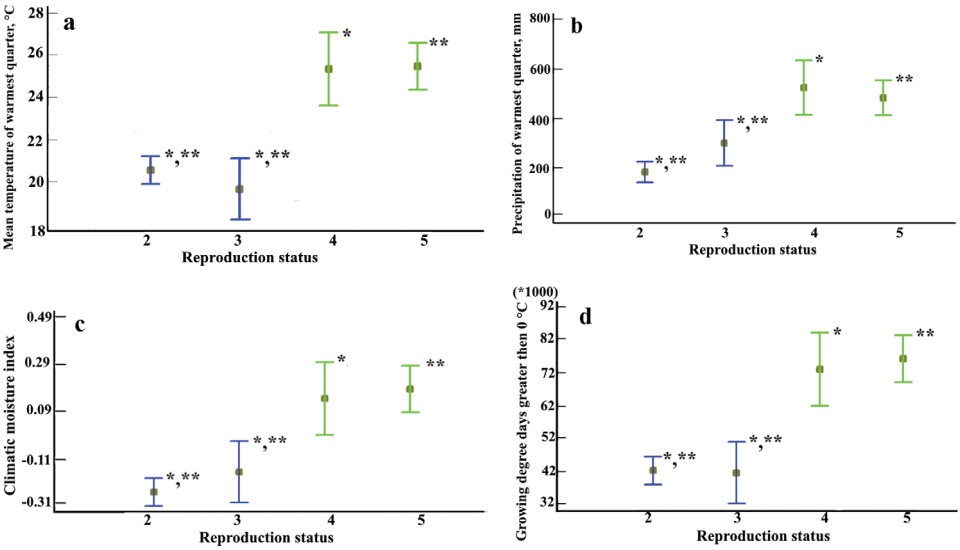

Figure 7. Comparison of mean values (± 95% Tukey HSD confidence intervals) of main predictor variables of terrapin habitats for records with different ecological/reproductive statuses. The results of one factor ANOVA based on General Linear Model (GLM) are presented. The GLM ANOVA tested the main effects of reproduction status (where 2 is confirmed successful overwintering; 3 is unsuccessful reproduction attempts, 4 is confirmed successful reproduction, 5 is established population): **a** F=23.5, df = 3, p < 0.01 **b** F = 20.92, df = 3, p < 0.01 **c** F = 19.7, df = 3, p < 0.01 **d** F = 24.4, df = 3, p < 0.01 (F is Tukey HSD test; p value is given for the factor effects). Statistically significant differences of means according to Post hoc Tukey HSD test between 4 and 2, 3 (separately) is marked by *; statistically significant differences of means between 5 and 2, 3 (separately) is marked by **. We did not compare means of categories 2 and 3 as they are rather similar. The same is true for 4 and 5.

Island, Japan), with detection in 1972 (Shimazu 2015). Soon after, this alien was also first detected in West Asia (Bethlehem, Israel) in 1975 (Bouskila 1986). Up to the beginning of 21st century, outdoor occurrence of the species under study was restricted mainly to Europe and East Asia, with less frequent reports in West Asia and Southeast Asia (Fig. 1b). Contrary to the invasion histories of some "classical" invaders such as the insect *Agrilus planipennis* or fish *Perccottus glenii* (e.g., Reshetnikov and Ficetola 2011; Orlova-Bienkowskaja et al. 2020), colonization by the red-eared slider did not have a limited number of initial introductions which became sources of secondary distribution with the potential establishment of invaded subranges. The geographical expansion of this reptile was driven by massive propagule pressure in different regions over the huge territory of Eurasia. Nevertheless, Europe and East Asia were the regions with earliest and greatest dissemination compared with other parts of the continent (Fig. 1b). To date, this terrapin species is present in almost all countries of Eurasia (Fig. 1a). It has been reported from 68 Eurasian countries. The original list of Eurasian countries colonized by red-eared slider is available in the Suppl. material 9.

Invasion ecology

Of course, data on ecological characteristics of the red-eared slider for some water bodies may be absent due to lack of appropriate observations. Nevertheless, our large-scale spatio-temporal approach (invasion within all of Eurasia during a 50-year period) reduces possible inaccuracies and allows us to reconstruct the invasion process within the studied continent. Our comprehensive database of primary data allowed us to compare ecological features of the red-eared slider in different parts of Eurasia. We found that the ecological niche of reproductive groups of the red-eared slider in East Asia differs from those in Europe and West Asia in terms of thermal energy and moisture (Fig. 6). This may be explained by the absence of the whole range of appropriate favorable environmental conditions in Europe and West Asia. Breeding groups of this invader are likely to occupy habitats with more favorable climatic conditions in East Asia, with higher temperature and humidity compared with other parts of Eurasia (Fig. 6). Despite the absence of appropriate records of reproductive success, our modelling confirms the existence of large territories favorable for reproduction in non-coastal regions of China and Azerbaijan, and southern Turkey, as well as limited regions of several other countries, including Kazakhstan (south), Iran (north), India, Nepal and others (Fig. 5).

Importantly, the red-eared slider inhabits mainly urban and rural environments (Fig. 2d) because the principal invasion vector is pet release (Semenov 2010; Banha et al. 2017). It is not surprising that synanthropic groups of this terrapin are more abundant, as it has been shown for Europe and West Asia. However, the distribution of red-eared sliders is not limited by territories of human settlements, where this terrapin is often used for decoration of ponds. This invader has already been detected in natural environments, i.e., outside human settlements, in most parts of Eurasia (Fig. 2a). In Europe and East Asia, the proportion of records in natural habitats reaches 16–17%. In West Asia, records in natural water bodies amount 13.7%. This reflects the unavoidable dispersion of these animals from points of initial introductions (e.g., urban and rural ponds) to other places. Pet terrapins can migrate to natural habitats both through the hydrological network and over land; however, at least in some cases, they were introduced directly into nature (e.g., Doñana National Park, Perez-Santigosa et al. 2008).

Recorded red-eared slider numbers may entirely (in regions without reproduction) or partly (in regions with reproduction) reflect past human activities, i.e., accumulation of human-released slider individuals, a phenomenon defined as "invasion debt" (Essl et al. 2011). Commonly, aquatic sites with red-eared sliders have one terrapin individual per water body, however the number varies and mean values are tens of individuals for different parts of Eurasia, with the highest abundance in East Asia, where the mean value is 62 individuals per water body. High numbers and biomass of this alien hydrobiont produces risks for native freshwater ecosystems (Cadi and Joly 2004; Lee et al. 2016; Salerno and van den Burg 2021). In Eurasia, the number of sliders

may reach thousands of individuals per aquatic site (Perez-Santigosa et al. 2008; Sancho and Lacomba 2013; Taniguchi et al. 2017; Gong et al. 2018). Therefore, this alien reptile became a target of eradication campaigns in this region from the early 2000s (e.g., Sancho and Lacomba 2013). However, despite possible local success, our review did not reveal any signs of decrease in terrapin abundance over the years, or signs of decreasing geographical range on the all-Eurasian scale (see Suppl. material 5; Fig. 1b).

Our results show a higher density of records of the slider in Europe and East Asia (Fig. 1b). The density of records may correlate positively with the density of human population (Banha et al. 2017). Propagule pressure (the number of release events) is often positively correlated with human population density, whereas survival and reproductive success of terrapins depends mainly on climate conditions, i.e., fundamental niche. Therefore, both climatic and anthropic factors are important to this terrapin for invasion. Analyzing invasion ecology, we found that many characteristics of invasion success (e.g., higher portion of inhabited natural water bodies, higher number of individuals per water body, successful overwintering, presence of juvenile individuals, successful reproduction and establishment of populations) tend to be present in coastal regions, such as the Mediterranean coast of southern Europe, the western part of West Asia, the Pacific coast of East Asia and islands. The coastal regions could have milder thermic and more favorable humidity regimes, which are important for the reproduction of this reptile.

Reproductive success depends on several key environmental parameters (Fig. 7). Assessing bioclimatic differences between presence and reproduction occurrence is important (Ficetola et al. 2009; Heidy Kikillus et al. 2010). For example, despite a great number of occurrence records in Europe, the establishment of self-sustained populations of this terrapin has been proved only for southern regions of Europe in Spain, Italy and southern France (Cadi et al. 2004; Perez-Santigosa et al. 2008; Ficetola et al. 2009; Crescente et al. 2014). On the other hand, specialists report successful reproduction in a larger number of localities and do not exclude the possibility of established populations in Portugal, Greece, Croatia, Slovenia, and Serbia, in locations where a similar Mediterranean climate is prevalent (Bruekers et al. 2006; Đorđević and Anđelković 2015; Standfuss et al. 2016; Koren et al. 2018; Martins et al. 2018; Tzoras et al. 2018; Urošević et al. 2019; our data). Of course, some observed groups of terrapin may be at different stages of invasion debt (Essl et al. 2011), with potential establishment of populations in the future, after the accumulation of human-released individuals of reproductive age and/or due to future climate alterations. In regions with suboptimal climatic conditions, e.g., lowland territories of Switzerland and Austria, and south Germany, the red-eared slider can also successfully reproduce but more rarely, only in some very hot summers (Bringsøe 2001; Wüthrich 2004; Pieh and Laufer 2006; Kleewein 2015; Schradin 2020). However, some above-mentioned data originate from open areas of zoos (Wüthrich 2004; Kleewein 2015), not from natural landscapes. Additionally, sometimes records of hatchlings from urban park ponds (Bringsøe 2001; Pieh and Laufer 2006) are difficult to separate from bought and released young-of-the-year juveniles (see facts and discussion in: Semenov 2010;

Ficetola et al. 2012). Registration of reproductive efforts, i.e., female egg-laying behavior, is the least informative ecological parameter because it characterizes neither success of reproduction, nor physiological adaptation to local geographical conditions. Therefore, despite multiple registrations of unsuccessful reproduction efforts in some more northern countries of Europe, e.g., Belgium, the Netherlands, Denmark, Czech Republic, and Poland (Bringsøe 2001; Najbar 2001; Herder 2007; Brejcha et al. 2010; Verbelen 2021), temperature conditions in those countries are, possibly, much less favorable for successful development of embryos at the present time (Fig. 5a).

In the current analysis (Fig. 1c), the northernmost countries of successful reproduction of this reptile in West Asia and East Asia are Turkey, Japan and Republic of Korea (Çiçek and Ayaz 2015; Taniguchi et al. 2017; Koo and Sung 2019). However, climatic conditions of even some more southern regions of Asia seem to be unsuitable for reproduction (Fig. 5a). We propose that cold mountain climates and lack of soil humidity of some other regions inhibit reproduction of the studied reptile. Indeed, the eggs of *T. scripta* have a skin envelope (Cagle 1944) and are less protected against desiccation compared with hard-shell eggs of some other terrapins (Tucker et al. 1998). Multi-year monitoring of groups of *T. s. elegans* individuals in an arid region do not reveal successful development of naturally laid eggs under extremely dry conditions (Drost et al. 2021), which further supports our hypothesis. Importantly, sex determination of embryos of the red-eared slider is temperature-dependent (Tucker et al. 2008). Only males appear under low incubation temperature; this feature is regarded as a possible limitation for the establishment of populations in northern regions, with insufficient thermal conditions for the production of both sexes (Cadi and Joly 2004; Heidy Kikillus et al. 2010). Additionally, red-eared sliders can inhabit thermal or heated water bodies with special microclimatic conditions and can benefit from a higher reproduction potential due to earlier maturation with greater body sizes, earlier start of the nesting season and larger clutch sizes (Thornhill 1982). For example, hatchlings of *T. s. elegans* may be recorded in thermal springs (e.g., in Bulgaria, Kornilev et al. 2020) outside areas of proven reproduction of this species. Among our dataset, the northernmost records of this slider in North Asia (e.g., West Siberia and Kamchatka peninsula) with rather severe climates are restricted to thermal reservoirs; however we have not found confirmation of survival and reproductive success in those localities (Fig. 1c).

Paradoxical expansion without reproduction

The results of all the species distribution models have some differences due to variations in datasets and climatic variable sets used. The calculated reproductive range of the red-eared slider in Eurasia in our study (Fig. 5a) is based on the most comprehensive dataset and significantly updates some earlier SDM prognoses of successful reproduction for this terrapin (Rödder et al. 2009; Heidy Kikillus et al. 2010). For instance, our model excludes England as an area favorable for reproduction. Analysis of the literature indirectly suggests our model may be suitable because there have not yet been reports confirming successful reproduction of the studied terrapin in England.

Nevertheless, current geographical occurrence of this terrapin (Fig. 1b) is not limited to areas climatically suitable for successful reproduction (Fig. 5a). As the main invasion vector and driver is pet releases (García-Díaz et al. 2015), the geography of initial introductions does not depend on climate features. Despite the reproduction of this terrapin being restricted to a few regions of Eurasia with comparatively high summer temperatures and sufficient air humidity (Fig. 1c), the released red-eared slider tolerates a wide range of temperatures and does not depend on air humidity around recipient water bodies. Individuals of this species activate their feeding behavior when water temperature is above 10 °C (Parmenter 1980). Many lowland freshwater aquatic sites of Eurasia reach such thermal conditions during summer. So, this terrapin becomes included in the food webs of local ecosystems immediately after its release. It is assumed that even a few big individuals of red-eared slider are capable of damaging low-component ecosystems of small isolated water bodies like artificial ponds (Semenov 2010). However, numbers of this invader often reach much higher values in Eurasian water bodies (Fig. 2b). Thus, this reptile demonstrates wide expansion without establishment of populations. Recruitment of new individuals to "pseudopopulations" of the red-eared slider takes place due to additional releases. Once released, individuals of this terrapin may inhabit a water body up to 30–31 years (Frazer et al. 1990; Castanet 1994). As a result, despite the absence of reproduction in the most regions of Eurasia (Fig. 5a), its occurrence area has enlarged considerably from the end of 1960s to the late 2010s and presently covers a considerable portion of Eurasia (Fig. 1b).

Conditional invasion

The invasive status of a species assumes 1) naturalization, i.e., establishment of populations, and 2) remarkable negative impact on native species/ecosystems (Cadi et al. 2004; Standfuss et al. 2016). Thus, invasive status, *sensu stricto*, of this reptile is not confirmed for the majority of Eurasian countries because established populations are registered only in a few regions (Fig. 1c). However, keeping in mind its abnormally high propagule pressure (García-Díaz et al. 2015), ability to survive under suboptimal conditions (Willmore and Storey 1997), long life duration (Castanet 1994), increasing numbers (without reproduction) due to progressive cases of releases and continuing geographical expansion, this aquatic reptile has acquired invasive status without the establishment of reproducing populations in areas where it can survive for more than one year. Because of the lack of such an important feature as establishment of populations, this new type of invasion may be defined as a "conditional invasion". This may be applied to this reptile within the area of successful wintering excluding the area of successful reproduction.

Wintering range as an important criterion for risk assessment

Successful wintering is registered for all parts of the continent (Figs 1c, 2d, 5b). The only hitherto known confirmation of wintering in North Asia is restricted to the Far

East region of Russia, with its mild marine climate. We do not have confirmation of successful overwintering in other regions of North Asia, which are characterized by a severe continental climate with low winter temperatures. Interestingly, during severe winters with subzero temperatures in southern regions, some individuals may die but others can survive in the same water body (Stoyanov 2015). On the other hand, wintering success can differ in different years depending on weather conditions (Reshetnikov and Sokolov 2020). Climatic thresholds for successful wintering may be explained by physiological restrictions. Red-eared sliders usually hibernate on the bottom of water bodies and the aquatic environment reliably protects them against subzero temperatures if a layer of water remains between the ice and bottom of the water body. Importantly, during hibernation, this terrapin can tolerate near-zero positive temperatures, as well as considerable deficit and even short-term absence of oxygen (Ultsch 2006); therefore, this species is sometimes regarded as a facultative anaerobe (Willmore and Storey 1997). Theoretically, crucial criteria for survival may be: 1) duration of winter ice-covering period because the red-eared slider does not survive if anoxic conditions last longer than 44–50 days (Ultsch 2006); 2) number of days with water temperature above 10 °C in the warm period, impacting the condition of the terrapin body prior to wintering, e.g., lipid reserve, necessary for long hibernation without exogenous feeding. Such body condition is difficult to reach in northern and mountainous regions with a brief warm season, as well as in internal areas of the continent with a severe continental climate. In such regions, climatic limitations of successful wintering may be non-direct: this animal survives under low water temperatures, but is deprived of the necessary physiological reserves that might prepare it to tolerate a prolonged period of unfavorable conditions. Calculated limitations of wintering in some regions in the south of Asia (Fig. 5b) are less understandable. Theoretically, the main limiting factors may be related to high temperatures and water deficit, especially for vast arid areas of Saudi Arabia, Yemen, Oman, Iraq and Afghanistan. However, we cannot exclude year-round existence of the red-eared slider in oases with permanent aquatic sites.

We propose the "range of successful wintering" as a territory at risk for true invasion as well as for conditional invasion. This non-standard (for a reptile) characteristic, i.e., wintering range, must be taken in account when planning eradication campaigns or other measures of control of the red-eared slider.

Conclusions

The geographical expansion of the red-eared slider started in the 1960–1970s from two opposite sides of Eurasia, i.e., Europe and East Asia, and was driven by massive propagule pressure in different regions over its huge territory. The invasive range of this terrapin enlarged gradually in Eurasia up to the beginning of the 2020s covering 68 Eurasian countries. In particular, we report original data outlining recent first detections of this alien terrapin in the following countries: Bangladesh, Georgia, Kazakhstan, Kyrgyzstan, Mongolia, Nepal, Pakistan, Tajikistan, as well as Russian Siberia (drainages of

rivers Ob and Yenisei). Regions of successful reproduction of this ectotherm in Eurasia are well-predictable on the basis of climatic features of the native geographic range but may be altered because of progressing global climate change. Analyses of invasion ecology confirm that coastal regions and islands show the most prominent expression of diverse signs of invasion success in terms of a higher portion of inhabited natural water bodies, higher number of individuals per water body, successful overwintering, occurrence of juvenile individuals, successful reproduction, and establishment of populations. Notably, a great number of established groups of this reptile in different regions of Eurasia do not meet the conditions for successful reproduction.

In this pet terrapin we have an excellent but rare example of wide geographic expansion without the establishment of (reproducing) populations but through the recruitment of new individuals to growing (non-reproducing) pseudopopulations due to additional releases. Therefore, we highlight the significance of the wintering range. This range must be taken in account when planning measures of control of this invader because non-reproducing groups of this terrapin may become a significant component of freshwater ecosystems with impact on native species. Thus, a cost-effective conservation strategy against the red-eared slider in large countries with a variety of climatic zones may differ for three geographical areas: 1) area of true invasion (within potential reproduction range), 2) area of conditional invasion (within potential wintering range but outside potential reproduction range), and 3) area without potential for reproduction and wintering. Nevertheless, some protective measures (i.e., banning of import and trade) are effective only on an all-country level and therefore must be applied at national levels. Finally, we encourage further accumulation of empirical knowledge on the invasion ecology of the red-eared slider in newly-invaded regions, especially in North Asia and South Asia, to establish a deeper understanding of its adaptive limits and role in Eurasian native ecosystems.

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Supplementary material 1

List of literature sources with records of red-eared slider in Eurasia

Authors: Andrey N. Reshetnikov et al.

Data type: Pdf file

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Link: https://doi.org/10.3897/neobiota.81.90473.suppl1

Supplementary material 2

Eurasian subregions as accepted in the current article
Authors: Andrey N. Reshetnikov et al.
Data type: Pdf file
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Link: https://doi.org/10.3897/neobiota.81.90473.suppl2

Supplementary material 3

Data base of georeferenced records of *Trachemys scripta elegans* in Eurasia
Authors: Andrey N. Reshetnikov et al.
Data type: xls file
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Supplementary material 4

Coding of collected field data
Authors: Andrey N. Reshetnikov et al.
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Link: https://doi.org/10.3897/neobiota.81.90473.suppl4

Supplementary material 5

Correlation matrix for ecological and other parameters of the red-eared slider *Trachemys scripta elegans* in water bodies of Europe (a), West Asia (b) and East Asia (c)
Authors: Andrey N. Reshetnikov et al.
Data type: Pdf file
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Link: https://doi.org/10.3897/neobiota.81.90473.suppl5

Supplementary material 6

Locations of the training areas based on the available occurrence records
Authors: Andrey N. Reshetnikov et al.
Data type: Pdf file
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Supplementary material 7

Evaluation metrics for MaxEnt models made across a range of feature-class combinations and regularization multipliers
Authors: Andrey N. Reshetnikov et al.
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Supplementary material 8

Comparison of mean values of the Log-transformed predictor variables
Authors: Andrey N. Reshetnikov et al.
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Link: https://doi.org/10.3897/neobiota.81.90473.suppl8

Supplementary material 9

Original list of 68 Eurasian countries colonized by the red-eared slider *Trachemys scripta elegans*
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Supplementary material 10

Additional list of 52 persons who kindly provided their observations of red-eared sliders in open water bodies of Eurasia
Authors: Andrey N. Reshetnikov et al.
Data type: Pdf file
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RESEARCH ARTICLE

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Status and distribution of an introduced population of European Goldfinches (*Carduelis carduelis*) in the western Great Lakes region of North America

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Abstract

Despite the importance of monitoring introduced species, reports of non-native birds are often initially dismissed by observers. This leads to serious information gaps about source localities, founding numbers, and growth and expansion of potential new populations. Here, we report on European Goldfinches in North America between 2001 and 2021, focusing on the western Great Lakes region. We compiled over 7000 records of European Goldfinches from multiple sources; over 3300 records were from the western Great Lakes. This species was initially reported widely in this region, but over time, birds were most consistently reported between Milwaukee, Wisconsin and Chicago, Illinois. They have been breeding in this area continuously since 2003 and the number of reported observations has increased in recent years. From our compiled records, we describe their distribution, breeding status, nesting phenology, and natural food sources. From import records, we provide evidence that the likely primary founding event of this population was release or escape from a cage bird importer in northern Illinois and provide information on possible origins. We briefly discuss possible ecological impacts. We highlight weaknesses in the way data on non-native species are currently collected and how it has impeded our ability to thoroughly reconstruct the recent history of this species in the western Great Lakes region. Formal study is needed on this population of European Goldfinches, including their potentially increasing population and range, ecology, and an evaluation of the potential effects on native ecosystems.

Keywords

establishment, naturalisation, non-native species, pet trade, release, songbird

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Introduction

Humans have been moving birds from their native ranges to locations around the globe for centuries. Prior to the early 20th century, bird translocations were primarily intentional releases. In particular, an acclimatisation movement peaking in the mid- to late 19th century was coincident with the European diaspora seeking to bring familiar plants and animals to their new homelands for sport or pleasure (Duncan et al. 2003). After that era, introduced birds have largely been the result of accidental releases from the cage bird trade (Blackburn et al. 2010), when there are ample opportunities for release or escape as birds move through the commodity market (Lockwood et al. 2019). The pet trade is now considered the primary conduit for the introduction of non-native birds worldwide (Carrete and Tella 2008; Cassey et al. 2015; Garrett 2018). The current trade volume of songbirds is largely unknown. Gilardi (2006) estimated that 5–10 million birds are taken annually from the wild for the pet trade and many countries have vast domestic markets comprised of hobbyists, larger private aviculturists and commercial breeders (FAO 2011; Lockwood et al. 2019).

There is much we do not know about the dynamics of previous introductions of non-native birds (Blackburn et al. 2015). This may be in part due to the tendency of birders (recreational birdwatchers) to disregard exotic species. Although ornithology has benefited from the efforts of amateurs for many decades, it suffers from a peculiarity of its most avid contributors: a disinterest or even loathing towards non-native species (Pranty and Garrett 2011). In North America, for example, many birders do not consider introduced species as countable on lists they maintain according to rules defined by the American Birding Association (American Birding Association 2020). With the rate of non-native bird introductions rising (Dyer et al. 2017), our ability to manage potential contemporary avian invasions requires increased vigilance and monitoring.

A brief history of European Goldfinch introductions

The efforts of the acclimatisation movement of over a century ago are perhaps best known for the introduction and establishment in many countries of two bird species that developed into serious pests: the House Sparrow (*Passer domesticus*) and European Starling (*Sturnus vulgaris*). Another species was also widely introduced during this period, the European Goldfinch (*Carduelis carduelis*). This attractive member of the Fringillidae is native to Europe, western Asia, and extreme northern Africa. Multiple subspecies are divided into two groups: the western, black-crowned *C. c. carduelis* group of west and central Europe and the eastern, grey-crowned *C. c. caniceps* group of west and central Asia (Cramp and Perrins 1994; Clement et al. 2020).

European Goldfinches were introduced to the Azores around 1860 (Clarke 2006), Australia in 1863 (Acclimatisation Society of Victoria 1863; Ryan 1906), New Zealand in 1864 (Anonymous 1864), Bermuda in 1885 or 1893 (Prentiss 1896; Verrill 1902) and Uruguay in 1913 (Dias 2000). Populations in all these areas persist

today, some of which have spread to nearby islands or countries (Dias 2000; Codesido and Drozd 2021).

The first introduction of European Goldfinches to North America was facilitated by Thomas S. Woodcock (Woodcock 1852). In late 1852, he brought 168 songbirds, amongst them 48 European Goldfinches, to New York City which were held in captivity over the winter (Woodcock 1853). Those that survived, including 16 European Goldfinches, were released on 20 April 1853 in Green-Wood Cemetery in Brooklyn (Woodcock 1853; Cleaveland 1866). None of the released birds was seen past late summer (Cleaveland 1866). The species first appeared in New York City's Central Park in 1879 (Adney 1886) purportedly having crossed the Hudson River from Hoboken, New Jersey, where birds were said to have been released the previous year (Eaton 1914; Cruickshank 1942 Austin 1963). European Goldfinches were later reported as common in parts of New York City, with a maximum report of 50 in winter 1902 (Abbott 1902). Griscom (1923) wrote that they were gone from Central Park by 1907 and that very few were reported anywhere in the New York City area by the early 1920s. They did continue to be reported from Long Island in Nassau County, New York (Nichols 1936; Lincoln 1998). The highest numbers published for that area were 17 in 1938 (Eynon 1940) and ~ 24 in the mid-1940s (Lincoln 1998). The population there persisted until the 1950s when they disappeared due to habitat changes related to development (Elliott 1968). European Goldfinches were also reported as common in eastern Massachusetts by 1880 (Brewer 1879; Allen 1880), but apparently never achieved a self-sustaining population (Brewster 1906; Strohbach et al. 2014).

Elsewhere in North America, a temporarily successful introduction occurred in Oregon, where 40 or more pairs were introduced around Portland in 1889, 1892 and 1907 (Anthony 1891; Pfluger 1896); they thrived for some years, but did not persist (Jewett and Gabrielson 1929). Unsuccessful attempts to establish European Goldfinches in North America occurred in St. Louis, Missouri in 1870 (Widmann 1907); Cincinnati, Ohio in 1872–1874 (Langdon 1881); and Vancouver, British Columbia in 1908 or 1910 (Carl and Guiguet 1972).

Over the latter half of the 20th century, scattered European Goldfinch sightings in North America were considered released or escaped birds. In the western Great Lakes region, Wisconsin had four published records prior to the 1990s (Jung 1936; Lound and Lound 1956; Frank 2004). In Illinois, up to seven European Goldfinches were reported in September 1953 in Chicago's Lincoln Park, Cook County, including adults and dependent young (Binford 1993). These furnished the first Illinois records (contra Smith and Parmalee 1955).

Around 2001, sightings of European Goldfinches in the western Great Lakes region of the United States began to increase beyond occasional reports, a situation suspected at the time to originate from a cage bird dealer in Illinois (Dinsmore and Silcock 2004). Craves (2008) compiled records through mid-2006 from this region, revealing nest building activity in 2003 and successful fledging of young in 2005. In the decades since, European Goldfinch reports have continued to increase, but a full treatment of their status is lacking.

Here, we compile occurrence records of European Goldfinches from 2001–2021 to describe their: 1) distribution, 2) breeding status and phenology, 3) natural food sources and 4) apparent introduction pathway. We also briefly discuss their potential ecological impacts. Our intent is to summarise the early phase of establishment and to prompt formal study of this species in North America.

Methods

To assess the recent distribution of European Goldfinches in North America and their breeding status in the western Great Lakes region, we assembled a database of European Goldfinch occurrences for the years 2001–2021, inclusive, for the United States and Canada. We compiled this dataset of observations from three citizen science projects: eBird (https://ebird.org), Project FeederWatch (https://feederwatch.org) and iNaturalist (https://www.inaturalist.org); a search of the grey literature; a review of online websites including social media and the photo sharing site Flickr (https://www.flickr.com); and observations received directly by JAC that were solicited for an earlier publication (Craves 2008).

eBird is a database of observations contributed by bird watchers, launched in November 2002 (Sullivan et al. 2009). We downloaded the eBird Basic Dataset (eBird 2022) which contains all records marked as approved for public output because they passed through a local checklist filter or were manually approved by volunteer regional reviewers. In some localities, European Goldfinch sightings were not approved and made public by eBird reviewers due to their introduced status; we requested these additional records. Recognising that many bird watchers do not consider introduced species as countable on lists they maintain according to rules defined by the American Birding Association (American Birding Association 2020), we also requested records input in ways that prevent exotic species from appearing on eBird lists, such as entering the record as a less precise taxon (for example, as finch sp. or goldfinch sp.) or using a count of zero. We included records which noted the observation referred to European Goldfinch in any of the comment fields.

On iNaturalist, started in 2008, contributors submit observations (primarily photos) of any taxa and propose or request an identification, which can then be verified by the community (Di Cecco et al. 2021). Project FeederWatch collects observations at feeding stations by participants across North America from November through April; the first winter using the current protocol was 1987–88 (Bonter and Greig 2021). We extracted European Goldfinch records from these sources.

Records received by JAC were solicited beginning in mid-2003 on social media, online listservs and the (now defunct) website of the Rouge River Bird Observatory. The request was specifically for records from January 2002 through August 2006 from the U.S. Midwest and north-eastern States. Reports from other States and dates were also received and retained. Nearly all records were from backyard birders who saw and/or photographed European Goldfinch(es) at their bird feeders, searched online for

the identification of this unfamiliar yet distinctive species, and found the request for information. After the publication of Craves (2008), JAC continued to receive reports, albeit in decreasing numbers, and they are included in the dataset.

We screened all records for accuracy, including any associated media. Duplicate records between data sources were removed, retaining the record containing the most data. We also removed all but one in a group of identical eBird checklists that were shared amongst multiple observers, but did not attempt to identify or remove records of what may have been the same bird at the same place submitted by different observers. Each resulting record is an observation of ≥ 1 European Goldfinch(es) at a particular time and place. Although we have confidence in the overall accuracy of the dataset for describing occurrence and range, the mixed unstructured and semi-structured nature of the dataset and the often incidental and sometimes duplicate nature of the observations make it difficult to conduct rigorous estimates of abundance.

From this continent-wide dataset, we delineated the western Great Lakes region as the area between 51° and 37.5° latitude and -96° and -81°longitude. This included all observations from the U.S. States of Minnesota, Iowa, Missouri, Wisconsin, Illinois, Michigan, Indiana, Kentucky, and Ohio, and adjacent parts of the Canadian Province of Ontario. To explore possible increases in population, we used simple linear regression to test for a relationship between mean count of birds per record (a metric that may be less subject to the sampling bias in our dataset) and year using R version 4.1.0 (R Core Team 2021).

To assess breeding status, we reviewed all records within the western Great Lakes region from March through August. We applied standardised breeding evidence codes used by eBird (eBird 2021), which are adapted from codes utilised by North American breeding bird atlas projects (Beck et al. 2018). These codes are grouped in categories, based on the strength of evidence, from merely Observed, to Possible, Probable, and Confirmed. We focused on the higher-level categories of Probable and Confirmed. The eBird dataset included records from Wisconsin's second Breeding Bird Atlas for the years 2015–2019, so these years have more even geographical coverage and precise estimates of breeding for that state. We summarised breeding records to the highest breeding category and plotted them within U.S. Geological Survey 7.5-minute quadrangles, a standard basis for most North American breeding bird atlases. We also plotted breeding codes by day of year to investigate breeding phenology.

To characterise natural food sources, we reviewed associated media from all records in eastern North America to record as many potential food plants as possible that are likely to occur in the western Great Lakes region. We identified plant taxa to species when possible.

To identify possible pathways of introduction for European Goldfinches to the United States, we obtained import data from the U.S. Fish and Wildlife Service's (USFWS) Law Enforcement Management Information System (LEMIS) database. These data come from declaration forms submitted to the USFWS for all incoming shipments of wildlife, self-reported by the importer with data generally not verified by USFWS (Smith et al. 2017; Eskew et al. 2020). The LEMIS data are only held by USFWS for 5

years and must be obtained by a Freedom of Information Act request. We obtained the available archived data for the years 2000–2014 maintained by the EcoHealth Allliance (Eskew et al. 2019; Eskew et al. 2020) by using the 'lemis' package (Ross et al. 2019) in R (R Core Team 2021) to query the LEMIS Wildlife Trade Database.

Results

Distribution

We compiled 7120 records of European Goldfinches across North America from 2001–2021 (Fig. 1). Observations were recorded in 41 U.S. States and nine Canadian Provinces (Suppl. material 1). The eastern, grey-crowned *C. c. caniceps* race made up < 1% of the entire dataset. The majority of records were from eBird (82%) and those directly received by JAC (9%). The bulk of the eBird records (88%) were accumulated from 2015–2021, while most of the directly reported records (71%) were from 2001–2006.

Forty-seven percent of all records were from the western Great Lakes region and the majority of those (n = 2919) were from Illinois and Wisconsin (Fig. 2). Similar to the overall dataset, 90% of the records for this region were from eBird and those directly received by JAC. The bulk of the eBird records (90%) were accumulated from 2015–2021, while most of the directly reported records (74%) were from 2001–2006. Of the 2467 eBird records for the western Great Lakes region, 80% were "complete" checklists, in which the users indicated they recorded all species they were able to identify. Ninety-four percent of these complete checklists were from 2015–2021. About 40% of all records from the western Great Lakes region were from the last week in March through May. Only about 4% of records were from mid-August through October.

The general pattern of records for the years 2007–2014 for both the overall dataset and the western Great Lakes region was a decreasing number of directly reported records and records in the grey literature and an increasing number of eBird records.

Initial records were loosely clustered in north-eastern Illinois and south-eastern Wisconsin with scattered outliers in neighbouring States. From 2004–2006, there were records across the entire region, after which outlying records declined, but continued in the vicinity of the original cluster (Fig. 3). Since about 2018, records were concentrated between the cities of Milwaukee, Wisconsin and Chicago, Illinois and mostly within 15 km of Lake Michigan.

In the western Great Lakes region, every year in our time range had records with counts of at least two birds. Beginning in 2009, each year had records reporting counts of five birds. From 2013 on, each year had counts of at least 10 birds. Starting in 2016, each year had records of 20 or more birds. All counts of European Goldfinch ≥ 20 individuals were in Illinois or Wisconsin and nearly all were in winter (November through February). There are six records of ≥ 50 European Goldfinches with the highest single count being 95 on 1 January 2021 in Lake County, Illinois. There was a significant increase from 2001 to 2021 in the mean count of birds per record (0.12 ± 0.02 [SE]; R^2 = 0.64, t = 5.8, df = 19, P ≤ 0.001). The mean number of European Goldfinches per record in 2021 was 3.6.

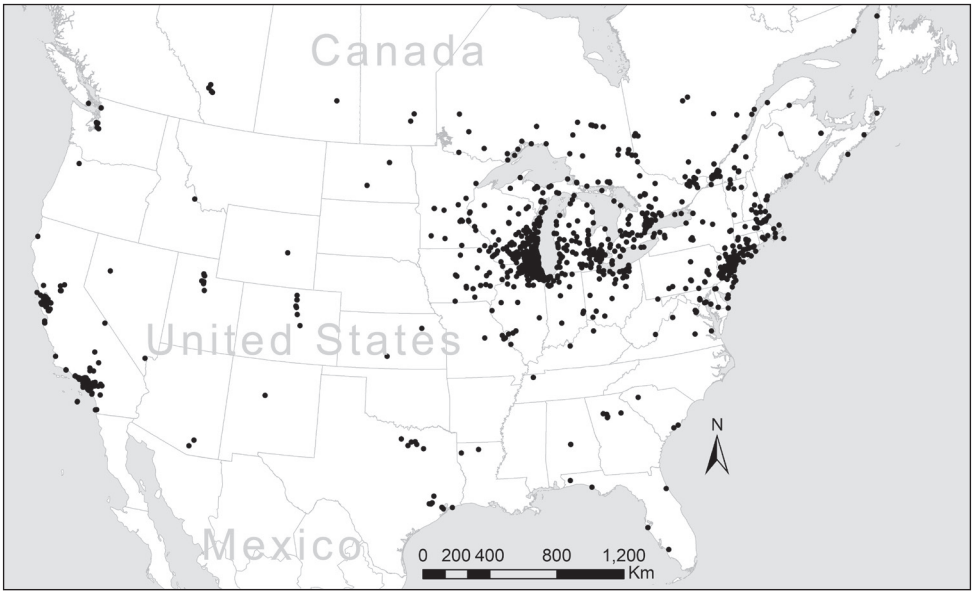

Figure 1. Locations of records of European Goldfinches in North America, 2001–2021. A table of the number of records by U.S. State and Canadian Province with county totals is in Suppl. material 1.

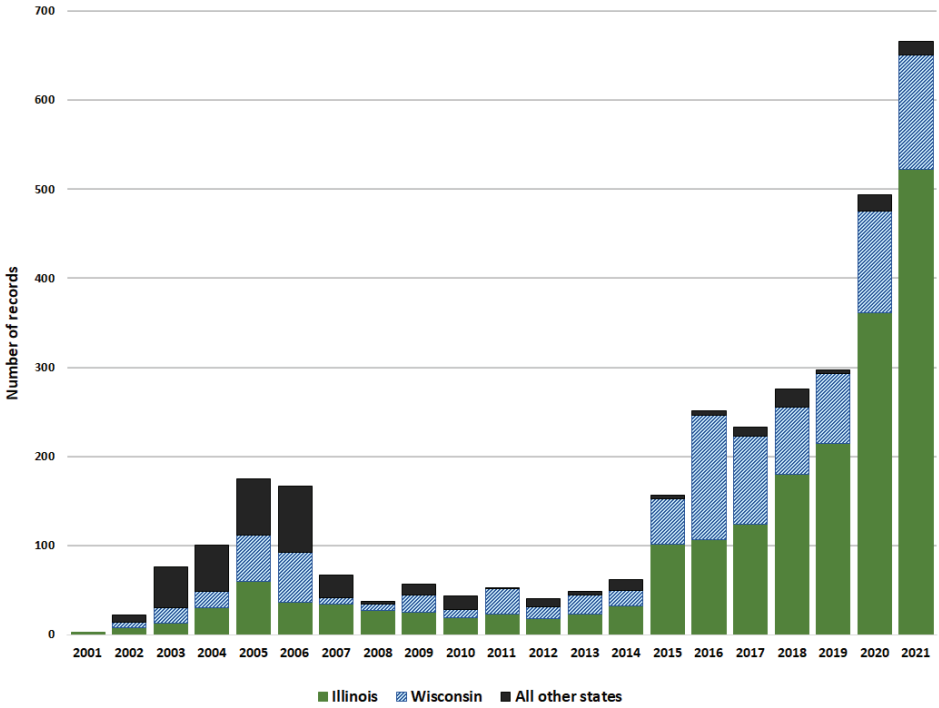

Figure 2. Number of records of European Goldfinches in the western Great Lakes region, 2001–2021. Stacked bars show proportions from the core population in Illinois and Wisconsin, and all other States (Minnesota, Iowa, Missouri, Indiana, Kentucky, Michigan, Ohio, and Ontario west of -81°longitude).

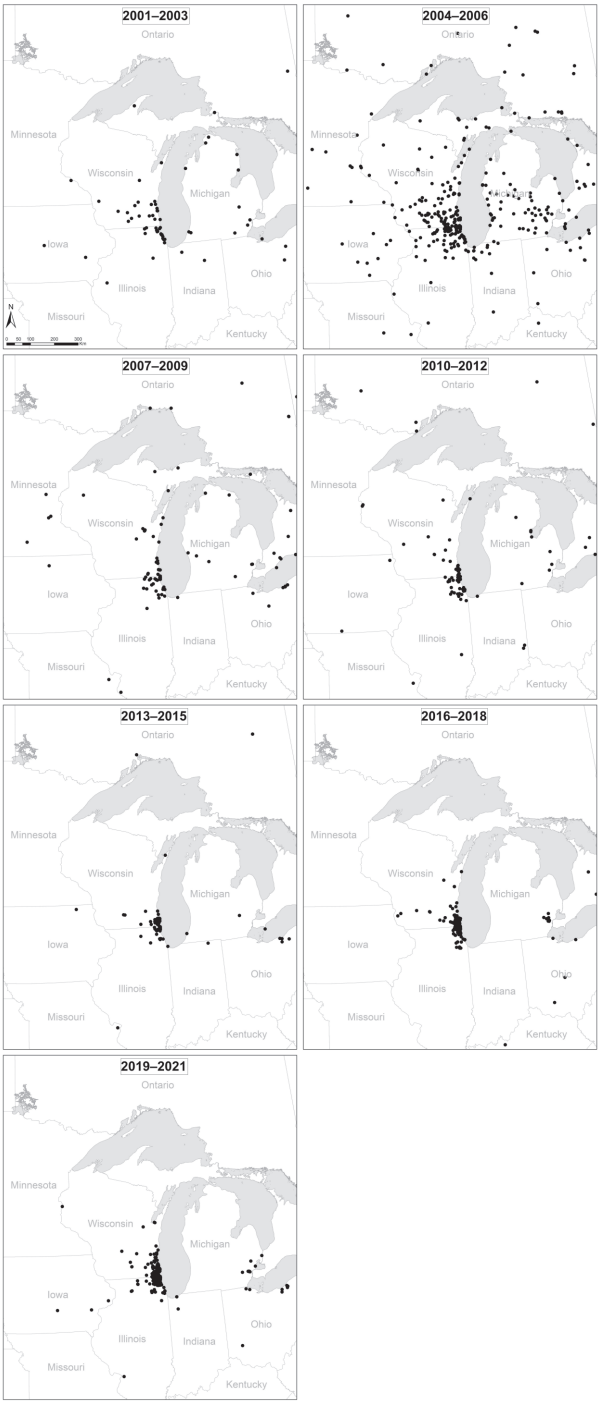

Figure 3. Records of European Goldfinches in the western Great Lakes region grouped in 3-year increments. Some points in these panels are outside our geographic boundaries of this region due to map projection distortions. An animated depiction of the accumulating records over time can be viewed at https://tinyurl.com/bdz8vxt3.

Breeding status and nesting ecology in the western Great Lakes region

We assigned breeding evidence codes for 2320 records in the western Great Lakes region from the months of March through August. Nineteen percent of these records were from March, 26% from April and 28% from May. The number of records decreased over the rest of the breeding period, with 12% in June and the remainder in July and August. The majority of these records were assigned codes in the Observed or Possible categories and, therefore, did not provide strong evidence of breeding (eBird 2021). The remainder (n = 274) were coded in the Probable or Confirmed categories. None of these birds was noted as *C. c. caniceps* either by the observer or in our review of media.

The majority (n = 268) of Probable or Confirmed records were located in northeast Illinois and southeast Wisconsin (Fig. 4). There was a single breeding record in the State of Ohio that falls outside the extent of Fig. 4: a pair of goldfinches frequented a feeder in Cuyahoga County in 2015, where an adult and immature were photo-

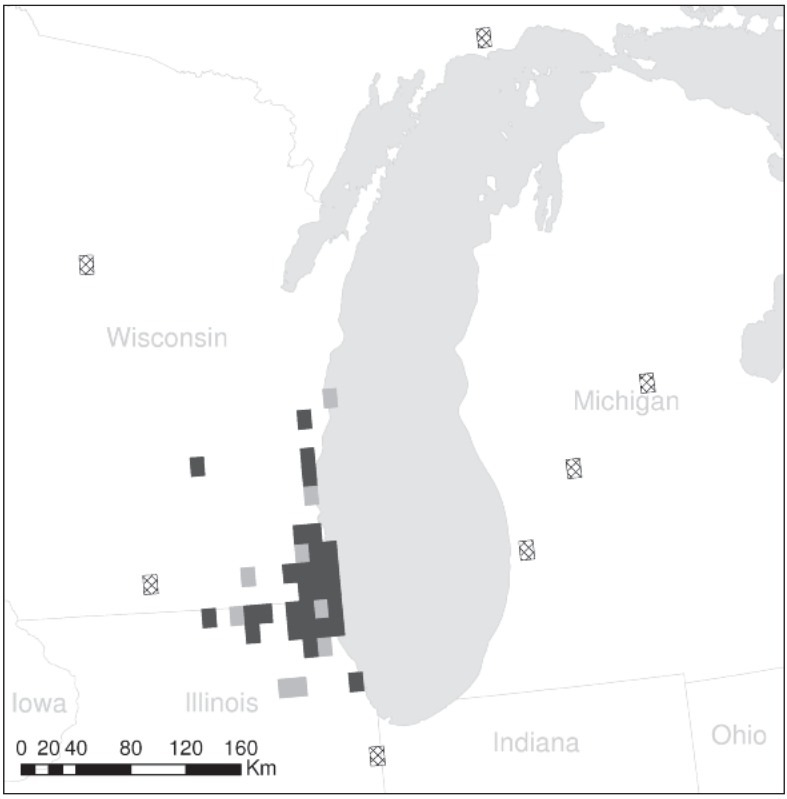

Figure 4. Locations with breeding evidence of European Goldfinches in the western Great Lakes region. From records categorised as Probable or Confirmed, the highest breeding evidence is plotted in USGS 7.5-minute quadrangles. Black represents Confirmed, grey represents Probable, crosshatched represents European Goldfinch pairs (Probable) recorded in 2006 in quads where no records of multiple birds occurred in later years. Quads may contain multiple breeding locations and some quads overlap county lines. A confirmed breeding record in Ohio is outside the map boundaries and not shown (see Results).

graphed on 22 August 2015. We plotted seven Probable records coded P (Pair in Suitable Habitat) from 2006 separately in Fig. 4; although pairs were initially present in these quadrangles, no breeding confirmations were ever reported in these areas and no records of multiple birds occurred in years after the initial reports. They are not included in the totals below.

Illinois had 155 records with high-level breeding evidence. European Goldfinches were confirmed in 13 quads in four counties and coded as probable in five additional quads and two more counties. The majority of the records (n = 141) were from Lake County. Breeding evidence, a pair constructing a nest, was first reported in the State in 2003, there have been Probable and/or Confirmed records in the State every year since.

In Wisconsin, there were 113 records coded Probable or Confirmed. European Goldfinches were confirmed breeding in 16 quads in seven counties. They were coded as probable in four additional quads. Most records were from Racine County (n = 62) and neighbouring Kenosha County (n = 33). Breeding evidence was first reported in Wisconsin in 2004 and there have been Probable and/or Confirmed records in the State every year since 2009. A link to a map file showing the Confirmed records with county boundaries is in the Suppl. material 2.

Records showed that nest building was initiated as early as 1 March, with nest building activities extending to 27 July (Fig. 5). Occupied nests were reported from 13 May though 8 July, and fledged young were reported from 22 May through 30 August (Fig. 5).

Natural food sources

Our examination of media associated with European Goldfinch records resulted in 125 observations of European Goldfinches utilising natural food sources in eastern North America. We identified all plants to at least genus (Suppl. material 3, which provides scientific names) and all 16 plant taxa occur in the western Great Lakes region (USDA NRCS 2022). Ten non-native plant taxa, all of Eurasian origin, made up 80% of the observations. The remaining six plant taxa are native to North America, but represent species or genera that have been introduced from North America into at least parts of the native range of European Goldfinches (Royal Botanical Gardens Kew 2022). Most observations (89%) and most plant taxa (69%) were herbaceous plants and the rest were trees. All observations were of European Goldfinches eating seeds, except for a video of a bird eating the flower buds of a bigtooth aspen tree.

Potential introduction pathway

Import data from LEMIS indicate that nearly 159,000 European Goldfinches were imported into the U.S. for the purpose of commercial trade from 2000–2014. This number is conservative, as it does not include potential European Goldfinches which may have been amongst the > 16,000 birds listed under *Carduelis* sp. or the thousands of birds listed under even more generic terms. The country of origin of most birds,

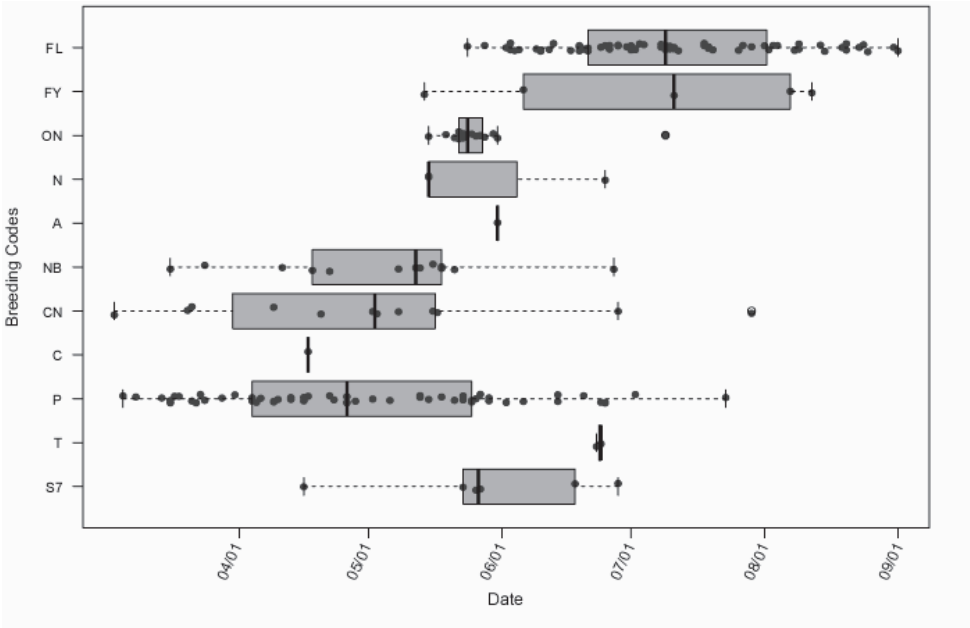

Figure 5. Phenology of breeding activities of European Goldfinches in the western Great Lakes region. Black vertical lines represent median dates. Boxes represent 1st and 3rd quartiles. Whiskers represents minimum and maximum dates, with solitary dots representing outliers. Breeding codes are as follows: FL (Recently Fledged Young), FY (Feeding Young), ON (Occupied Nest), N (Visiting Probable Nest Site), A (Agitated Behaviour), NB (Nest Building), CN (Carrying Nesting Material, C (Courtship Display or Copulation), P (Pair in Suitable Habitat), T (Territorial Defence), S7 (Singing Bird Present 7+ Days). Full definitions and application of these codes can be found at eBird (2021).

60%, was given as Australia, all of which were coded as captive-bred. Another 34% were from Russia, of which 67% were coded as captive-bred and the rest having been taken from the wild (Fig. 6).

Over 99% of the European Goldfinches were imported by three entities. The largest quantity, 39%, was imported by a company headquartered in McHenry County (Illinois Secretary of State 2022). This company was the sole importer of the European Goldfinches from Russia, receiving > 53,000, all in the years prior to 2006. From 2008–2013, the Illinois company received ~ 6100 wild-caught birds from Uzbekistan and 50 captive-bred birds from the same country in 2014. They also received a small number, < 3% of their total imports, of captive-bred birds from Spain ≥ 2005.

Another 30% of the total were imported by a California company which acted as the sales office of the Illinois company (California Secretary of State 2022; Moody's Analytics 2022), all were from Australia. A second California company received 30% of total imports, which were also all from Australia, with the exception of 500 captive-bred birds from New Zealand.

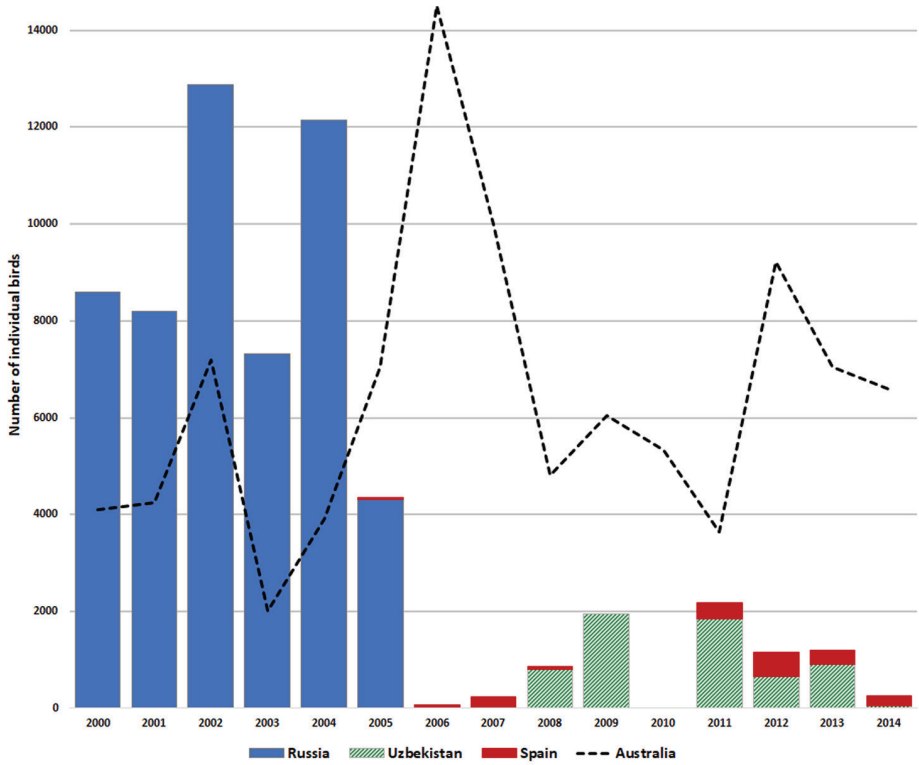

Figure 6. Country of origin and number of European Goldfinches imported into the United States for the purpose of commercial trade, 2000–2014 (all available data). Dashed line represents birds imported from Australia by two California companies. Bars represent birds imported by a single Illinois company. Not shown are < 1700 birds imported from Canada, China, and New Zealand by four other entities.

Discussion

Our compilation of occurrence records of European Goldfinch in North America was derived primarily from two sources: directly reported records solicited primarily from the Great Lakes region, mostly covering the period through mid-2006; and eBird records, submitted under various protocols which were mostly accumulated from 2015 through 2021. Although all sources contributed records to most years, the early years of our study were dominated by presence-only records with no effort metrics, submitted by casual birders, often from residential feeders. The later years were characterised by increasing numbers of eBird records, some of which were complete checklists and/or included effort metrics, that were concentrated in popular birding locations. Each of these opportunistic, unstructured, or semi-structured sources has shortcomings, but the accounting of European Goldfinches over the past two decades would be incomplete and misleading without considering them as a whole. Although the extreme heterogeneity and biases of the available data did not allow for robust population or

spatial analyses, the sheer number of records merits attention and cannot be dismissed as simply an amalgamation of escaped pets.

We believe the > 7,000 records in our dataset to be conservative due to the strong bias by birders against reporting introduced bird species. Two-thirds of birders who keep lists of species they observe do not include "uncountable" exotic species (Callaghan 2017). Most of our records came from eBird, where 90% of checklists are submitted from the most active 10% of users (Wood et al. 2011). Active participants are those who tend to be motivated by achievements, such as keeping a life list (Rosenblatt et al. 2022). Although eBird has encouraged users to enter introduced species, it has been estimated that 36% of eBird users only input those that are countable and 11% do not report them at all (Callaghan and Brooks 2020).

The second-most common source of records were reports from people responding to requests for information made online, which limited replies to those active online. Similarly, we obtained European Goldfinch records from many other online sources. Due to the large number of these types of sites, their variable membership or privacy settings, and their often-ephemeral nature, this search was not exhaustive and undoubtedly some records were missed.

Distribution

The initial increase in reports of European Goldfinches in the western Great Lakes region began around 2002. This was followed by a large increase in the number of European Goldfinch and other non-native cage bird records in the Great Lakes region over the years 2004–2006 (Fig. 2, David 2005; Craves 2008). At that time, it was rumoured that an Illinois dealer (the same one we identified through import records) was either purposely releasing birds or had lax husbandry practices (Dinsmore and Silcock 2004; Fiske 2004). We believe a global outbreak of pathogenic avian influenza H5N1 may have also played role. The outbreak originated in Asia in late 2003 and wild migratory birds were implicated in its spread (Gauthier-Clerc et al. 2007). In 2005, there was a total embargo imposed on imports of birds from Russia (HHS/CDC 2006), the source of nearly all European Goldfinches imported by the Illinois company up to that point (Fig. 6). We speculate that a substantial number of European Goldfinches and other species may have been released by the Illinois company during this period due to concerns about captive birds having, getting, or transmitting avian influenza; the potential need for additional inspections or health screening; and/or possible restrictions on sales (Gilardi 2005; Senni 2005; Romagosa 2015).

Reports diminished between 2007 and 2014. This may have been due to the discontinuation of solicited records by JAC in 2006, or an actual decline in the number of birds in the region. Beginning in 2006, the number of European Goldfinches imported by the Illinois company was also greatly reduced because of the import embargoes, from a mean of around 8900 birds annually prior to 2006 to fewer than 900 a year thereafter (Fig. 6). If the Illinois company was the source of the European Goldfinches in the region, perhaps the reduced inventory resulted in fewer releases or escapes.

Beginning in 2015, the number of reported observations began to increase substantially in the western Great Lakes region, mostly in Illinois and Wisconsin. In part, this may be attributed to the rising usage of eBird, including the debut of their mobile app (Team eBird 2015). European Goldfinch records were also approved for public display on eBird maps in some parts of Wisconsin and Illinois around this time, thus increasing awareness. Additionally, participants in the Wisconsin Breeding Bird Atlas were specifically instructed to watch for the species and report them via the eBird atlas portal (Anich and Craves 2015).

The steady increase in reports may also reflect the start of a period of population growth after an initial lag phase (Crooks 2005; Aagaard and Lockwood 2014), similar to the pattern that occurred after the introduction of the House Finch (*Haemorhous mexicanus*) into eastern North America ~ 1940. After a ban on the sale of these protected migratory birds, native to western North America, at least one New York area dealer apparently released their stock (Elliott and Arbib 1953). The founding population was estimated at 80 birds (Veit and Lewis 1996). The eastern population of House Finches was estimated at 280 birds in 1951 (Elliott and Arbib 1953). Numbers increased 10-fold from 1962–1971, coincident with rapid range expansion (Bock and Lepthien 1976; Veit and Lewis 1996).

The distribution of European Goldfinch records from 2001–2006 (Fig. 3), appears to show widespread dispersal from north-eastern Illinois and south-eastern Wisconsin, a pattern that supports our theory of a substantial release of birds around 2005 originating in that area. The reduction in records and apparent geographic contraction that followed may represent the failure of scattered individuals to establish satellite populations away from the northern Illinois source. There is a possibility that the observed pattern might also be influenced by the increasing number of eBird records which are concentrated closer to population centres and popular birding sites and the discontinuation of solicited records, many of which came from more rural counties that have less eBird coverage.

Breeding status and nesting ecology in the western Great Lakes region

With well over a decade of continuous breeding in Illinois and Wisconsin, it appears that European Goldfinches are establishing a self-sustaining population in this area. Our data indicate the nesting ecology of European Goldfinches in the western Great Lakes region is similar in many respects to those of previous North American populations as well as in the native range.

Cruickshank (1942) gave egg dates ranging from 26 April to 4 June for birds in the New York region. Our records of nest construction activities in March suggest a slightly earlier commencement of breeding, perhaps due to an advancement in egg laying over the ensuing decades. This has occurred in Britain, where the mean laying date of European Goldfinches moved up 20 days over the period 1968–2019 (Walker et al. 2020).

Cruickshank (1942) and Elliott (1968) reported several nests being built or with eggs in July. From this, Cruickshank concluded European Goldfinches were single-brooded, while Elliott felt these late nests indicated double-brooding. We had just two

records of nests being constructed or occupied after late June in our dataset. Given that only 26% of our breeding season records were from June–August, we hesitate to draw any conclusions on how many broods are attempted by European Goldfinches annually in the western Great Lakes region.

Natural food sources

Various methods have been used to study the diets of wild European Goldfinches or granivorous passerines, including prolonged field observations, gut flushing, and post-mortem stomach content analysis (Middleton 1970; Campbell 1972; Moeed 1975). The use of web-sourced photographs has recently been used to explore the diets of birds (Naude et al. 2019; Panter and Amar 2021). This method may suffer from bias, such as being photos more likely to be taken along roadsides, in open habitats, or in lower vegetation levels, but it can provide insight into a time- and cost-effective manner (Berryman and Kirwan 2021; Panter and Amar 2022). Our compilation of natural food sources derived from media associated with records from eastern North America (Suppl. material 3) suggests European Goldfinches may prefer the seeds of plant species not native to this region, but indigenous to their native range.

European Goldfinches are nearly entirely granivorous, specialising in the seeds of composites (Asteraceae) in their native range, strongly favouring thistles, burdocks, knapweeds, dandelions, and ragworts (*Senecio* spp.) (Newton 1967; Newton 1972 Cramp and Perrins 1994). Half of the plant taxa noted in our media review were composites, including all the taxa listed above, except for *Senecio* spp. All non-native taxa we identified except the grass *Bromus inermis* have been reported as food items by European Goldfinches in their native range (Newton 1967; Newton 1972; Cramp and Perrins 1994). A reliance on introduced Eurasian plants is a pattern noted in other regions where European Goldfinches have become established (Middleton 1970; Campbell 1972; Dias 2000). European Goldfinches that were previously established in North America in the New York region reportedly fed on burdocks, thistles, grasses, various garden composites, grasses, sweetgum, and larch (*Larix* spp.) (Elliott 1968), comparable to our findings.

There are many records of European Goldfinches at feeding stations. Many – especially those of multiple birds – are from feeders adjacent to appropriate habitats, such as parks or vacant land, including natural areas with known populations of European Goldfinches. Flocks of European Goldfinches, including juveniles, feeding on natural food sources much of the year suggest that while this species will utilise feeders, they readily adapt to and make use of widely available natural food sources and do not seem likely to be dependent on human provision of food.

Potential introduction pathway

We believe there is substantial evidence that the main source of the European Goldfinches in the western Great Lakes region was a dealer located in McHenry County, Illinois, ~ 80 km northwest of the city of Chicago (Illinois Secretary of State 2022).

This company was the largest importer of European Goldfinches into the U.S. for the years 2000–2014, imported many other cage birds (Eskew et al. 2019) and was the only company with a direct connection to this region. In April 1998, there was a report of a European Goldfinch from rural Walworth County, Wisconsin at a home < 10 km from the McHenry County address of the Illinois importer (Frank 1998). Between 2001 and 2004, there were also records of Common Chaffinches (*Fringilla coelebs*), Eurasian Blue Tits (*Cyanistes caeruleus*) and Great Tits (*Parus major*) in McHenry and Walworth counties and in nearby Racine County, Wisconsin; these and other cage-bird species were generally found < 200 km from the importer's location (David 2002; David 2004; Craves 2008). In her report of nesting Great Tits in McHenry County in 2003, Fiske (2004) suggested that the source of the birds was the McHenry County bird importer either accidentally or intentionally releasing exotic birds.

The majority of European Goldfinches imported into the U.S. from 2000–2005 were from Russia; all these birds were imported by the Illinois company. The country of origin listed in import records may not have been where wild-caught birds were actually collected, but rather the location from where birds harvested across a wider area are consolidated and exported (Eskew et al. 2020; Sinclair et al. 2021). It seems likely that many of the European Goldfinches imported by the Illinois company prior to 2006 were collected somewhere in eastern Europe and central Asia and perhaps from multiple locations throughout these regions.

Potential impacts

Thus far, most non-native bird species have failed to develop permanent populations in their new environments (Zenni and Nuñez 2013; Aagaard and Lockwood 2016). Those species which have become successfully established have interacted with many other taxa, with varying impacts on the recipient ecosystems (Blackburn et al. 2009). For birds, the most important impacts include predation; competition for resources, including food and nest sites; hybridisation; interaction with other non-native species, usually the spread of invasive plants via frugivory (Baker et al. 2014; Evans et al. 2016); and disease transmission (Springborn et al. 2014; Martin-Albarracin et al. 2015). Despite this potential for disruption, relatively few introduced bird species, particularly songbirds, have had severe impacts, especially outside of island settings (Bauer and Woog 2011; Strubbe et al. 2011; Baker et al. 2014).

Our data offer limited insight into potential impacts of European Goldfinches on native ecosystems. European Goldfinches are not predatory and they appear to be compatible with native songbirds. Comments included with many records indicated European Goldfinches were only occasionally aggressive towards other birds and were more often described associating with other finches, especially American Goldfinches (*Spinus tristis*). European Goldfinches are not cavity nesters and are unlikely to compete for nesting sites.

The primary natural food sources we documented being used by European Goldfinches in eastern North America are common weedy species, such as burdocks, teasels, and various thistles which are considered invasive in North America (EDDMapS

2022). Given the large variety of widespread, abundant plants suitable for European Goldfinches and native granivorous birds, it seems doubtful that competition for food resources could be problematic. Studies of European Goldfinches and related granivores indicate they are seed predators with few viable seeds being passed through their digestive tracts (von Mariluan 1895; Roessler 1936; McCallum and Kelly 1990; Heleno et al. 2011). European Goldfinches are not frugivorous and, thus, highly unlikely to disperse fleshy-fruited non-native plants. Dispersal of troublesome plants is presumably minimal, but data on foraging ecology are needed to assess unforeseen biotic interactions.

Hybridisation is considered a potential threat introduced birds may impose on native species (Baker et al. 2014). While European Goldfinches are frequently crossed with other finches in captivity, these hybrids are apparently nearly always sterile and wild hybrids are rare (Hinde 1956a, b; McCarthy 2006), suggesting the potential for negative impacts is low. The asynchrony in the breeding cycles of American and European Goldfinches may reduce the opportunity for hybridisation between these species; in eastern North America, American Goldfinches do not begin nesting until late June with a peak in the second half of July (Nickell 1951; Middleton 1978).

Our data shed little light on the potential role of European Goldfinches as reservoirs of disease or pathogens. There were no comments in the over 7000 records we compiled nor any images in the media we reviewed suggesting a sick bird, which might indicate infection with West Nile virus or *Mycoplasma gallisepticum*, the bacteria that cause conjunctivitis in House Finches and related Fringillids (Farmer et al. 2005). Pathogen screening and surveillance studies are needed to determine any disease risks posed by European Goldfinches.

In other countries where they have become established, European Goldfinches are not considered a major threat. They are not listed as an invasive species in Bermuda (Bermuda Department Environment and Natural Resources 2022) or the Azores (Marchante et al. 2020) and they are not included on the New Zealand Pest Register (Biosecurity New Zealand/Tiakitanga Pūtaiao Aotearoa 2022). In Australia, they are considered a "low interest" exotic species (DCCEEW 2007). Uruguay lists them as an invasive species of medium priority undergoing risk assessment (Aber et al. 2012) with no data on impacts (Aber et al. 2014).

Conclusions

Our data demonstrate that European Goldfinches are currently resident in the western Great Lakes region of North America. They have been breeding in an area between Milwaukee, Wisconsin and Chicago, Illinois continuously since 2003 and are now present in numbers that have established them as part of the local avifauna. Despite an earlier article published in the continent's journal of ornithological record drawing attention to this nascent population (Craves 2008), interest by birders and researchers has been limited. Thus, we lack high-quality, standardised datasets to allow us to rigorously and accurately interpret the history of these birds in the region. Nor do we have

information on many aspects of their ecology, such as seasonal movements, foraging ecology, clutch size, number of broods, or nesting success.

The lack of comprehensive data on a non-native bird species is not unique to European Goldfinches; insufficient knowledge is a common theme in literature (e.g. Blackburn et al. (2015)). Full understanding of the dynamics of non-native species successes and failures would benefit greatly from a change in the mindset of the birding community, who may disregard non-native species they encounter. The large and active birding community is ideally positioned to provide prompt detection of non-native bird species, a crucial phase in the establishment process for assessing and mitigating impacts. Yet, it is during these early stages that non-native birds are most likely to be ignored, as birders are discouraged from counting species that have not been present in a self-sustaining population for at least 15 years (American Birding Association 2020).

With the pet trade now the main source of avian introductions, even presumed escaped cage birds should not be ignored. In mid-2022, eBird initiated changes which encourage the reporting of all non-captive species, distinguish amongst several categories of exotic status, displaying them on range maps and will eventually segregate these species on user life lists (Team eBird 2022). We hope these developments spur a change in birder culture, reducing the current bias and offering a clearer picture of introduced bird source localities, founding numbers, and population growth. This seems especially urgent, given that several other non-native species we believe originated from the same source as the European Goldfinches are still being reported in the western Great Lakes region. Small numbers of Great Tits, a cavity-nesting species with potentially greater ecological impact, are successfully nesting in Wisconsin (https://ebird.org/atlaswi/map/gretit1), while much less easily recognised species such as Common Chaffinch or European Greenfinch (*Chloris chloris*) may be gaining a foothold largely unmonitored.

Although they have been present in the western Great Lakes region for at least 20 years and have years of breeding success, more detailed research is needed on European Goldfinches to fully assess their potentially increasing population and distribution, understand their basic ecology, and thoroughly evaluate their potential for range expansion and impacts on native species and ecosystems. The data we present here provide a foundation to build upon and an outline for further studies.

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Supplementary material 1

Records of European Goldfinches in North America, 2001–2021, by state/province with county totals. Records represent observations, not individual birds. Regions included in the western Great Lakes region are in bold

Authors: Julie A. Craves, Nicholas M. Anich

Data type: Spreadsheet file (.xls)

Explanation note: The data summarized here from eBird (https://ebird.org/data/download), Project FeederWatch (https://feederwatch.org/explore/raw-dataset-requests), iNaturalist (https://www.inaturalist.org/observations/export), and the United States Fish and Wildlife Service (USFWS) Law Enforcement Management Information System (LEMIS) database (https://zenodo.org/record/3565869) are available for download from each of those sites. Data summarized here that originated from social media, photo sharing sites, or those records provided directly to the authors from individuals are not publicly available due to privacy restrictions. Please contact the corresponding author for inquiries [29 kb].

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Link: https://doi.org/10.3897/neobiota.81.97736.suppl1

Supplementary material 2

Mapped locations of confirmed breeding European Goldfinches in the western Great Lakes region, 2001–2021

Author: Julie A. Craves

Data type: Google Earth compressed keyhole markup language file (.kmz)

Explanation note: Single points on the map may represent many records assigned to a single location (e.g., a "hotspot" in eBird representing a larger area, observations of a pair of birds over several days). Clicking on a point will display any multiple records. Clicking on individual records will show the breeding code (see text for descriptions) and year of record; ID code is for author reference. Light blue points indicate imprecise coordinates placed at a town center. County names and boundaries are in yellow. Counties that do not contain points are those that had breeding records coded as Probable, not confirmed. Counties recording pairs of birds in 2006 only are not included (see text) [34 kb].

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Supplementary material 3

Natural food sources of European Goldfinches in eastern North America

Author: Julie A. Craves

Data type: Document file (.docx)

Explanation note: Compilation is based on photographic records of birds actively foraging of plant material, not birds merely perched on food plants. Records that included multiple photos of a foraging bird were counted only once. Bold indicates a taxa not native to North America. Taxonomy follows the World Checklist of Vascular Plants version 8 (WCVP 2022), nativity data from U.S. Department of Agriculture's PLANTS Database (USDA, NCRS 2022). Abbreviations: CT = Connecticut, GA = Georgia, IL = Illinois, MA = Massachusetts, NY = New York, OH = Ohio, ON = Ontario, QC = Quebec, VA = Virginia, WI = Wisconsin [15 kb].

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RESEARCH ARTICLE

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Effects of the invasive leafy spurge (*Euphorbia esula* L.) on plant community structure are altered by management history

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Abstract

Invasive species threaten biodiversity and ecosystem functioning, often causing changes in plant community composition and, thus, the functional traits of that community. Quantifying changes in traits can help us understand invasive species impacts on communities; however, both the invader and the plant community may be responding to the same environmental drivers. In North America, leafy spurge (*Euphorbia esula* L.) is a problematic invader that reduces plant diversity and forage production for livestock. Its documented effects on plant communities differ amongst studies, however, potentially due to differences in productivity or land management. To identify the potential effects of leafy spurge on plant communities, we quantified leafy spurge abundance, plant species richness, forage production, functional group composition and community weighted mean traits, intensively at a single site and extensively across ten sites differing in management. We then tested how leafy spurge abundance related to these variables as a function of site management activities. Leafy spurge abundance was consistently associated with fewer plant species, reduced forage production and more invasive grass. Community-weighted specific root length also consistently increased with leafy spurge abundance, suggesting that belowground competition may be important in determining co-existence with leafy spurge. Other changes were dependent on management. Native forbs were excluded as leafy spurge became more abundant, but only in grazed sites as these species were already absent from ungrazed sites. Taller plants better persisted in dense leafy spurge patches, but only in grazed sites, consistent with either facilitation of taller species via associational

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defences or competitive exclusion of shorter species in ungrazed sites and dense leafy spurge patches. These results show that, despite some emergent properties of invasion, management context can alter invasion impacts by causing changes in the plant community and its interactions with the invader.

Keywords

co-existence, competitive exclusion, ecosystem function, exotic species, functional traits, invasion impacts, overgrazing, passenger-driver, plant height, specific root length

Introduction

Invasive plants can have strong effects on the structure and function of plant communities. When abundant, invasive plants exclude or suppress many plant species, which can reduce the diversity and functioning of resident plant communities (Levine et al. 2003; Vilà et al. 2011). In addition to driving changes in plant communities and ecosystems, invasive species can also be passengers of such change, increasing in abundance as a consequence of past land-use or management and any consequent ecosystem degradation (DiTomaso 2000; MacDougall and Turkington 2005; Carboni et al. 2016; Riibak et al. 2020). Isolating the effects of invasive plants on community structure and function is, therefore, challenging as it is unclear whether the invaders are driving or responding to community and ecosystem changes (White et al. 2012). By studying how invasive plant abundance is associated with changes in the plant community across environments and different management histories, we can potentially unravel some of these complexities, especially if we consider changes in the functional composition of the community.

Changes in the average functional traits of the species in the community, weighted by their relative abundance (the community weighted trait means), can be used to infer the ecological processes affecting community assembly as environmental and biotic filters select for specific traits (Laughlin 2014; Kraft et al. 2015; Bennett et al. 2016). Quantifying trait changes along gradients of invader abundances can also help understand invader impacts (Sodhi et al. 2019). Inferences on invader impacts may be obscured, however, if comparing amongst systems differing in their management (e.g. grazed or not) or ecology (e.g. differences in resource limitation) (White et al. 2012). For example, in productive ecosystems, increases in the average height of the remaining plant species in dense invader patches suggests that shade-intolerant shorter species were excluded due to competition for light (Hejda et al. 2019). Increases in plant height with invader abundance may not be possible in less productive systems if resource limitation limits the establishment of tall species (Daou et al. 2021) or when herbivory rates on taller species are high (Diaz et al. 2007), especially if the invader is not consumed and herbivory pressure remains constant (enemy release; Gross et al. (2015)).

In this study, we explore the effects of invasive species on plant community structure and ecosystem function focusing on leafy spurge (*Euphorbia esula* L.), a problematic invader throughout much of the North American Great Plains (Bradley et

al. 2009). Leafy spurge is an aggressively clonal plant with a deep root system from which it can generate new shoots (Best et al. 1980). Leafy spurge is also unpalatable to cattle (Hein and Miller 1992) which reduces forage production for livestock and, thus, ecosystem function, in grazing systems and makes it an economically important invasive species (Leistritz et al. 2004). When combined with its deep root system, low palatability may allow leafy spurge to flourish in systems like the Great Plains where water is often limiting and livestock grazing pressure is often intense (Epstein et al. 1997). Additionally, leafy spurge benefits more from mycorrhizal fungi, which provide plants with nutrients and other benefits in exchange for carbon, than most species in the Great Plains (Reinhart et al. 2017) and may increase the abundance and diversity of mycorrhizal fungi (Lekberg et al. 2013) to its advantage. Consequently, leafy spurge can form dense patches with reduced plant species richness, reduced forage production and significant alterations to other ecosystem functions (Belcher and Wilson 1989; Butler and Cogan 2004; Larson and Larson 2010; Gibbons et al. 2017).

Despite being associated with declines in plant diversity, leafy spurge effects on the composition and function of invaded communities are unclear. Results are often inconsistent at the functional group level, with some studies finding leafy spurge to be associated with a loss of native grasses and others showing a negative association between leafy spurge and native forbs (Belcher and Wilson 1989; Larson and Larson 2010). Inconsistency in results amongst studies may be due to differences in past management, especially if leafy spurge is not driving changes in community structure, but simply invading already degraded ecosystems (i.e. it is a passenger; MacDougall and Turkington (2005)). Overgrazing at some sites could facilitate leafy spurge invasion by reducing grass abundances, resulting in negative relationships between leafy spurge and native grasses (DiTomaso 2000; Li et al. 2017). Leafy spurge is also positively associated with invasive grasses (Belcher and Wilson 1989) that can increase with overgrazing (DiTomaso 2000) and cause loss of native grasses and forbs (Bennett et al. 2014), potentially obscuring any leafy spurge effects on the plant community. Historical control of high-density leafy spurge invasions with herbicides or small ruminant grazing can also reduce the abundance of non-target forbs, which could result in a negative association between leafy spurge and forb abundances if leafy spurge recovers more rapidly than the native forbs (Thilmony and Lym 2017). Accounting for land management activities when assessing the effect of leafy spurge on the resident community is thus important.

Quantifying the relationship between leafy spurge abundance and community-weighted trait means may also help us develop hypotheses about how leafy spurge affects the plant community and associated ecosystem functions (Castro-Díez et al. 2016). Given the ecology of leafy spurge and grassland ecosystems, we focus on traits related to competition, grazing response and mycorrrhizas. Changes in the community mean traits towards more resource acquisitive and competitive values could suggest that only competitive species can co-exist with leafy spurge or that leafy spurge does better in high resource environments. Changes in these traits towards those associated with stress tolerance and grazing avoidance could suggest that either species that tolerate increased grazing pressure can co-exist with leafy spurge or that leafy spurge tends

to invade stressful environments. Alternatively, an increase in community root thickness and tissue density could suggest that stress tolerant species or those that exploit mycorrhizal fungi best co-exist with leafy spurge or that leafy spurge is more likely to invade areas where these plants are found. We include height, leaf area and specific leaf area (SLA) as taller plants with larger leaves that are produced with less tissue investment can improve competition for light (Pérez-Harguindeguy et al. 2013; Bennett et al. 2016). Similarly, we include root diameter and specific root length (SRL) as narrower roots that require less investment in tissue can increase foraging ability and competition for soil resources (Freschet et al. 2015; Bennett et al. 2016; Bergmann et al. 2020). Some of these traits (height and SLA) are also associated with herbivory avoidance and shorter plants with tougher leaves may indicate stronger effects of grazing pressure (Diaz et al. 2007), whereas others (low SRL and high root diameter) can be associated with reliance on mycorrhizal fungi (Bergmann et al. 2020). By comparing these relationships amongst environmentally diverse sites that differ in their management and, thus, differ in their expected traits, we can determine whether leafy spurge is consistently associated with specific changes in the trait composition of the community and use those changes to develop hypotheses about the mechanisms by which leafy spurge may cause community change.

To explore the association amongst leafy spurge abundance, species richness, the trait composition of the resident community and forage production for livestock producers, we use two different surveys: one in which a single heavily invaded 9,300 ha site was intensively sampled and a broader survey that covered 10 different sites across 600 km. Sites in the multi-site survey differed in their usage (cattle grazing versus recreational) and weed management protocols (herbicide versus non-herbicide), allowing us to infer whether land management affects the association between leafy spurge and the plant community. In each survey, we collected plant composition and abundance data to test whether leafy spurge was negatively associated with species richness and forage production (measured as graminoid abundances and nutrient content) as estimates of ecosystem function relevant to local land managers. We also test for leafy spurge abundance associations with functional group composition and community-weighted trait means. We use these analyses to infer leafy spurge effects on plant community structure and how the observed relationships may be altered by land management.

Methods

Intensive survey

The intensive survey was conducted at the Elbow community pasture (51.0°N, -106.3°W), a 9,300-ha former government pasture now managed by a local cattle producer group. The Elbow site was selected due to its large leafy spurge invasion across a broad area. Leafy spurge has been managed at Elbow since 1991 through small ruminant (sheep and goats) grazing, complemented by the release of biocontrol agents

(*Aphthona* spp.) in some areas and herbicide application along trails and boundaries. All areas of the pasture are lightly grazed by cattle, but not all areas are grazed by small ruminants due to heterogeneity in leafy spurge and difficulties managing small ruminants in wooded areas. Vegetation is typical of sandy soils in the mixed grass ecoregion of Saskatchewan (Thorpe 2014), but there are areas with high tree and shrub cover and others that were aerially seeded to *Agropyron cristatum* approximately 40 years ago, but since managed extensively. To focus on leafy spurge invasion in grasslands, areas dominated by woody plants were avoided. Areas with *Agropyron cristatum* were included, although a lack of data on where seeding occurred meant that we could not separate seeded from unseeded transects. Areas where herbicide was used were avoided, but transects included areas grazed by small ruminants (24 transects) and those not grazed by small ruminants (six transects).

In 2018, we identified 18 stratified random sampling locations to maximise spatial spread across the site. We identified each grassy area of the pasture using georeferenced aerial photos and selected one to three locations within each area haphazardly, with the number of locations dependent on grassy patch size. We then travelled to these locations and identified the nearest leafy spurge patch to use for our survey. We also sampled four locations that were used historically for monitoring the site (22 total locations in 2018). In 2019, we returned to these sampling locations and added eight new locations using the same protocols as above (30 total locations in 2019). At each sampling location, we established two perpendicular 20 m transects that intersected at the centre of the leafy spurge patch. To quantify the plant community in both years, we estimated percent cover in a 0.25 m^2 quadrat at the transect intersections and at 5 m intervals in each cardinal direction (nine quadrats per transect). Of these quadrats, four were excluded from these analyses as they were placed within grazing cages and, thus, differed in grazing history. As a result, we used 194 quadrats in 2018 and 266 quadrats in 2019. We used these same quadrats to measure leafy spurge stem density as an additional estimate of leafy spurge abundance. In 2019, we clipped four additional 0.1 m^2 quadrats to 2 cm stubble height to collect plant biomass, with quadrats placed 2 m from the centre of the transect in each direction. These samples were sorted into litter, graminoids, forbs, shrubs and leafy spurge, before drying them at 60 °C for 72 h and weighing. We then calculated herbaceous biomass as the sum of graminoid, forb and spurge biomass, which served as an estimate of site productivity to include as a covariate in our models. As these lands are primarily managed for livestock, forage production is the primary ecosystem function of concern to land managers. We, therefore, estimated forage production as graminoid biomass and, to assess forage quality, we ground the graminoid samples and measured nitrogen content using a LECO 628 elemental analyser (LECO Corporation, St. Joseph, Missouri, USA).

Multi-site survey

For the multi-site study, we selected three regions in addition to Elbow where leafy spurge invasion is common. These areas cover approximately 600 km from NW to SE

along the northern boundary of the Great Plains and were centred on the following locations: west (52.7°N, -109.1°W); central (52.0°N, -106.8°W); and south (49.3°N, -104.0°W). In each region, we visited sites where leafy spurge invasion had been reported to municipal and provincial governments. Sites were selected if we were able to find a leafy spurge patch of at least 25 m^2 where leafy spurge did not exhibit signs of recent herbicide application. These patches were designated as blocks for inclusion in a separate experiment and, for grazed sites only, were fenced to exclude growing season grazing for the duration of the study. At some sites, we created multiple blocks if we found multiple physically distinct (non-contiguous) patches that were at least 10 m apart. Experimental plots were not used in the current analyses. In total, we created five blocks in the Elbow region, 10 in the central region, five in the west and five in the south. Three blocks were intensively disturbed over the course of the study (see Suppl. material 1: table S1) so were excluded from our analyses. Blocks from the Elbow region were at least 200 m from any transects in the intensive survey conducted at that site. All sites were classified as mixed grass prairie historically, although many were now dominated by invasive grasses (primarily *Bromus inermis*, *Poa pratensis* or *Agropyron cristatum*). Soils were variable amongst blocks, although most would be characterised as sandy dark brown or black chernozems (Suppl. material 1: table S1).

Past management and usage were variable across the sites. For management, we grouped sites into two categories: herbicide and other. We focus on herbicide application as broadleaf specific herbicides were commonly used (11 blocks) and have strong effects on community structure. Sites in the other category included sites with unknown management, but without any evidence of herbicide application (seven blocks), targeted small ruminant grazing (five blocks) and mowing (two blocks). For usage, we grouped sites into two categories: cattle grazing (18 blocks) and recreation (seven blocks). Past grazing intensity was unknown and, therefore, not accounted for.

As with the intensive survey, we estimated percent cover of all vascular plant species in 0.25 m^2 quadrats in late June and early July of 2018 and 2019. We collected six percent cover estimates per block in 2018 (144 quadrats), but this was reduced to 3–5 plots per block in 2019 due to time constraints (88 quadrats). All quadrats were placed within the fenced area for grazed sites or within 2 m of an experimental plot for ungrazed sites. Quadrat locations were selected to represent uninvaded areas and high leafy spurge densities within the block, although uninvaded areas were not always available, so we selected lowest density areas in those cases.

In both years, we clipped plant biomass in one 0.1 m^2 quadrat per block to obtain estimates of productivity as in the single site survey. Following weighing, we ground the graminoid biomass for nutrient analysis to explore changes in forage for cattle. We measured nitrogen as in the intensive survey in 2018, but measured nitrogen and phosphorus in 2019 as we were interested in phosphorus concentrations for the associated experiment. Nitrogen and phosphorus were analysed using an AA1 Autoanalyser (Seal Analytical Inc., Mequon, Wisconsin, USA) following Kjeldahl sulphuric acid digestion. Given that soil properties can have strong effects on the composition and traits of the plant community (Conradi and Kollmann 2016), we also collected ten soil samples

(2 cm wide and 15 cm deep) from within each block in 2019. These samples were pooled at the block level and homogenised prior to analysis. We analysed a subsample for texture using the hydrometer method (Bouyoucos 1962). Additional subsamples were ground and analysed for total carbon using a LECO C632 Soil Carbon Analyser (LECO Corporation, St. Joseph, Missouri, USA) and total nitrogen and phosphorus using the same procedure as for leaf tissues.

Trait measurements

For our trait analyses, we focus on five traits – average height, average leaf area, SLA, average root diameter and SRL – due to their associations with resource acquisition and tolerance strategies. For some species, plant traits were measured at the study sites, whereas trait data for others were taken from similar sites in Saskatchewan (Letts et al. 2015) or the neighbouring Province of Alberta (Kembel and Cahill 2011; Cahill 2020). Given that only two of the data sources measured the average height, we also included height data taken from the Flora of Alberta (Moss and Packer 1994). No single trait source included all species in the current study (see Suppl. material 1: table S2), so we used the average values across the data sources. We took the average across individuals, irrespective of source; however, we excluded all outliers, defined here as values greater or less than three times the standard deviation from the mean based on log transformed traits.

For traits measured in situ, we used standard protocols (Pérez-Harguindeguy et al. 2013) and focused on the most common species. We selected up to five individuals per species for analysis, although the number of plants measured was lower for less common species. Height was measured as the maximum vegetative height in situ for each plant. For height data taken from the flora, we used the average of minimum and maximum heights as an estimate of the average height for that species. Leaf area was measured as the average area of three mature leaves per plant using a Li-3000C leaf area meter (LI-Cor, Lincoln, Nebraska). All leaves were placed in sealed plastic bags with moist paper upon collection to prevent dehydration and shrinkage until they could be analysed. These leaves were then dried at 60 °C for 72 h and weighed to determine SLA. We also excavated each individual and collected a haphazard sample of their fine roots, which were stored in 70% ethanol solution until processing. Root samples were carefully washed over a 1-mm sieve then scanned at 400 dpi using an Epson Perfection V800 Photo scanner. Root diameter and root length were calculated using WinRHIZO Pro 2013a (Regent Instruments Inc.). The root samples were then dried at 60°C for 72 h and weighed to calculate SRL.

Functional groups and community weighted trait means

Using the quadrat level cover data, we calculated species richness as the number of vascular plant species. We then classified species into five groups: native forbs, native grasses, native shrubs, exotic forbs and exotic grasses. There were no exotic shrubs. We then calculated the proportion of species and total cover belonging to each functional

group. Using the percent cover data and the trait data described earlier, we also calculated the community weighted mean for each of the five focal traits using the R package FD (Laliberté and Legendre 2010). Leafy spurge was excluded from these calculations to avoid biasing the results. If we had included leafy spurge, the results would simply converge on the functional group or trait values of leafy spurge as it increased in abundance. To avoid results that were not actually representative of the community, we also excluded quadrats from the trait-based analyses if the available trait data represented less than 75% of the non-leafy spurge cover in that quadrat, resulting in the exclusion of 18/233 quadrats for the multi-site survey and 142/460 quadrats for the intensive single site survey.

Data analysis

To better understand how changes in functional group composition relate to changes in community weighted trait means, we ran five ANOVAs testing how each of the five traits (height, leaf area, SLA, root diameter and SRL) differed amongst the plant functional groups. Traits were the response variables and plant functional group was the fixed effect. Leaf area, SLA and SRL were log transformed to normalise the residuals.

For the remainder of our data analyses, we focused on testing the relationship between leafy spurge abundance and the following aspects of the plant community: 1) species richness, 2) graminoid forage production and nutrient content, 3) proportional abundance and richness of different functional groups and 4) community weighted means of the five traits. In these models, we also included multiple covariates to account for environmental influences on the leafy spurge-plant community relationships, so we ran additional analyses to see whether leafy spurge abundance also covaried with these variables. In all cases, the intensive single site survey and the multi-site survey were analysed separately. All data were analysed at the quadrat level, except for forage production, which was analysed at the transect or block level depending on the survey.

For the single-site survey, we analysed leafy spurge associations with species richness, the relative richness and abundance of the different functional groups and each of the community weighted trait means using separate mixed models in the lme4 package (Bates et al. 2015) in R v.4.1.2 (R Core Team 2021). In each model, we included leafy spurge abundance as either percent cover or stem density as the primary predictor. We decided which of the two predictors to use, based on the model having the lower Akaike's Information Criterion (AIC) score (Suppl. material 1: table S3). Additionally, we tested for non-linearity in the relationship by selecting the model with the lowest AIC score when leafy spurge abundance was included as a linear or quadratic predictor. We included an interaction between leafy spurge abundance and small ruminant grazing, but removed it if it increased AIC scores. Herbaceous plant biomass was also included as a covariate to represent variation in productivity amongst transects at the site and was square-root transformed to reduce the influence of outliers. Transect identity and year were included as random variables to account for the spatially and temporally repeated sampling. To test whether leafy spurge abundance covaried with the other predictors, we ran two additional mixed models with either leafy spurge cover or leafy

spurge stem density as the response variables. Small ruminant grazing and herbaceous biomass were included as fixed effects and transect identity and year were included as random variables. Amongst the models testing for associations between leafy spurge and different functional groups, we excluded exotic forbs as exotic forbs other than leafy spurge were only present in 15% of plots, whereas all other functional groups were present in at least 50% of plots. Native forb and exotic grass relative abundances were square-root transformed to normalise the residuals. When testing for leafy spurge associations with forage production data, we used linear models with either graminoid biomass or graminoid nitrogen content (as a proxy for quality) as response variables because forage production data were collected at the transect level. Graminoid biomass was square-root transformed to normalise the residuals.

The models for the multi-site survey were similar to those used for the single-site survey. For these models, however, we included two management variables (past usage [cattle or recreation] and leafy spurge management [herbicide or other] and three additional covariates because more environmental data were collected. The covariates included: herbaceous biomass (square-root transformed to reduce the influence of outliers), soil sand content, soil carbon and soil phosphorus. Soil silt, clay and nitrogen were collected, but not included as they were highly collinear with the selected covariates. To test whether management or the environment affected leafy spurge abundance, we used a mixed model with leafy spurge cover as the response variable and the environmental and management variables as predictors. The random structure included the block nested within a region and the year of sampling. We initially included site as a random factor in all analyses from the multi-site survey to account for multiple blocks within a single site, but removed it from our final analysis because only some regions had multiple sites and only some sites had multiple blocks. Additionally, its inclusion in the model typically increased the AIC score. Most models testing for leafy spurge associations with the plant community were similarly structured as above, but included leafy spurge cover and its interactions with past usage and management as fixed effects. Interaction terms were removed if they increased AIC scores. The response variables were the same as the single-site survey, except we did not analyse shrub richness or abundance as shrubs were only present in 28% of plots. Unlike the single-site survey, the forage models were analysed as mixed models. Forage production and nitrogen content were analysed as other multi-site models; however, phosphorus content was only measured in 2019, so year of sampling and block identity were not included as random effects because there was no repeated sampling.

Results

Trait differences amongst plant functional groups

Average height ($F_{4,88} = 10.96$, $P < 0.001$), SLA ($F_{4,76} = 3.00$, $P = 0.024$) and root diameter ($F_{4,78} = 3.27$, $P = 0.016$) differed amongst the functional groups, whereas leaf area ($F_{4,75} = 1.35$, $P = 0.258$) and SRL ($F_{4,77} = 1.04$, $P = 0.391$) did not (Fig. 1). Shrubs were

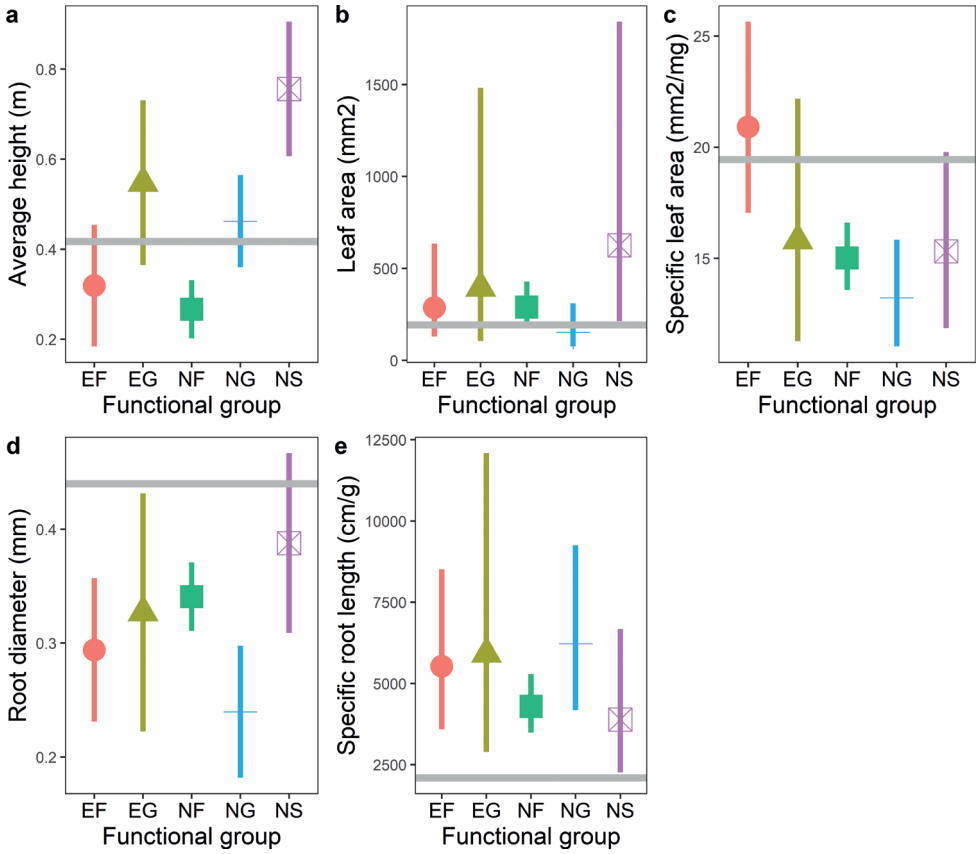

Figure 1. Differences in height (**a**), leaf area (**b**), specific leaf area (**c**), root diameter (**d**) and specific root length (**e**) amongst the functional groups considered in this study. Functional groups are abbreviated as follows: EF – exotic forb, EG – exotic graminoid, NF – native forb, NG – native graminoid, NS – native shrub. Points represent means and lines 95% confidence intervals. Solid grey horizontal lines denote the mean trait values for leafy spurge (*Euphorbia esula*).

tallest, with graminoids intermediate and forbs shortest, regardless of origin (Fig. 1a). Exotic forbs had greater SLA than all other functional groups, which did not differ from each other (Fig. 1c). Native shrubs also had the thickest roots, while native graminoids had the thinnest and other functional groups were intermediate (Fig. 1d).

Leafy spurge associations with management and the environment

We found no significant relationships between leafy spurge relative cover and small-ruminant grazing or productivity in the single-site survey or between leafy spurge cover and any management or environmental variables in the multi-site survey (Table 1), suggesting that leafy spurge relative abundance is relatively independent of the measured covariates. We did find a positive relationship between leafy spurge absolute

Table 1. Mixed model results testing for the relationship between leafy spurge abundance and management or environmental covariates in the single-site and multi-site surveys.

Survey	Response	Factor	Estimate	SE	df	t	P
Single-site	Cover	Grazing	0.011	0.042	27.8	0.27	0.790
		Productivity	0.012	0.007	27.8	1.63	0.115
	Density	Grazing	1.228	1.492	25.9	0.82	0.418
		Productivity	0.589	0.264	25.9	2.23	0.035
Multi-site	Cover	Grazing	-0.068	0.041	68.5	-1.62	0.111
		Herbicide	0.039	0.042	26.0	0.94	0.356
		Productivity	0.007	0.007	100.5	1.02	0.309
		Soil C	-0.028	0.032	12.9	-0.87	0.402
		Soil P	-0.002	0.074	61.7	-0.03	0.980
		Soil sand	-0.002	0.002	89.5	-0.93	0.362

abundance, measured as stem density and productivity in the single-site survey, indicating that leafy spurge does become more abundant in more productive sites. Stem density was unrelated to small ruminant grazing, however (Table 1).

Species richness and ecosystem function

Leafy spurge was negatively associated with plant species richness in the intensive single site survey ($F_{2,450}$ = 28.14, P < 0.001; Fig. 2a) and the multi-site survey ($F_{2,194}$ = 3.63, P = 0.028; Fig. 2b). For the multi-site survey, the negative leafy spurge-species richness relationship was consistent across management actions despite greater richness in sites grazed by cattle ($F_{1,20}$ = 5.79, P = 0.026; Fig. 2b). The only other significant predictor of plant species richness was soil phosphorus, where richness declined with phosphorus concentrations (see Suppl. material 1: fig. S1, table S5). Leafy spurge was also associated with a loss of ecosystem function as graminoid forage production declined with leafy spurge abundance in both the single ($F_{2,25}$ = 3.84, P = 0.035; Fig. 2c) and multi-site surveys ($F_{1,42}$ = 7.55, P = 0.009; Fig. 2d). Otherwise, graminoid biomass unsurprisingly increased with overall productivity in both the single-site and multi-site surveys (see Suppl. material 1: tables S4, S5, fig. S2). Interestingly, graminoid phosphorus content increased marginally with leafy spurge abundances ($F_{1,20}$ = 3.84, P = 0.064; Fig. 2e) in the multi-site survey, whereas graminoid nitrogen was not associated with leafy spurge abundance in either survey (see Suppl. material 1: tables S4, S5).

Functional groups

In both the single ($F_{2,442}$ = 6.07, P = 0.003; Fig. 3a) and multi-site surveys ($F_{2,199}$ = 6.78, P = 0.001; Fig. 3e), exotic graminoids became proportionally more abundant as leafy spurge increased. Increases in leafy spurge and exotic graminoids corresponded with a loss of native forbs ($F_{2,445}$ = 8.88, P < 0.001; Fig. 3c) and shrubs ($F_{1,400}$ = 4.68, P = 0.031; Fig. 3d) in the single-site survey, while native graminoid abundance was

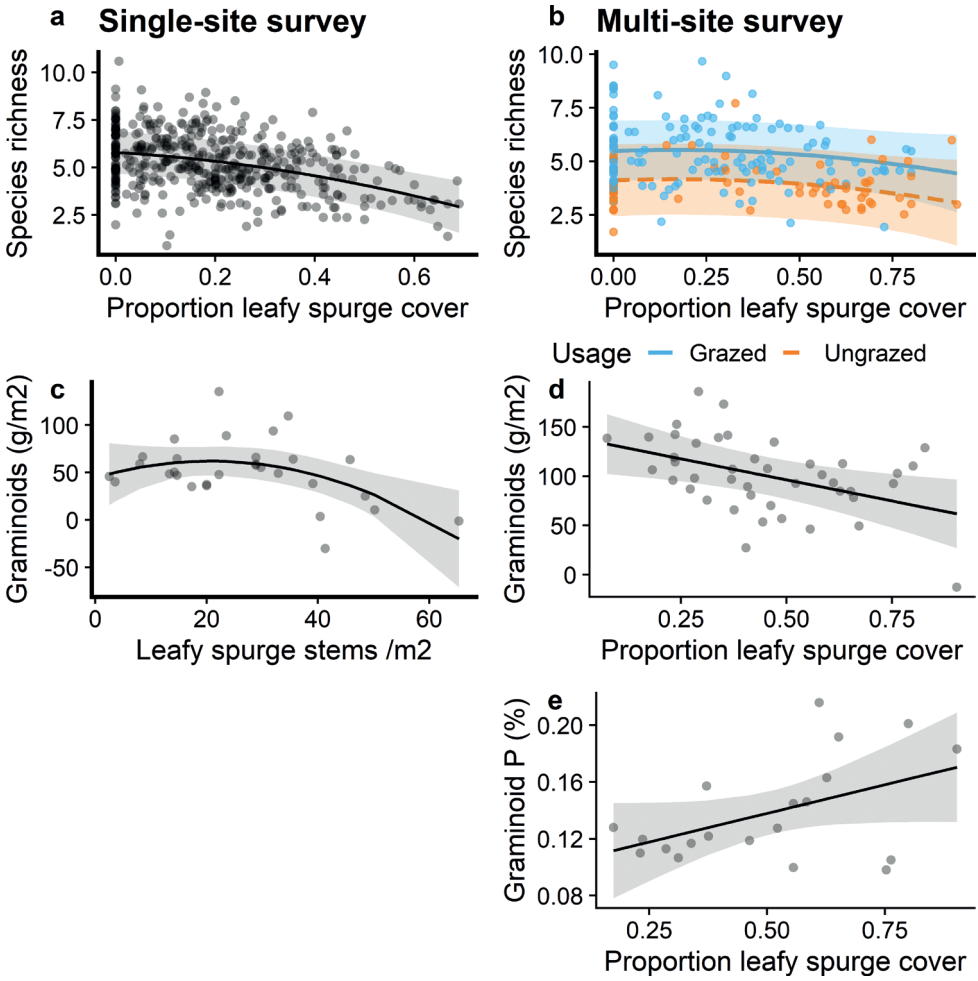

Figure 2. The relationship between leafy spurge cover, plant species richness and forage production. The relationship between leafy spurge and total species richness are shown for the intensive local survey (**a**) and the multi-site survey (**b**). Forage production was assessed for graminoid biomass for the single (**c**) and multi-site (**d**) surveys and as graminoid phosphorus content, but only for the multi-site survey. Management actions are colour-coded as per figure legends. There were no significant relationships between leafy spurge abundance and graminoid nitrogen content in either survey (not shown). Leafy spurge abundance was typically assessed as proportional cover, except leafy spurge stem density was a better predictor of graminoid biomass in the single-site survey (**c**). Plots are partial residual plots and fitted lines show the results of quadratic (**a–c**) or linear (**d–e**) regressions with 95% confidence intervals.

unaffected ($F_{1,450}$ = 2.15, P = 0.143; Fig. 3b). Interestingly, the proportion of species that were native graminoids increased at high leafy spurge abundances, but only if the transect was grazed by small ruminants (Fig. 4a). We found no direct relationships between functional group abundances and either small ruminant grazing or

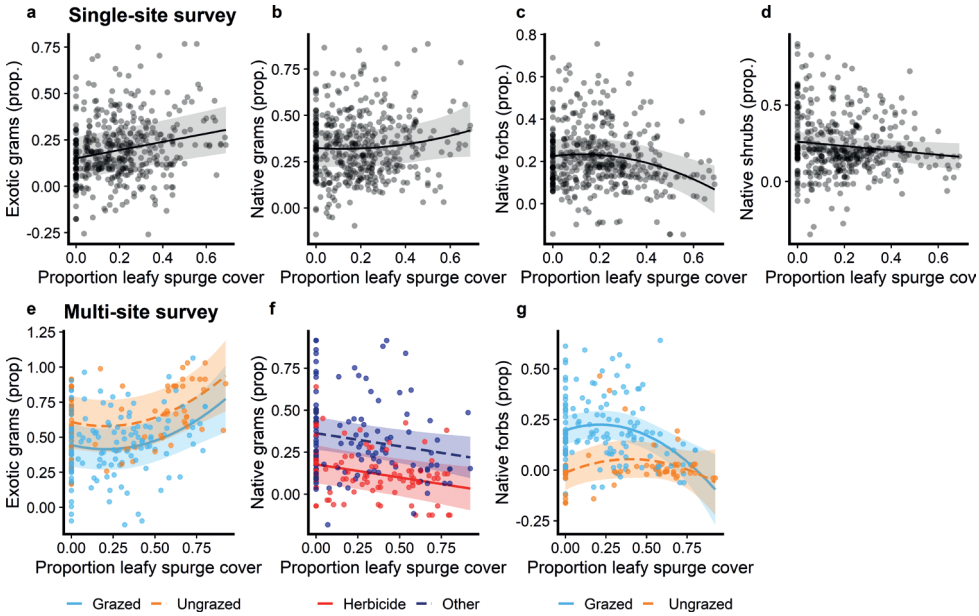

Figure 3. The relationship between leafy spurge cover and the relative abundance of different functional groups in the single (**a–d**) and multi-site (**e–g**) surveys. Shown are the relationship with the proportional cover of exotic graminoids (**a, e**), native graminoids (**b, f**), native forbs (**c, g**) and native shrubs (**d**). Native shrubs were too rare in the multi-site survey to analyse. For the multi-site survey, points and lines are colour-coded by whether the site was grazed by cattle or treated with herbicide to control leafy spurge as shown in the legend. Plots are partial residual plots and fitted lines show the fitted linear (**a, b, d, f**) or quadratic (**c, e, g**) regressions with 95% confidence intervals. All relationships, except for native forbs in the single-site survey, were significant at $P < 0.05$.

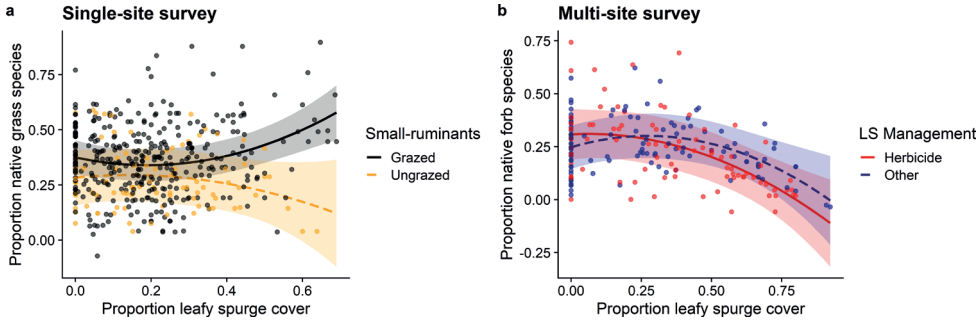

Figure 4. The relationship between leafy spurge cover and the proportion of species classified as native graminoids (**a**) and forbs (**b**). Leafy spurge effects on native graminoid relative richness are shown from the single-site survey, colour-coded as a function of small ruminant grazing. Leafy spurge effects on native forb richness are shown from the multi-site survey and colour-coded as a function of whether herbicide is currently used to manage leafy spurge. Plots show partial residuals. Lines represent best fit lines and shaded areas the 95% confidence intervals around those fits.

Table 2. Summary statistics comparing the single-site and multi-site surveys.

		Single-site survey				Multi-site survey			
Response variable		**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Leafy spurge		0.20	0.16	0.00	0.95	0.27	0.27	0.00	0.92
Diversity									
Species richness		5.0	2.0	1.0	12.0	4.2	2.2	1.0	12.0
Site productivity									
Herb. mass (g/m^2)		112	51	35	268	183	97	50	532
Forage graminoids	Mass (g/m^2)	50	34	8	156	94	80	13	374
	N (%)	1.5	0.2	0.8	2.2	1.2	0.2	0.8	1.8
	P (%)					0.14	0.04	0.09	0.21
Functional groups proportions									
Exotic graminoids	Richness	0.19	0.18	0.00	1.00	0.40	0.30	0.00	1.00
	Cover	0.22	0.24	0.00	1.00	0.51	0.31	0.00	1.00
Native graminoids	Richness	0.34	0.21	0.00	1.00	0.27	0.25	0.00	1.00
	Cover	0.32	0.25	0.00	1.00	0.23	0.27	0.00	1.00
Native forbs	Richness	0.24	0.18	0.00	0.83	0.18	0.21	0.00	0.80
	Cover	0.20	0.21	0.00	0.88	0.16	0.20	0.00	0.78
Native shrubs	Richness	0.17	0.17	0.00	0.75	0.07	0.13	0.00	0.67
	Cover	0.22	0.26	0.00	0.98	0.07	0.14	0.00	0.63
Exotic forbs	Richness	0.03	0.09	0.00	1.00	0.03	0.10	0.00	0.67
	Cover	0.02	0.07	0.00	1.00	0.02	0.09	0.00	0.63
Community weighted trait means									
Height (m)		0.40	0.11	0.21	0.78	0.36	0.13	0.21	0.95
Leaf area (cm^2)		5.46	0.52	1.85	6.57	5.55	0.59	4.24	6.94
SLA log(cm^2/g)		2.52	0.15	1.80	2.99	2.61	0.08	2.34	2.86
Root diam (mm)		0.33	0.05	0.18	0.59	0.27	0.08	0.16	0.48
SRL log(cm/g)		8.34	0.45	7.32	9.28	8.85	0.43	7.51	9.46

productivity. In contrast to the single-site survey, native graminoids declined ($F_{1,202}$ = 7.41, P = 0.007; Fig. 3f) and native forbs only declined in grazed systems (interaction $F_{2,206}$ = 3.81, P = 0.024; Fig. 3g) in the multi-site survey, likely because these systems generally had greater forb cover (Table 2). Grazed sites also had less exotic graminoid cover ($F_{1,22}$ = 6.53, P = 0.018), independent of leafy spurge (Fig. 3e). Unexpectedly, sites where leafy spurge is primarily managed through broadleaf specific herbicide had less native grass ($F_{1,22}$ = 21.97, P < 0.001), while forbs cover was unaffected ($F_{1,14}$ = 0.01, P = 0.944). Native forb richness did decline, however, in herbicide-treated sites when leafy spurge cover was high (interaction $F_{2,202}$ = 4.91, P = 0.008; Fig. 4b). Otherwise, the relationship between leafy spurge abundance and the richness of each functional group was similar to the relationships found for proportional cover (see Suppl. material 1: tables S6, S7). In addition to the relationships between functional group abundances and leafy spurge, we found that soil carbon and soil phosphorus affected the relative abundances of the functional groups. Native graminoids increased and native forbs declined with increasing soil carbon, whereas exotic graminoids decreased with productivity and increased with soil phosphorus (see Suppl. material 1: fig. S3, table S7), indicating that the measured environmental covariates were important for community assembly despite having no effect on the abundance of leafy spurge.

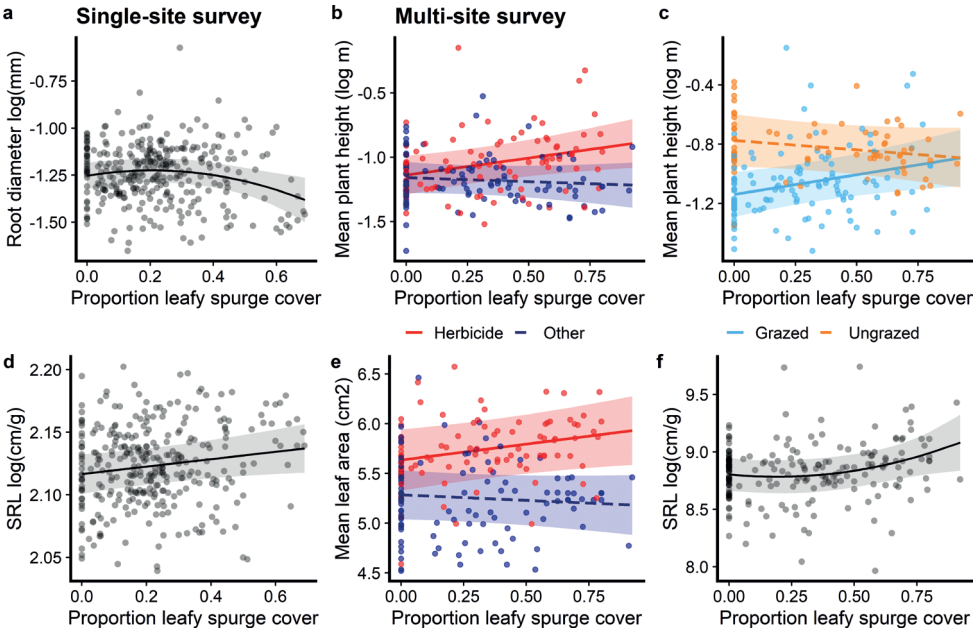

Figure 5. Significant relationships (P < 0.05) between leafy spurge cover and community weighted trait means in the single-site (**a, d**) and multi-site surveys (**b, c, e, f**). In the single-site survey, root diameter declined (**a**) and specific root length (SRL) increased (**d**) with leafy spurge abundance. In the multi-site survey, the relationship between leafy spurge cover and average height was dependent on both the leafy spurge management strategy (**b**) and whether the site was grazed (**c**), whereas the relationship with leaf area was dependent only on management strategy (e) and the relationship with specific root length (SRL) was independent of other factors (**f**). Management and grazing are colour-coded as in the legends. All plots are partial residual plots. Lines represent best fit lines and shaded areas the 95% confidence intervals around those fits.

Community-weighted trait means

Leafy spurge cover was negatively associated with community-weighted mean root diameter ($F_{2,313} = 3.45$, $P = 0.033$; Fig. 5a) and positively associated with SRL ($F_{1,308} = 4.58$, $P = 0.033$; Fig. 5d) in the single-site survey, although root diameter only declined at higher leafy spurge abundances. Otherwise, no traits were significantly associated with leafy spurge abundance (see Suppl. material 1: table S8). In the multi-site survey, SRL also increased at higher leafy spurge abundances ($F_{2,182} = 3.76$, $P = 0.025$; Fig. 5f). The relationship between leafy spurge abundance and plant height was more complex. Plant height increased with leafy spurge abundances in herbicide-treated (Fig. 5b) and grazed systems (Fig. 5c), whereas it was not significantly associated with leafy spurge abundance otherwise (spurge by management interaction $F_{1,185} = 7.56$, $P = 0.007$; spurge by grazing interaction $F_{1,182} = 10.94$, $P = 0.001$). The relationship between mean leaf area and leafy spurge cover also depended on leafy spurge management, increasing in herbicide-treated systems, but unrelated in others (spurge by management interaction $F_{1,182} = 4.45$, $P = 0.036$; Fig. 5e). Neither SLA nor root diameter were associated

with leafy spurge abundances in the multi-site survey (see Suppl. material 1: table S9). We found no significant relationships between any of the other covariates and any community-weighted means in either survey (see Suppl. material 1: tables S8, S9).

Discussion

The relationships between leafy spurge abundance and plant species richness and forage production were relatively consistent. As these relationships were found in multiple surveys and after accounting for management differences and underlying environmental relationships, this suggests that leafy spurge invasion drives the loss of species and ecosystem function. Some unmeasured factor may still drive ecosystem degradation and leafy spurge invasion occurs as a result, as invasive grasses positively covaried with leafy spurge, although we lack such evidence. Amongst the traits measured, only community SRL consistently covaried with leafy spurge abundance, indicating some role of belowground interactions during leafy spurge invasion. All other functional groups and trait relationships with leafy spurge abundance either differed between the two surveys (declines in native graminoids, changes in root diameter) or depended on site management (loss of native forbs, changes in plant height and leaf area). Combined, these results suggest that broader impacts of invasion, like the loss of species and changes in ecosystem function, may be relatively consistent amongst locations. Any effects on plant community functional structure largely depend on both the scale of the investigation, as well as the management history of the locations included, suggesting that deciphering leafy spurge effects on community traits may be challenging using only surveys.

Consistent impacts of leafy spurge

Declines in plant diversity and ecosystem function are a commonly observed consequence of invasion, both in general (Vilà et al. 2011) and for leafy spurge specifically (Belcher and Wilson 1989; Butler and Cogan 2004; Larson and Larson 2010). We found consistent negative relationships between leafy spurge abundance and both species richness and forage production, consistent with these findings. Whether the declines in richness and forage production are linked is unclear. Declining biodiversity due to invasion can lead to declines in ecosystem function (Linders et al. 2019), which may help explain the declines in forage production. In the current study, it is more likely that leafy spurge dominance reduces graminoid productivity because productivity is typically resource limited in grassland ecosystems (Stevens et al. 2015). Interestingly, the phosphorus content of the forage produced increased marginally alongside leafy spurge abundance. As leafy spurge abundance was unrelated to soil phosphorus, this suggests some change in how the graminoids access nutrients. Leafy spurge invasion can increase the abundance and diversity of mycorrhizal fungi (Lekberg et al. 2013), which can transfer large amounts of phosphorus to their host plants (Delavaux

et al. 2017). If the remaining graminoids can exploit the mycorrhizal fungi, this would explain the increase in phosphorus content. Nonetheless, increased phosphorus appears insufficient to allow the graminoids to competitively suppress leafy spurge.

Despite declines in overall graminoid biomass, exotic graminoids were consistently composed of a greater portion of the resident community at high leafy spurge abundances. Similar positive associations between leafy spurge and exotic grasses have been reported elsewhere (Belcher and Wilson 1989; Larson and Larson 2010). Exotic species can aggregate in invaded areas (Stotz et al. 2020). Positive associations amongst exotic species may be because exotic species can better tolerate competition (Golivets et al. 2018), because they facilitate each other (i.e. invasional meltdown; Simberloff and Von Holle (1999)) or because degraded systems allow for increased invasion (more passengers) regardless of species identity (MacDougall and Turkington 2005). Each of the main exotic grasses in our study (*Poa pratensis*, *Bromus inermis*, *Agropyron cristatum*) can reduce plant diversity when they invade and are considered strong competitors (Henderson and Naeth 2005; Bennett et al. 2014; Toledo et al. 2014). Being able to compete with leafy spurge is not likely to drive the positive leafy spurge-invasive grass association, however, as native and exotic grasses can compete similarly with leafy spurge (Rinella and Sheley 2005) and native grasses are not positively associated with leafy spurge. We cannot rule out facilitation between leafy spurge and invasive grasses as all of these species can cause diversity declines, which could reduce biotic resistance and facilitate later arriving invaders (Byun et al. 2018). Both leafy spurge and the grasses could also invade grasslands degraded for unrelated reasons (Chabrerie et al. 2008; White et al. 2012), but we found no evidence that current management affects positive relationships amongst invasive species, suggesting that a purely passenger model is unlikely. We lack information on the intensity and frequency of those management actions or historical management in these systems. Overgrazing or overuse of herbicides, either currently or in the past, could cause ecosystem degradation leading to greater invasion (DiTomaso 2000; Lekberg et al. 2017), so we cannot completely rule out the passenger model. More directed experiments would be required to differentiate amongst these mechanisms.

Leafy spurge invasion was also consistently associated with high SRL in the neighbouring plants, which is associated with acquisitive belowground strategies (Freschet et al. 2018; Bergmann et al. 2020). High SRL in species co-existing with leafy spurge suggests that these species need to be effective in taking up soil resources. As we found no relationships between any of the measured soil variables and leafy spurge abundance, we hypothesise that species with high SRL are more effective in competing with leafy spurge rather than having both SRL and leafy spurge abundance covary along an environmental gradient. As SRL and root diameter are typically negatively correlated (Bergmann et al. 2020), this may be why root diameter declined in the single-site survey, although it is unclear why a similar relationship was not found in the multi-site survey. An increase in acquisitive root traits also suggests that limiting similarity (MacArthur and Levins 1967) drives co-existence during leafy spurge invasion, as leafy spurge typically has thicker fine roots with lower SRL than the resident species (Fig. 1).

Conversely, leafy spurge induced increases in mycorrhizal fungi (Lekberg et al. 2013) likely do not benefit other thicker-rooted species to the extent that allows co-existence.

The positive relationship between acquisitive root traits and co-existence with leafy spurge are likely partially independent of the changes in functional group composition. Exotic graminoids increased with leafy spurge abundance, but varied greatly in root diameter and SRL. Native graminoids had the thinnest roots of any functional group, but declined with leafy spurge abundance in the multi-site survey and were largely unrelated to leafy spurge in the single-site survey. Interestingly, native graminoid richness increased with leafy spurge abundance when leafy spurge was grazed by small ruminants, but declined in the absence of leafy spurge control. Grazing can reduce the competitive ability of most species, including leafy spurge (Rinella and Bellows 2016), by reducing light interception capability and reducing resource allocation to root systems (May et al. 2009). Reductions in above- and belowground competition may be sufficient for native graminoids with acquisitive root traits, which are typically more competitive with thicker-rooted species like leafy spurge (Bennett et al. 2016), to persist when leafy spurge is otherwise dominant. Nonetheless, native graminoids do not comprise a large proportion of cover, potentially due to displacement by invasive grasses (Bennett et al. 2014). More abundant invasive grasses (Table 2) may also explain the lack of persistence of native graminoids in the multi-site survey.

Land management and leafy spurge effects on community structure

Despite some consistency amongst land uses and control strategies, the observed relationships between leafy spurge and the plant community also changed with land management. Invasion and land management both have well documented and, sometimes, divergent effects, on plant communities (Diaz et al. 2007; Saar et al. 2017; Hejda et al. 2019; Sodhi et al. 2019). When multiple processes act upon community assembly, the signal of any one process can be lost (Spasojevic and Suding 2012; Bennett and Pärtel 2017). As each of the land management actions altered community structure and the observed relationship between leafy spurge abundance and the functional composition of the community, this suggests that the management regime may affect conclusions drawn about how leafy spurge affects the plant community. Whether these differing conclusions actually reflect context-specific impacts of leafy spurge or if both leafy spurge and the plant community are responding to the same set of cues would likely vary case by case.

Cattle grazing was the factor most associated with differences in the relationship between leafy spurge and the plant community, suggesting that failing to consider grazing may result in erroneous conclusions. Grazed sites had more species and a greater abundance and diversity of forbs than ungrazed sites, consistent with models and data showing that moderate cattle grazing increases species richness and forb abundances by limiting graminoid dominance (Milchunas et al. 1988). Interestingly, we also found less invasive grass in cattle-grazed pastures than ungrazed pastures. As invasive grasses are a major cause of biodiversity loss in the northern Great Plains (DiTomaso 2000), grazing of the invasive grasses by cattle may help conserve plant biodiversity, as has

been shown in some targeted grazing studies (Rhodes et al. 2021). As many forbs were absent from ungrazed sites even at low leafy spurge abundances, we detected no relationship in these sites, suggesting that most of the forb loss in invaded pastures may be caused by invasive grasses which were more abundant when ungrazed. The lack of forbs across ungrazed sites and heavily invaded patches suggests that both leafy spurge and invasive grasses can cause the loss of forbs from invaded communities. Other management actions may still drive the abundances of both invasive species and forbs. Without further information on how invasive and native populations change over time or experimental manipulation of management regimes (Sokol et al. 2017; Kulmatiski and Beard 2019), it will not be possible to differentiate amongst these mechanisms.

We hypothesised that plant traits would help clarify how cattle grazing mediates the relationship between leafy spurge and the plant community, but many of these relationships were inconsistent, especially when considering plant height. In the multi-site survey, plant height increased with leafy spurge abundance in grazed sites, but decreased with leafy spurge in ungrazed sites, whereas, in the intensive survey, we found no relationship between plant height and leafy spurge abundance. There are many mechanisms that could account for these patterns. A positive relationship between leafy spurge abundance and plant height could represent competitive exclusion of shorter species (Hejda et al. 2019) or it could result from associational defences (Callaway 1995) where avoidance of leafy spurge patches by cattle (Kronberg 1993) reduces grazing on taller plants (Diaz et al. 2007). The intensively studied site, however, was less productive, which could limit any inference about invasion impacts if the range of conditions surveyed were too narrow (Pyšek et al. 2012). The intensive site also had more tall shrubs, which were negatively related to leafy spurge abundance. Exclusion of leafy spurge from shrub-dominated areas would also result in taller plants at low leafy spurge densities. By contrast, the loss of short forbs in ungrazed sites due to competition with tall invasive grasses (Cadotte 2017) may result in the plant community being taller when leafy spurge is at low densities. While they remain conjecture, each of these hypotheses can be tested by manipulating grazing at sites differing in both productivity and leafy spurge abundance and monitoring shifts in the plant community.

As with cattle grazing, herbicide use was associated with multiple changes in the plant community. Broadleaf specific herbicides are usually used for leafy spurge control and typically result in forb losses and increased grass growth (Lym and Messersmith 1985; Thilmony and Lym 2017). Surprisingly, native graminoids were much less abundant in herbicide treated sites, whereas the diversity of native forbs declined, but only at high leafy spurge abundances. Herbicide usage can result in secondary invasions that can have detrimental effects on native species (Pearson et al. 2016); however, we found no evidence that herbicide increased other invaders, leaving the mechanism for native grass loss unclear. Herbicide resistance may allow some forb species to increase following herbicide application (Thilmony and Lym 2017), which could account for the lack of a difference in forb abundance between treated and untreated sites. That forb richness declined at higher leafy spurge densities could result from the combined effects of herbicide and competition (Adcock and Banks 1991) or cumulative herbicide injury if herbicides were more frequently applied in more invaded areas (Simmons et al.

2007). Plant communities at herbicide-treated sites also increased in height and leaf area as leafy spurge abundance increased. Frequent herbicide use may increase nutrient flushes as plants die, increasing the resources available to unaffected species (Gaupp-Berghausen et al. 2015), which could increase the abundance of faster growing species which tend to be taller with larger leaves (Reich 2014). Current herbicide usage may also be correlated with other unmeasured management factors which may bias our interpretation of the results; however, we lack the data to make any such conclusions.

Conclusions

Although the mechanisms may be unclear, management differences amongst sites undoubtedly can alter conclusions drawn when using survey-based approaches to infer the effects of invasive species. That some relationships were consistent across different management regimes suggests that some effects of invasive species, such as losses of diversity and ecosystem function and association with other invasive species, are likely characteristic of leafy spurge invasion and strong enough to overcome any noise due to differences amongst sites. By accounting for different management regimes, however, we can develop hypotheses about scenarios under which leafy spurge may be the driver or passenger of community change. These hypotheses can then be tested by manipulating management activities along environmental and leafy spurge invasion gradients to improve our understanding of the causes and consequences of leafy spurge invasion.

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Supplementary material 1

Supplemental information and results from Groff Liu et al. Management efffects on leafy spurge invasion impacts

Authors: Catherine Liu, Terava Groff, Erin Anderson, Charlotte Brown, James F. Cahill Jr, Lee Paulow, Jonathan A. Bennett

Data type: tables and figures

Explanation note: Approximate location of each site used in the multi-site survey. The number of trait values extracted from each of the sources. AIC scores for models testing whether leafy spurge cover or leafy spurge density was a better predictor of the various response variables in the single-site model. Model results showing the relationship among leafy spurge abundance, species richness and forage production in the single-site survey. Model results showing the relationship among leafy spurge abundance, species richness and forage production in the multi-site survey. Plant species richness as a function of soil phosphorus. Graminoid productivity as a function of site productivity in the single site (A) and multi-site (B) surveys. ANOVA tables showing leafy spurge abundance effects on the proportional richness and abundance of different functional groups in the intensive single site survey. ANOVA tables showing leafy spurge abundance effects on the proportional richness and abundance of different functional groups in the intensive single site survey. Environmental covariate relationships with functional group relative abundances. Leafy spurge effects on community weighted means and functional dispersion of height, leaf area, specific leaf area (SLA), root diameter and specific root length (SRL) in the intensive single site survey.

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RESEARCH ARTICLE

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Advancing research on alien species and biological invasions

A bug's tale: revealing the history, biogeography and ecological patterns of 500 years of insect invasions

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Abstract

The arrival of Europeans to the Americas triggered a massive exchange of organisms on a continental scale. This exchange was accelerated by the rapid increase in the movement of people and goods during the 20th century. In Chile, scientific and technical literature contains hundreds of records of non-native insect species established in different parts of the territory, from the hyperarid Atacama Desert to the Magallanes Region. Here, we analyse temporal trends, taxonomic diversity, biogeographic origin and main impacts of these species on different sectors in Chile from the European arrival to the present. Our task includes a review of old records in museum catalogues, libraries, collections, expedition records and catalogues. Almost 600 species of non-native insects have been reported to be established in Chile. Introductions started with the very arrival of Europeans to the central valley of Chile and underwent a huge acceleration in the second half of the 20th century. The order Hemiptera was the most prevalent amongst non-native insects. Most species are linked to agriculture and forestry. Species are of Palearctic origin in more than 50% of the records. In terms of temporal trends, the rate of established non-native species shows an abrupt increase at the beginning of the 1950s. This change may be associated with the strong development in agriculture and forestry in Chile after World War II and the increase in intercontinental air traffic. We believe that the understanding of past patterns of introductions is an important component in the design of current policies to minimise the impact of invasive insects.

Keywords

biological invasions, Chilean fauna, insect pests, invasive species, non-native insects

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Introduction

The advance of civilisations, human migration and the proliferation of trade between different regions have led to a strong increase in species movement (Buckland 1981). This exchange was accelerated by the rapid increase in the movement of people and goods during the 20th century (Seebens et al. 2017). Indeed, the exchange of different species of insects has intensified in the last 200 years, together with the great transcontinental movements of people, goods and services (Mack et al. 2000; Chapman et al. 2017; Liebhold et al. 2017). Today, all countries have hundreds or thousands of non-native species established in their ecosystems (Mack 2003; Langor and Sweeney 2009; Seebens et al. 2017); however, in many cases, it is difficult to determine the origin, pathway and date of the introduction. Furthermore, recent estimates indicate that observational bias means that many non-native pest species still go unreported (Bebber et al. 2019).

Social and economic factors are key components in the increase in propagule pressure or species introductions (Santini et al. 2013; Bacon et al. 2014), whereas ecological and biogeographical factors are the main determinants of establishment (Santini et al. 2013; Schulz et al. 2019). In the first case, accelerated economic growth, the agricultural or ornamental use of non-native plants, connectivity (e.g. the number and availability of ports) emerge intuitively as important variables to explain the rate of insect species arriving in a new country (Dehnen-Schmutz et al. 2007; Hulme 2009; Banks et al. 2015; Chapman et al. 2017; Seebens et al. 2018; Bebber et al. 2019). On the other hand, biogeographic similarity (including climatic similarity), host availability and community invasibility have been described as the most important factors to explain the establishment of new insect species (Shea and Chesson 2002; Bacon et al. 2014; Burns 2015; Schulz et al. 2019). Thus, it is the particular combination of these factors that will define the composition of the non-native fauna in a region. For example, the pool of non-native insects in a country could be dominated by species whose origins are in biogeographic regions with environmental conditions that match those of the new habitats. An alternative scenario is a pool of non-native insects that arrived using pathways mainly associated with the main economic activities of the country, regardless of their biogeographic origin.

In a similar vein, it is not only the species' identities that can reflect different processes structuring the non-native assemblages. Diversity of orders or families may or may not respond to ecological factors. Non-native insect assemblages can be a reflection of the global richness of these groups, with the representation of orders or families being proportional to their world richness or the non-native richness may be biased towards a group associated with some particular pathway, socioeconomic or ecological variables (Sailer 1978, 1983; Yamanaka et al. 2015; Liebhold et al. 2016; Bebber et al. 2019).

In the Americas, the arrival of Europeans triggered a massive exchange of organisms on a continental scale. Accidental and intentional introductions of plants and animals promoted the establishment of new insect species, especially those associated

with crops of foreign origin (Prado 1991). In continental Chile (excluding oceanic islands), new food and crops were introduced in the 16th century (Prado 1991); however, few non-native insects were reportedly established in the country until the 19th century (Prado 1991; Artigas 1995; González 2012). Other pathways of introduction of insects were the establishment of ornamental plants, forestry, livestock and accidental transport in human baggage (see results). An important intentional pathway for insect introductions to Chile, especially during the 20th century, was the implementation of biological control programmes (González and Rojas 1966; Zúñiga 1985; Rojas 2005). The introduction of these beneficial insects was a response to the increasing impact that non-native pests had on food production.

In Chile, the scientific and technical literature contains hundreds of records of non-native insect species in different parts of the territory, from the hyperarid Atacama Desert to the Magallanes Region. Using this information, here we analyse the biological patterns of establishment of non-native insects to Chile from the first European arrival to the present. In particular, we analyse temporal trends, taxonomic diversity, biogeographic origin and main sectors impacted by each species. Through the description of these patterns, we can obtain a better understanding of the process involved in biological invasions over a timescale of centuries.

Materials and methods

Database

We collected records of non-native insects established in continental Chile from scientific articles, museums, libraries, collections, Chilean governmental reports, expedition records and catalogues. A primary online search using the words "exotic insect", "invasive insect", "insect pests" and "Chile" and their equivalents in Spanish was performed in Google Scholar. However, this search provided few results. For example, the Alien Species First Records Database 1.2 (Seebens et al. 2017) contains only 18 records of insects for Chile. We reviewed complete journal series and specialised sites (Revista Chilena de Entomología, Acta Entomológica Chilena, Revista Chilena de Historia Natural, Anales de Zoología Aplicada, Boletín del Museo de Historia Natural, Gayana, Anales del Museo de Historia Natural de Valparaiso, Publicaciones Ocasionales del MNHN, Agricultural Técnica, Anales de la Universidad de Chile, ISC, EPPO Bulletin, EPPO Reporting Service, CABI, SAG Reports, amongst others), specialised books (Prado 1991; Artigas 1995; CONAMA 2008, amongst others), museum and private collection catalogues and reports from expeditions (for a complete list, see the Supplementary files). We consulted specialist entomologists for some specific taxonomic groups. Most references were obtained (through loans or purchases) in a paper format outside Chile. When a mention of a non-native species was detected, we tracked back the literature for the original report. At least the page with the reference for each spe-

cies can be obtained in a digital format upon request from authors. First, we searched for explicit statements and dates of first records of non-native insects in the country. In some cases, we included the year of the first mention of the species in Chile when the authors explicitly recognised that the specific year of introduction or establishment is unknown. We selected the low limit when the publication indicates a range of years because reports usually are published several years after the real date of introduction/establishment of the species. We included species that were eradicated by governmental initiatives, but that were originally successfully established in the country. We collected species name, taxonomic position and year of first report. After we obtained our list, we completed our database by reviewing the literature to determine origin, type of impact and whether the species was used for biological control. For origin, we used the classification of biogeographic Realms from Olson et al. (2001). Given that a species can belong to more than one realm, we considered all realms including the native distribution ordered by area occupied in each one. For type of impact on human activities, we searched for publications where some type of direct and indirect impact was mentioned for the species. We included current and potential descriptions of impact in any country or region. In this sense, our classification was comprehensive and it does not mean that all these impacts have been reported in Chile, but the classes used are an approximated representation of the most critical areas/industries in the country. We used the following categories: agriculture, forestry, ornamental plants, environmental (impacts on biodiversity, endangered or endemic species or ecosystems), livestock, human health and infrastructure (damage to artificial structures, roads, ports, heritage buildings etc.). In some cases, when no description of impact was found in the scientific or technical literature, we recorded the impact as unknown (~ 5%).

Analysis

First, we estimated several descriptive statistics. We calculated the percentage of insects belonging to each order and family of non-native insects and also the distribution of orders as a function of the dominant realm of origin. We compared the frequency distribution of the number of species per order of non-native insects with the proportional number of insect orders in the world and Chile. For world data of insect richness, we used Stork (2018); for Chilean insect richness, we used CONAMA (2008). In addition, we compared the Palearctic component with the database of invasive insects of North America (Yamanaka et al. 2015). We only included in the analysis Palearctic species because Nearctic and Neotropical realms involve native species for each region and the other realms show too few species for a meaningful comparison. In the same vein, we estimated the frequency distribution of the number of species per type of impact.

We used the common species-time approach to examine temporal trends in insect dates of first report (e.g. Preston (1960); White (2004, 2007); White et al. (2006)). The accumulated number of species was calculated for the complete dataset, main orders (more than 40 species) and for those insects considered biological control species

(despite an intentional or accidental introduction). For the complete dataset and main orders, we evaluated three hypotheses of the temporal evolution in species accumulation (S). We compared linear, exponential and segmented trends. A linear accumulation suggests that the rate of accumulation is constant through time (t), independent of changes in population movement, economic growth and/or market changes (no acceleration). Exponential accumulation indicates that species accumulation shows a smooth acceleration ($S = a*\exp(b*t)$), where S is the number of species, t is time and a and b are parameters to be estimated. Finally, a segmented trend points to an abrupt change in the acceleration of species accumulation, which may be the result of abrupt changes in population movement, economic growth and/or market changes, amongst other factors. To avoid the noise due to few records in the first centuries, we started our analysis with the number of species accumulated to 1850. We tested these hypotheses by fitting each model to our dataset and selecting the best one using the Bayesian Information Criterion (BIC) in the R environment using function lm and nls (R Core Team 2022).

Results

Our review identified 591 non-native insect species established in Chile. Three of them were eradicated after establishment (see Suppl. material 1). From this total, we found the date of the first report for 572 species. The non-native insect fauna of Chile is dominated by the order Hemiptera, with almost 40% of the species (Fig. 1a). Coleoptera and Hymenoptera each represent approximately 20% of the total species (Fig. 1a). Amongst the families of Hemiptera, Aphididae (23% of all species) and Diaspididae (5%) were the most frequent. In Coleoptera, Curculionidae (7%) was the dominant family. The distribution of families in Hymenoptera was more homogeneous, with most species acting as a biological control agent of insect pests. The origin of the non-native species was strongly biased to Palearctic insects. Species from this realm represent more than 50% of the non-native insects. In a secondary position and well behind the Palearctic origin, Nearctic and Neotropical species made important contributions to the non-native insect fauna of Chile (Fig. 1b). For Palearctic, Australasian, Indomalayan and Nearctic species, the dominant order was Hemiptera (Fig. 1b, c). Only for Neotropical and Afrotropical species, Coleoptera was the dominant order (Fig. 1b, c). From the Palearctic component, 53% of the species already established in Chile are also established in North America.

When comparing the relative richness of the non-native insects established in Chile and world richness of species per Order, we observed a disproportionate representation of orders Hemiptera and Hymenoptera and a strong underrepresentation of the orders Coleoptera, Diptera and Lepidoptera (Fig. 2a). The same pattern was observed when comparing non-native established insects with Chilean native insect richness (Fig. 2b). Most non-native insects are described as having an impact on agriculture, forestry and

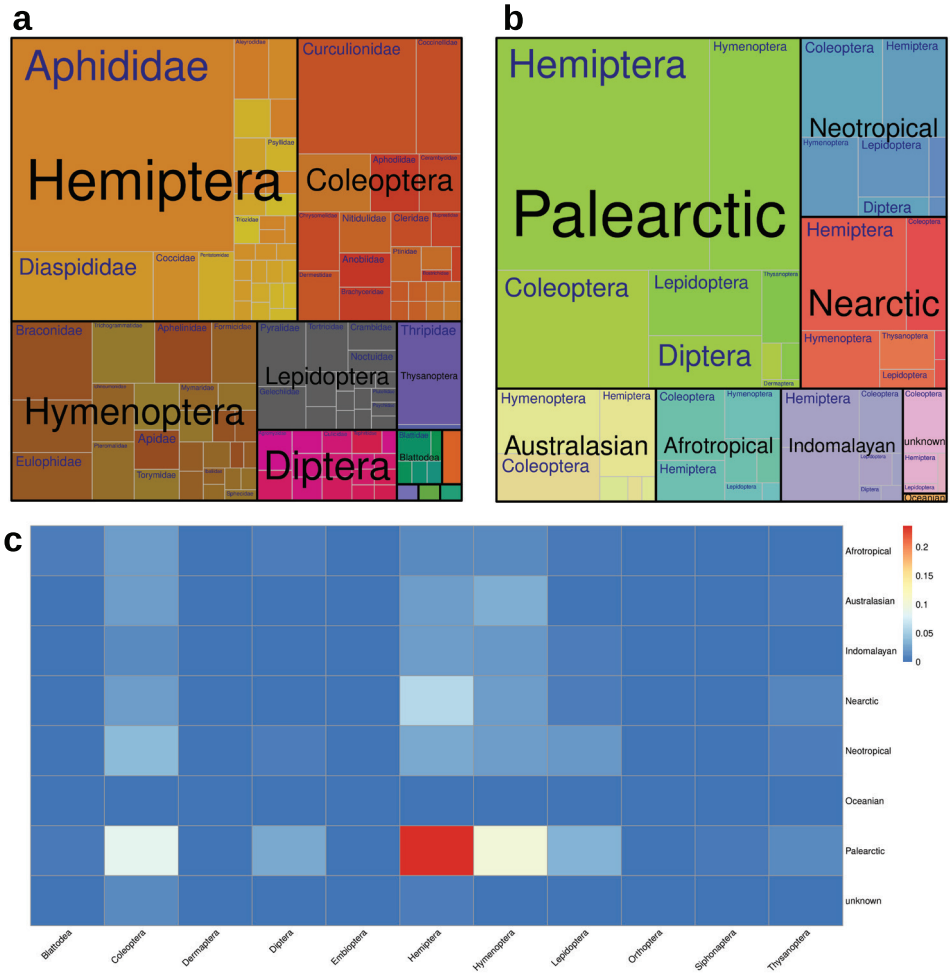

Figure 1. Taxonomic and biogeographic patterns of the non-native insect fauna of Chile **a** proportional representation of species belonging to each order and family **b** proportional representation of the biogeographic realms of origin of orders of the species **c** Heatmap showing the bivariate distribution (%) of orders and origins of the species.

ornamental activities (Fig. 3). The frequency of non-native species with an impact on other areas shows a minor representation. Biological control agents correspond to 17% of all species.

When we analysed temporal trends of the total accumulated number of non-native species, the best model was the segmented regression (Table 1). The best model showed an abrupt increase in the rate of non-native species recorded around 1949. Starting in that year, the species accumulation rate increased more than three times (Fig. 4a). When we look at the more abundant orders, we see that Coleoptera, Hymenoptera and Lepidoptera show the same pattern of increase (segmented model) (Table 1, Fig. 4b).

Table 1. Results for models fitted to the total number of accumulated non-native insects in Chile considering all species and the main orders separately.

Model	Formula	Parameter	R2	BIC
		All orders		
Linear	S = a+b*t	a = -6216; b = 3.310	0.90	1472.7
Exponential	S = a*exp(b*t)	a ≈ 0; b = 0.017	0.99	1107.1
Segemented	Si = ai+bi*t, with i= 1,2	a1 = -2797; b1 = 1.512; a2 = -11260; b2 = 5.854	0.99	1031.3
		Coleoptera		
Linear	S = a+b*t	a = -1160; b = 0.624	0.87	1136.0
Exponential	S = a*exp(b*t)	a ≈ 0; b = 0.015	0.99	837.0
Segemented	Si = ai+bi*t, with i= 1,2	A1 = -399.7; b1 = 0.221; a2 = -2010; b2 = 1.054	0.99	746.0
		Hemiptera		
Linear	S = a+b*t	a = -2104; b = 1.126	0.82	1363.2
Exponential	S = a*exp(b*t)	a ≈ 0; b = 0.019	0.99	933.6
Segemented	Si = ai+bi*t, with i= 1,2	A1 = -661.0; b1 = 0.3611; a2 = -4411; b2 = 2.291	0.99	1006.4
		Hymenoptera		
Linear	S = a+b*t	a = -6216; b = 3.310	0.71	1267.1
Exponential	S = a*exp(b*t)	a ≈ 0; b = 0.017	0.99	831.4
Segemented	Si = ai+bi*t, with i= 1,2	a1 = -2797; b1 = 1.512; a2 = -11260; b2 = 5.854	0.99	788.2
		Lepidoptera		
Linear	S = a+b*t	a = -6216; b = 3.310	0.89	825.2
Exponential	S = a*exp(b*t)	a ≈ 0; b = 0.017	0.98	619.0
Segemented	Si = ai+bi*t, with i= 1,2	a1 = -2797; b1 = 1.512; a2 = -11260; b2 = 5.854	0.98	557.9

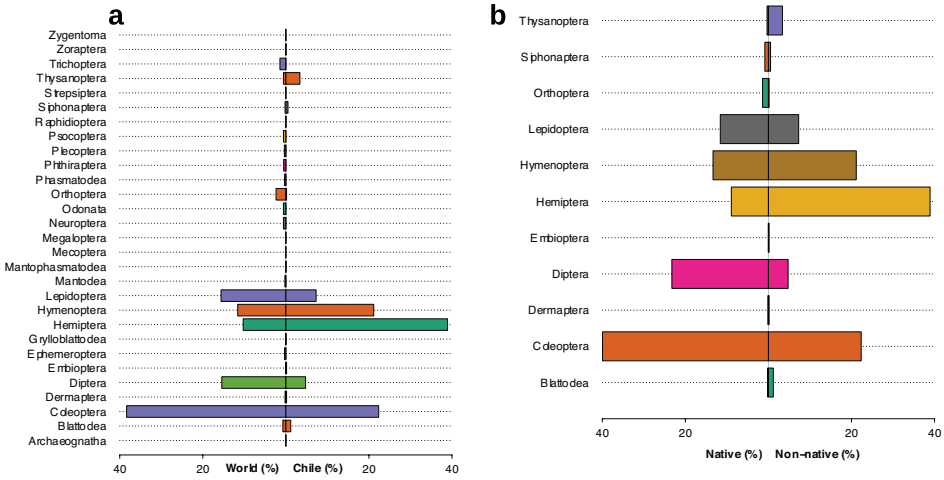

Figure 2. Comparison of the frequency distribution of insect orders in the **a** World fauna and **b** Chilean fauna, with the pool of non-native insects established in Chile.

However, Hemiptera species accumulation shows an exponential increase (Table 1, Fig. 4b). The number of biological control agents shows an accelerated increase since the 1950s (Fig. 4c).

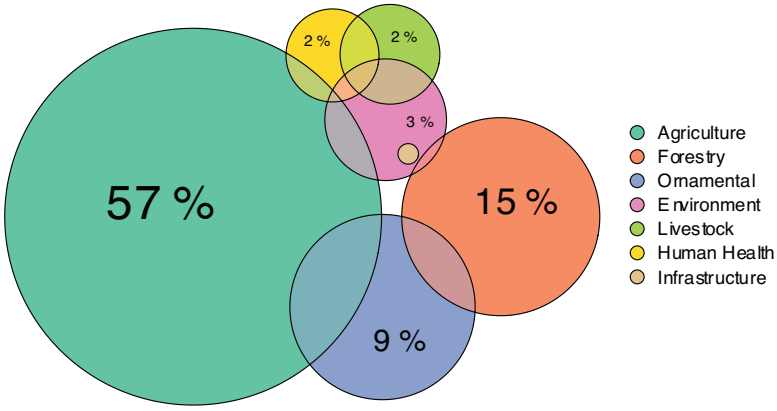

Figure 3. Percentage of non-native insect species established in Chile with the impact on each category of human activity, according to global literature. Unknown categories are not shown. Overlap areas correspond to the percentage of species with more than one category of impact (n = 565).

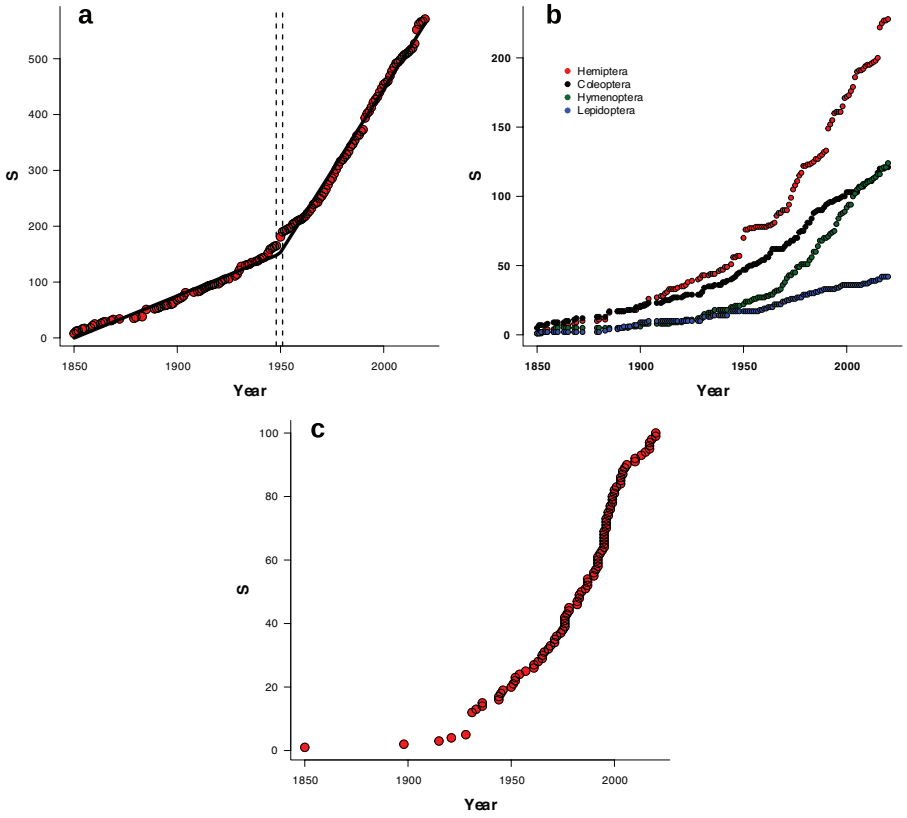

Figure 4. Temporal trend of the accumulated number of non-native species in Chile (S) **a** total number of species. Points correspond to observed data, the black line corresponds to the fit of the regression model and the dashed lines indicate the 95% confidence interval for the break-point in the segmented regression **b** number of species of the most abundant orders **c** number of species identified as biological control agents.

Discussion

The history of insect invasion in Chile follows the common trend observed all around the world (e.g. Sailer (1983); Yamanaka et al. (2015)). The arrival of Europeans to the country started major transitions in the insect fauna mainly due to the introduction of non-native plants. For example, the introduction of new crops, such as wheat, began as early as 1541. However, because most non-native plants were introduced as seeds, few insects were detected and very few became a phytosanitary issue before the 19th century (Prado 1991), a similar situation to the one described by Sailer (1983) for the USA. Fruit crops and vines were also introduced early on in colonial times (Lacoste 2004; Lacoste et al. 2011), but major pests of these crops also arrived in Chile during the 19th and 20th centuries (Artigas 1995; González 2012).

Our results show that the composition of non-native insect fauna in Chile is strongly biased to groups associated with agriculture and forestry. This is a common situation in other parts of the world (Bradshaw et al. 2016; Liebhold et al. 2016). For example, Sailer (1978, 1983) and Yamanaka et al. (2015) also showed that most non-native species in North America belong to the order Hemiptera. Waage et al. (2008) also found that Hemiptera (Homoptera in the original) is the order with the most species introduced in Europe and Africa. According to Stork (2018), Hemiptera globally is only the fifth order in terms of the number of species, but it is the most intercepted order in borders of several countries of the world because its association with crops, forestry and fruit or ornamental trees (Gippet et al. 2019; Turner et al. 2021).

In terms of the origin of the non-native insects, most of them show a Palearctic origin. Again, this situation has been observed in other parts of the world. Miller et al. (2005) described similar results when they analysed the richness of non-native scale insects in the USA, all of them associated with agriculture. Yamanaka et al. (2015) also found that, in North America and Japan, most of the non-native insects are of Palearctic origin. This result is not surprising given that more than 50% of the non-native plants in Chile are of European origin (Fuentes et al. 2014). Barriga et al. (1993) and Fuentes-Contreras et al. (1997), in their analyses of Coleoptera and Aphids, respectively, report that, with only two exceptions, non-native insects feed on non-native plants, which supports the hypothesis that the non-native-plant/non-native-insect association is the key promoter of the introduction of arthropods (Liebhold et al. 2018). This is reinforced by the fact that most non-native insects are associated with agricultural, forestry and ornamental plants. Moreover, most early alert systems in the world have been designed to detect non-native insects of economic importance (agriculture, forestry etc.).

We detected an abrupt increase in the rate of introductions recorded around 1950. Many studies have shown an exponential increase in the rate over years, especially in the last century (see examples in Seebens et al. (2017)) and even the timing of this acceleration has been observed in other taxa at global scale (Seebens et al. 2017). In our case, this abrupt change can have several explanations. First, the change in the rate can be a by-product of the increase in Hemiptera introductions in the same years following

the growth in agricultural production post-World War II during the "Green Revolution" (Díaz et al. 2016). Bonnamour et al. (2021) describe this moment as the second wave of globalisation, where international trade began to increase significantly. A second explanation comes from the major development of biological control programmes of plant pests in Chile in the second half of the 20th century, with particular relevance for the parasitoid Hymenoptera (Rojas 2005). Both explanations make reference to changes in agricultural production, but a third alternative is related to the strong increase in air transport (Díaz et al. 2016). The use of international air transport by Chileans showed a marked, strong growth at the beginning of the 1950s. Furthermore, international trade in Chile also increased in the last decades of the 20th century, along with globalisation. In particular, such a recent increase in trade with Asian countries could be incorporating new regions with new pools of potential invasive species (Seebens et al. 2018). Finally, observational bias in the report of new non-native species is probably present in our analyses (Bebber et al. 2019). For example, at the beginning of the 1950s and 1990s, three specific reports seem to add a significant number of records, creating jumps in the accumulated series (Essig 1953; Prado 1991; Starý et al. 1993). However, the segmented model detects changes in the intercept and slope of the two segments of the series. Reports of new non-native species of insects require trained entomologists and international collaboration with specialist taxonomists. For Chile in the 19th century, these human resources were a few foreign naturalists working in the country. The first applied entomologists appeared at the end of 19th and the first half of the 20th century. Finally, a more robust and permanent process of training and networking of applied entomologists and agriculturalist scientists was promoted only during the second half of the 20th century (Artigas 1995; del Pozo et al. 2021). All these variables might be associated with the increase in non-native species, but more detailed analyses are needed to evaluate their relative contribution.

Nowadays, climate change has acted as a promoter of the range expansion of many insect species. For non-native species, ongoing and future climate change could facilitate the short distance dispersal of non-native insects across national borders (Pearson 2006; Hulme 2017). However, for some authors, climate-tracking species should not be considered non-native or invasive (Urban 2020).

Conclusions

In this study, we reconstructed the main patterns of insect introductions to Chile. The order Hemiptera was the most prevalent amongst non-native insects, with species linked to agriculture and forestry industries. Species are of Palearctic origin in more than 50% of the records. Temporal trends show an abrupt increase at the beginning of the 1950s. This change may be associated with the strong development in agriculture and forestry in Chile after World War II and the increase in intercontinental air traffic. We believe that the understanding of past patterns of introductions is an important

component in the design of current policies to minimise the impact of invasive insects. This database is the first attempt to compile this information, but this is essentially a work in progress. It has to be updated and improved by governmental agencies, academics and specialists for a better understanding of it. We think that some of the results presented in this study may be representative of other countries in South America. Similarities with other regions suggest that the processes behind insect introductions are common around the world and their detailed description can be a fundamental tool for managing current introductions and preventing major economic, social or environmental damage.

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Supplementary material 1

Database: exotic insects of Chile

Authors: Daniela N. López, Eduardo Fuentes-Contreras, Cecilia Ruiz, Sandra Ide, Sergio A. Estay

Data type: table (excel file)

Explanation note: Excel file containing records of exotic insects in Chile.

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