NeoBiota 23: 17–64 (2014)
doi: 10.3897/neobiota.23.7745
http://neobiota.pensoft.net/

RESEARCH ARTICLE

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

A biography of an invasive terrestrial slug: the spread, distribution and habitat of *Deroceras invadens*

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Academic editor: *Ingolf Kühn* | Received 17 April 2014 | Accepted 10 June 2014 | Published 2 September 2014

Citation: Hutchinson JMC, Reise H, Robinson DG (2014) A biography of an invasive terrestrial slug: the spread, distribution and habitat of *Deroceras invadens*. NeoBiota 23: 17–64. doi: 10.3897/neobiota.23.7745

Abstract

The article reviews distribution records of *Deroceras invadens* (previously called *D. panormitanum* and *D. caruanae*), adding significant unpublished records from the authors' own collecting, museum samples, and interceptions on goods arriving in the U.S.A. By 1940 *D. invadens* had already arrived in Britain, Denmark, California, Australia and probably New Zealand; it has turned up in many further places since, including remote oceanic islands, but scarcely around the eastern Mediterranean (Egypt and Crete are the exceptions), nor in Asia. Throughout much of the Americas its presence seems to have been previously overlooked, probably often being mistaken for *D. laeve*. New national records include Mexico, Costa Rica, and Ecuador, with evidence from interceptions of its presence in Panama, Peru, and Kenya. The range appears limited by cold winters and dry summers; this would explain why its intrusion into eastern Europe and southern Spain has been rather slow and incomplete. At a finer geographic scale, the occurrence of the congener *D. reticulatum* provides a convenient comparison to control for sampling effort; *D. invadens* is often about half as frequently encountered and sometimes predominates. *Deroceras invadens* is most commonly found in synanthropic habitats, particularly gardens and under rubbish, but also in greenhouses, and sometimes arable land and pasture. It may spread into natural habitats, as in Britain, South Africa, Australia and Tenerife. Many identifications have been checked in the light of recent taxonomic revision, revealing that the sibling species *D. panormitanum* s.s. has spread much less extensively. A number of published or online records, especially in Australia, have turned out to be misidentifications of *D. laeve*.

Keywords

Biological invasion, pest slug, Pulmonata, Agriolimacidae, *Deroceras panormitanum*

Introduction

Some terrestrial slugs and snails have been inadvertently spread by man well beyond their natural range (Hanna 1966, Barker 1999, Robinson 1999, Cowie 2001, Herbert 2010). They may become very common and cause significant economic damage. For instance, in much of North America the commonest slugs in disturbed habitats are not native species but European slugs such as *Deroceras reticulatum* (Müller, 1774) and several species of *Arion* (e.g. Chichester and Getz 1969). These species have also colonised less disturbed habitats. In these cases much of the spread likely occurred well before anyone was observing the process.

The current paper gathers data on the spread of the slug *Deroceras invadens* Reise et al., 2011, which has often been reported (under various different names) as turning up in new places over the last century, thus revealing something of the colonisation process. Many relevant publications are widely dispersed in local journals, so there seems merit in reviewing these accounts in the hope of identifying global patterns. A better knowledge of the colonisation process may help in restricting or slowing the further spread of this and other slug species. The commonest sort of relevant data is the first occurrence in a country or administrative division. Unfortunately this is rather an unreliable statistic, because when a species first arrives its rarity makes its discovery very much a chance event, and because most local malacologists may not recognise the species until its first occurrence in their region has been published. Accordingly, we have tried also to assess rates of spread following the first discovery; unfortunately such monitoring is uncommon.

Our second object is to establish how far *D. invadens* has spread; several records of our own and unpublished information from museum collections significantly expand the known range. Conversely, some records turn out to be erroneous. Besides the value to those battling pest slugs in affected countries, a fuller knowledge of the range of climates that the species can tolerate may allow us to predict other regions that are at risk of being colonised. Thirdly we are interested in what habitats *D. invadens* occupies, particularly whether it invades agricultural and natural habitats. A fourth issue is how common the species gets, which can be assessed at various scales, such as proportion of grid squares occupied, proportion of sampling sites at which it is found, or number of animals collected. Here we will often compare with comparable data on *D. reticulatum*, a usually commoner congener that is found in similar synanthropic habitats but has spread earlier and more widely. Occurrence of *D. reticulatum* thus provides a proxy for estimating sampling effort (i.e., confirming the activity of someone interested in recording slugs).

The diversity of climates within the introduced range of *D. invadens* prompts the question of whether several cryptic species might be hidden within the diaspora. Therefore another aim has been to check the species identity of introduced populations. To understand the issues, it is helpful to review the taxonomic background. *Deroceras* is the largest genus of terrestrial slugs, with over 100 species described (Wiktor 2000). Although the genus is originally Palaearctic, two species, *D. reticulatum* and

D. laeve (Müller, 1774) have spread globally; in the case of *D. laeve* it is thought that its invasion of America has been natural. Another species, *D. sturanyi* (Simroth, 1894), is spreading widely in Europe. In much of western Europe and elsewhere in the world malacologists can recognise *D. invadens* in the field, because it is a different colour to *D. reticulatum* (although this difference can disappear in alcohol) and larger than *D. laeve*. However, dissection is required to be sure because *D. laeve* can sometimes grow large (particularly outside Europe), because *D. invadens* is externally indistinguishable from *D. sturanyi*, and because there are other more local species in Europe that are also externally similar, and which also might have spread. In particular, *D. invadens* was until recently confused with *D. panormitanum* s.s., a species common in Sicily and Malta (Reise et al. 2011); the vast majority of identifications in the literature predate this splitting. *Deroceras caruanae* (Pollonera, 1891) is a junior synonym of *D. panormitanum* (Reise et al. 2011).

Material and methods

Besides checking literature in our own collections, we carried out online searches for "*caruanae*", "*panormitanum*" and "*invadens*" particularly in combination with the names of specific countries. We also searched for the most recent species lists or distribution maps of likely host countries. We checked online museum catalogues, and personally screened the natural history museums in London and Wrocław. A.J. de Winter kindly selected relevant material from the Naturalis Biodiversity Centre, Leiden, and we have also borrowed material from the Rähle collection in the Stuttgart State Museum of Natural History, the Field Museum Chicago, the Florida Museum of Natural History, the Museum Victoria, the Queensland Museum, the Australian Museum, and the University Museum of Zoology Cambridge.

We have incorporated into the account results from our own fieldwork. Specimens collected by HR and JMCH are in the Senckenberg Museum of Natural History at Görlitz (SMNG). DGR has collected separately and specimens are in the collection of the U.S. Department of Agriculture (USDA) at the Academy of Natural Sciences in Philadelphia. Furthermore we have accessed the USDA collection of material intercepted arriving at U.S. ports (Robinson 1999, Reise et al. 2006). M.A. Nash and G.M. Barker provided the SMNG with numerous samples from Australia and New Zealand; other collectors who responded to our requests are listed in the Acknowledgements.

HR confirmed identities using characters of the genitalia (Reise et al. 2011). Table 2 lists the collection details of previously unpublished records that extend the distribution of *D. invadens* significantly. To avoid confusion in subsequent work, we mention identifications of *D. invadens* in museums or in publications that have proved to be incorrect or were based only on unreliable external characters. Unrecognised misidentifications may affect some of the other records that we analyse or map, but where we had suspicions we have endeavoured to borrow voucher specimens, or we state where further checking would be desirable.

Literature commonly refers to *D. invadens* as *D. caruanae*, *D. panormitanum* or *D. pollonerae* (older literature also uses the genus name *Agriolimax*). Moreover, because the separation of *D. invadens* from *D. panormitanum* s.s. is recent, much literature is ambiguous to which species it refers. We have found it least confusing here to refer to all such ambiguous records as *D. invadens*, which is by far the more widespread species, rather than to distinguish unconfirmed records as "*D. panormitanum* s.l." Table 1 states, for each country or island, how many populations we have confirmed are *D. invadens* rather than *D. panormitanum* s.s. Fig. 4A also makes this distinction. The text highlights the very few records outside of Malta and Sicily that were *D. panormitanum* s.s. This low incidence of *D. panormitanum* s.s. justifies our working assumption throughout that ambiguous records are of *D. invadens*. But in no region have we examined enough samples to be confident that some *D. panormitanum* s.s. are not mixed in; others should continue to check.

Table 1. List of countries and oceanic islands dealt with in the text (in the same order). The second column summarises the date *D. invadens* was first found (outdoors, unless specified). The '≤' symbol indicates when a publication does not give a date of first collection. Dates of interception describe when the species was found on goods derived from that country. The third and fourth columns give the number of sites (or interceptions) for which we are sure that *D. invadens* rather than *D. panormitanum* s.s. occurs or vice versa; usually this evidence is our dissections, other cases are from publicly available COI sequences (indicated if this is the only evidence), otherwise the source is cited. We use '–' instead of '0' if there is no evidence of either species.

Location	First known occurrence of *D. invadens*	Sites confirmed	
		D. invadens	***D. panormitanum* s.s.**
Europe			
Italy	native	mainland 48, Sardinia 2, Sicily 5, Lipari Is >12	mainland 1, Sicily 21
San Marino	2013	2	0
Malta	no record	0	Malta 5, Gozo 2
Great Britain	1930	England 25, Wales 5, Scotland 7	Wales 1 (Rowson et al. 2014a, b)
Island of Ireland	1958	4	0
France	≤1945	12	0
Monaco	2012	1	0
Belgium	1968	8	0
Netherlands	1969	9	0
Luxembourg	1997	0	0
Germany	1979	18	0
Switzerland	1982	1	0
Austria	≤1977	2	0
Czech Republic	1996	1	0
Slovakia	(greenhouse 2003)	1 (Dvořák et al. 2003)	0
Poland	2001	1	0
Lithuania	erroneous record	–	–
Hungary	no reliable record	–	–

Location	First known occurrence of *D. invadens*	Sites confirmed	
		D. invadens	***D. panormitanum* s.s.**
Romania	erroneous record	–	–
Bulgaria	no reliable record	–	–
Greece	2011	1 (COI)	0
Denmark	1937	0	0
Sweden	≤1980 (greenhouse 1957)	4	0
Norway	1983–84 (greenhouse c. 1967)	2	0
Finland	(greenhouse ≤1961)	0	0
Portugal	1977	0	0
Spain	1974	12	0
Africa			
Egypt	2005	0	0
South Africa	1963	2	0
Kenya	interception 2012	1 interception	0
Asia and Australasia			
Sri Lanka	erroneous record	–	–
Australia	1936	NSW 8, Victoria 4, Tasmania 1, S. Aus. 1, W. Aus. 2	0
New Zealand	1974, or maybe ≤1891	8	0
Americas			
USA	1940	Washington State 3, Oregon 2, California 4, Colorado 7, Utah 5, Washington DC 1	0
Canada	1974 (greenhouse 1966)	British Columbia 10, Newfoundland 1	0
Mexico	1974	1	0
Costa Rica	2006	1	0
Panamá	(interception 2007)	2	0
Colombia	1975	1, 1 interception	0
Ecuador	2012 (interception 2004)	1	0
Peru	(interception 2012)	1 interception	0
Chile	≤2003	3	0
Argentina	2010	1 (COI)	0
Brazil	1991	1 interception	0
Oceanic islands			
Faroe Islands	1970	0	0
Madeira	1980	17	2
Azores	1957	São Miguel 4, 1 interception	1 interception
Canary Islands	1947	9	0
Tristan da Cunha	1982–83	1	0
Raoul Island	1973	2	0
Chatham Islands	1976	0	0
Marion Island	1972	1 (COI)	0
Juan Fernández Islands	1962	1	0
Lord Howe and Norfolk islands	erroneous records	–	–

Results

This section considers each country in turn. Countries are grouped by continent; within continents the ordering is mostly so that geographically close countries are dealt with together; Table 1 can be used as an index to the order of presentation. Oceanic islands are dealt with separately at the end, independently of their political affiliation.

Europe

Italy and San Marino

The native range of *D. invadens* is thought to be in Italy (Reise et al. 2011), but the species might nevertheless be an introduction in parts of that country. Our recent collections and their genetic analysis support this hypothesis, but the results will be published elsewhere. To summarise, we have found that *D. invadens* is widespread throughout mainland Italy and occurs also in Sicily and Sardinia. It is easiest to find in synanthropic sites, as in other countries, but we also found it in undisturbed woodland. Several other, less frequent, species occur which are externally indistinguishable from *D. invadens*. Only in one garden in northwest Italy was *D. invadens* found co-occurring with *D. panormitanum* s.s. (Table 2); the latter replaces *D. invadens* in parts of Sicily.

Table 2 details the first two records (2013) of *D. invadens* in the Republic of San Marino (a tiny state surrounded by Italian territory).

Malta

Reise et al. (2011) argued that Pollonera's (1891) original description of *D. caruanae* from the capital Valletta referred to *D. panormitanum* s.s. Our collecting in 2000 on Malta and Gozo (supplemented by that of T. Backeljau in 1994: see Reise et al. 2011) was targeted at *Deroceras* but never encountered *D. invadens*; *D. panormitanum* s.s. and *D. golcheri* (Altena, 1962) were widespread.

Great Britain

Deroceras invadens was first found about 1930, in Cornwall, but by 1932 also from South Wales, central southern and northeast England, and Scotland (Ellis 1950, Quick 1960, Kerney 1999). This wide distribution implies that it had been overlooked for some time. Formerly, some supposed that *D. invadens* was native in Britain (Ellis 1951, Hayward 1954), but we are now more aware of how well the species can spread, and further work (Reuse 1983) established that the shell is insufficiently distinctive for us to trust Hayward's (1954) identification of fossils.

The Conchological Society of Great Britain and Ireland publishes lists annually of vice-counties in the British Isles from which species have been newly recorded and the identity confirmed by experts. If we restrict attention to England and Wales (Scotland and Ireland were more sporadically recorded), the number of vice-counties increased only slowly to 13 by 1964, then jumped to 54 within 10 years (presumably at least partly

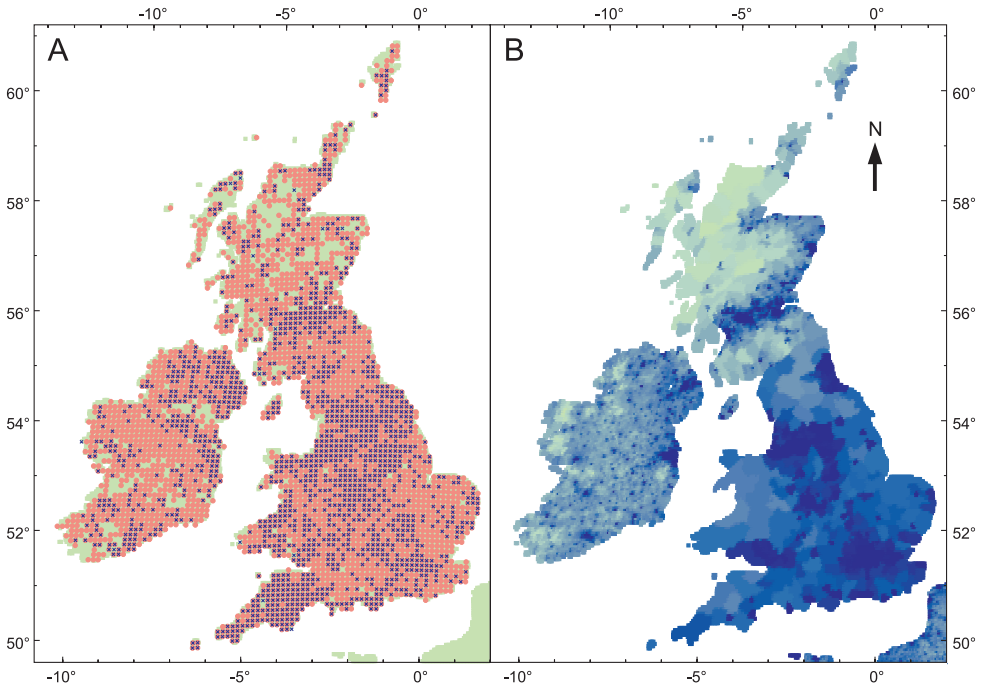

Figure 1. The distribution of *D. invadens* in the British Isles. **A** Records of *D. invadens* (blue cross) and *D. reticulatum* (red circle) for each 10 km square (accessed from NBN gateway 24.xi.12) **B** Human population density (pale green = low, dark blue = high); sourced from Center for International Earth Science Information Network (Columbia University), Centro Internacional de Agricultura Tropical. 2005. Gridded Population of the World Version 3: Population Density Grids. Palisades, NY: Socioeconomic Data and Applications Center (SEDAC), Columbia University. Downloaded from http://sedac.ciesin.columbia.edu/gpw Nov. 2012.

an artefact of increased sampling effort in preparation of a distribution atlas). Over the next 25 years, Kerney (1999) considered that it had continued to spread rapidly. Today, confirmed records are lacking in only one of the 70 vice-counties (for which there are unconfirmed records) and the distribution now spans all of Great Britain, including such offshore islands as Orkney, Shetland, the Western Isles, the Isle of Man, Lundy, and the Scilly Isles.

At a more local scale, *D. invadens* has been recorded from 1849 10 km grid squares in Great Britain; this is 0.44 as many as the almost ubiquitous *D. reticulatum* (access of NBN gateway on 24.xi.12; https://data.nbn.org.uk). The distribution map still shows some regions of scarcity (Fig. 1). Some correspond to areas where absent records of *D. reticulatum* suggest light recording activity, but these are also often areas of low human population density, which itself might have hindered the spread of a synanthrope. Areas in the west with low human population densities nevertheless show a dense distribution of *D. invadens*. A higher abundance in the west was noted by Kerney (1999) and may derive from the milder climate (both warmer winters and wetter summers).

Some regional differences in abundance are certainly not artefacts of recording intensity. For instance, in Suffolk (eastern England, sparsely populated) *D. invadens* was not reported until 1982 and a particularly thorough survey up to 1990 found it to be relatively scarce, with scattered localities across the county but concentrated in a couple of areas and generally only in gardens and disturbed ground (Killeen 1992). Contrast this with a 1987–88 survey of gardens in Greater Manchester (northwest England, densely populated), which found it to be the slug species occurring in the most gardens (258 out of 372 gardens) and in the greatest numbers (North and Bailey 1989). Similarly, in a diverse sample of 16 gardens in southeast Scotland, *D. invadens* occurred in 14; *D. reticulatum* was the only mollusc occurring in more (Sumner 2002).

Kerney (1999) nicely summarises where *D. invadens* is most often found (writing of the British Isles, but it is typical elsewhere too): "A species of disturbed habitats, and associated with roadside rubbish, farmyards and gardens. It often shelters under stones, pieces of wood, cardboard and other litter in bare or sparsely vegetated waste ground". He also reported the species occurring in wilder places such as woods and hedgerows but only in climatically mild areas such as the South West; in our experience this is also the case in the South East. In a survey of eight ancient woods on the Isle of Man, it was found in seven and was the only widespread non-native species (Alexander and Dubbeldam 2013). Likewise, in northeast England *D. invadens* occurred in 9 out of 17 woods (all contained *D. reticulatum*: Wardhaugh 1996). Dirzo (1980) reported the absence or rarity of *D. invadens* in habitats dominated by grass. It occurs in some arable fields (Quick 1949, Foster 1977, Dirzo 1980, Vernavá et al. 2004, Howlett 2005 Chapter 8), where it sometimes dominates, but usually other slugs are the more important pests. However, *D. invadens* was the dominant slug pest in 10 selected English nurseries growing "hardy nursery stock" (Anon. 2003; the dearth of information about this survey does raise a concern that *D. laeve* might have been confused sometimes). An ability to thrive in the damp warm environment of modern nurseries would predispose the species to spread into gardens nationwide.

Rowson et al. (2014a, b) reported the occurrence of *D. panormitanum* s.s. from a garden in Cardiff. The single occurrence of this species contrasts with the 37 British populations of *D. invadens* that we have checked or from which COI sequences appear in Genbank (Table 1).

Island of Ireland

The first records were in 1958, from several sites around Cork, and in 1959 from Newcastle, County Down, at the other end of the island and in a different country (Makings 1959). These dates are surprisingly late, considering the close links with Great Britain and that malacologists familiar with the species there were collecting in Ireland in these 29 years after its discovery in Britain.

Today in Ireland the number of 10 km squares occupied by *D. invadens* is a similar proportion of those occupied by *D. reticulatum* as in Great Britain (0.38 vs 0.44; access to NBN gateway on 24.xi.2012; https://data.nbn.org.uk). In an interesting contrast with Britain, Ross (1984) observed that it was commoner to the east and north; this

might be explicable by a correlation with higher population densities (Fig. 1). At least in the north, the explanation for such a correlation is not an absence of collecting activity towards the west (Anderson 1983). Ross (1984) reported that its occurrence in less disturbed sites such as woodlands and marshes was increasing. By 1996, it was "widespread and abundant in disturbed habitats, woodland and marshes throughout Northern Ireland. A notable pest in gardens" (Anderson 1997). Around Cork, even soon after its first discovery, 7–27% of slugs collected in gardens were *D. invadens* (Makings 1959, 1962).

France

In 1910 Simroth described *Agriolimax scharffi* collected in 1903 from La Giandola in the extreme southeast of France. Some (e.g. Bishop 1980, Gavetti et al. 2008) have argued that this refers to the slug we call *D. invadens*, which would then be the first record of the species in France or anywhere else and give the species name *scharffi* priority. Unfortunately the description is so casual ("... fand ich neben der gemeinen Ackerschnecke eine kleinere helle Form, die nicht retikuliert, sondern fein dunkel punktiert war": I found together with the common *D. reticulatum* a smaller pale form which was not reticulated but with fine dark dots) that it could refer to other species known from the area (Bodon et al. 1982), such as *D. bisacchium* Bodon, Boato and Giusti, 1982, *D. rodnae* Grossu and Lupu, 1965, or a form of *D. reticulatum*. Also the sibling species *D. panormitanum* s.s. occurs only 23 km away at Bordighera, Italy (Table 2). We visited La Giandola in 2013 and did find *D. invadens*, which in itself is not so informative because the species could well have spread there since Simroth's visit. More significant is that *D. invadens* at this site is not paler than the *D. reticulatum*. Conversely some of the *D. reticulatum* were of a somewhat unfamiliar appearance to us and did fit the description of "pale ... not reticulated ... with fine dark dots". And also in La Giandola itself we found another species fitting this description; anatomically it matched local *D. rodnae* s.s. but its mating behaviour was distinct. Altogether there seems plenty enough uncertainty to follow Reise et al. (2011) in regarding *A. scharffi* as a nomen dubium and not to treat this as a record of *D. invadens*.

The first clear reports of *D. invadens* from France are from Hameury (1958), listing two sites near Brest (NW France) from 1956. Quick (1960) had examined specimens from the Pyrenées Orientales (SW France). Later Reygrobellet (1963) described a new species *D. meridionale*, now considered a synonym of *D. invadens* (Reise et al. 2011); she mentioned it occurring in southeast France (departments of Var, Bouches-du-Rhône, and Alpes-de-Haute-Provence, without details of localities or dates). More specifically, Chevallier (1973) published an occurrence of *D. invadens* from this region (Marseille) from 1948. Reygrobellet (1963) also referred to work by Abeloos (1945) demonstrating the existence of two forms of *Deroceras* near Poitiers (western France), one of which she and Abeloos had subsequently agreed was *D. meridionale* (i.e. *D. invadens*). To summarise, the species occurred at two distant sites in France already in the 1940s and was widespread at least by 1963.

A map prepared in 1972 by Chevallier (1973) showed many localities throughout the western half of France and around Paris; their absence on the eastern half of the map, except in the south, was explained by this region not having been surveyed. However

Chevallier also stated that the species seemed more at home in coastal regions than inland, and emphasised that it occurred along the very edges of sea shores, estuaries and lagoons as well as by freshwater habitats. In contrast to other habitat descriptions of *D. invadens*, he mentioned only in the last sentence that it was also sometimes found in gardens.

The first two records from Corsica were from 1977 (Holyoak 1983); these were identified by A. Wiktor but it would be desirable to scrutinise specimens from this island further given the taxonomic complexity of the genus on the adjacent Tuscan archipelago (Giusti 1976). The online database of the Inventaire National du Patrimoine Naturel (INPN) (http://inpn.mnhn.fr/espece/cd_nom/163204/tab/rep) shows *D. invadens* now to occur also widely in northeast France. Cucherat and Demuynck (2006) describe it as widespread and sometimes locally abundant in the northeast departments of Nord and Pas du Calais. Comparison of INPN maps of *D. invadens* and *D. reticulatum* suggests that the continuing absence of records from areas of central and eastern France at least partially reflects an absence of recent recording. However, there certainly are still areas of France where *D. invadens* is uncommon. Thus, Boulord et al. (2007) found it to be rare to uncommon in Maures (NW France), occurring in only six 5 km squares compared with the 44 with *D. reticulatum* (ratio = 0.14). And in a review of slugs in Alsace (E France), Hommay (2000) could report *D. invadens* only from greenhouses near Colmar.

Monaco

We believe that the first record of *D. invadens* from Monaco is our finding in 2012 under bushes in a park at a spot irrigated by an automatic watering system (Table 2).

Belgium

The first finding of *D. invadens* in Belgium was in 1968 in a Brussels garden (Van Goethem 1974). The species was not found again until 1972, when a project mapping terrestrial Mollusca began. Van Goethem et al. (1984) mapped on a 10 km grid all findings of *D. invadens* and *D. reticulatum* for each year from 1972–83. Again we divide the number of grid squares in which *D. invadens* had been found by the number for *D. reticulatum* (thus controlling for collecting coverage); this yields a ratio of 0.65, comparable with figures of 0.44 and 0.38 for Britain and Ireland.

Van Goethem et al. (1984) also displayed the total number of records of *D. invadens* and *D. reticulatum* within each grid square. *Deroceras reticulatum* occurred in almost every square, so for each grid square the ratio of number of records of *D. invadens* to those of *D. reticulatum* provides a local measure of commonness of *D. invadens* adjusted for collecting effort. (Only a small proportion of the records for *D. reticulatum* predate the occurrence of *D. invadens*.) By this measure *D. invadens* is rarer in the southeast (Fig. 2). As in Britain and Ireland, the pattern is a good match at a coarse level to human population density (Fig. 2). A partial exception is the paucity of records around the city of Liege, interesting because in 2012 we failed to find the species in this city despite screening public gardens and allotments that looked ideal habitat.

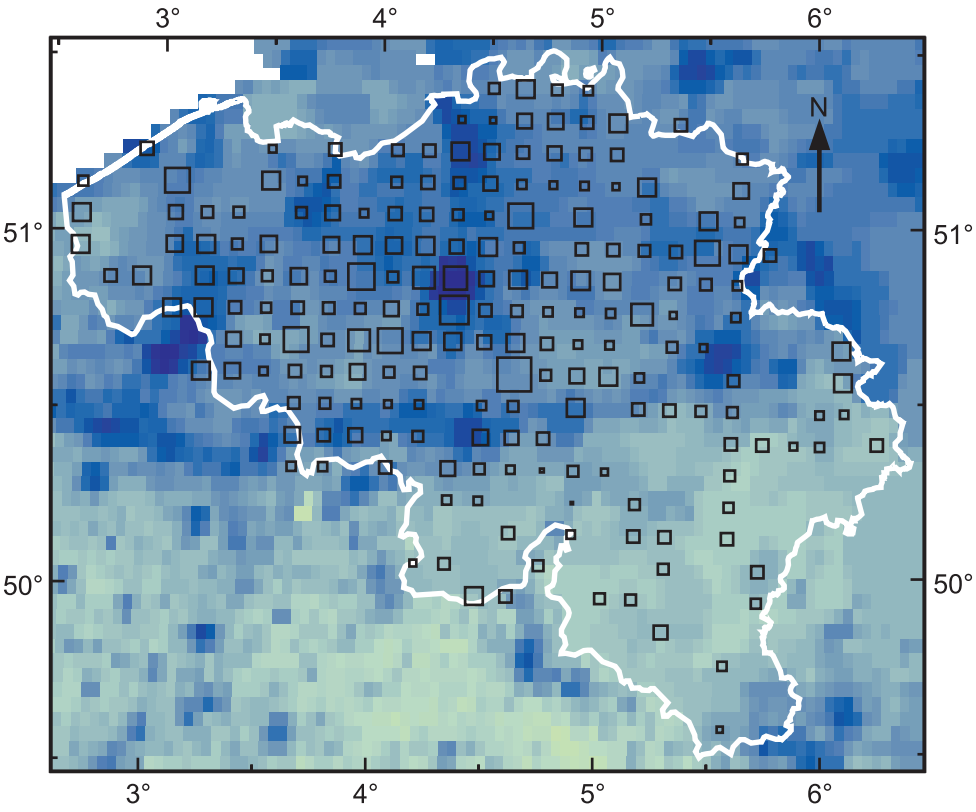

Figure 2. Incidence of *D. invadens* in Belgium (white outline) 1968–83. Based on surveys by Van Goethem et al. (1984). Size of the square in each 10 km grid square is proportional to the ratio of the number of records of *D. invadens* to that of *D. reticulatum* (the very few squares with no record of *D. reticulatum* show no symbol). This is superimposed on a map of population density (pale green = low, dark blue = high; same source as in Fig. 1).

Additionally the Belgian data provide the number of grid squares in which each species of *Deroceras* was found each year. Surprisingly, the ratio between the counts for *D. invadens* and *D. reticulatum* does not increase over the period 1972–83 (Fig. 3, $\tau = -0.30$, $P = 0.19$), suggesting that the species was already well established by 1972 despite only one record predating this. Even when we considered only the apparently less saturated southeast, the ratios did not suggest an increase. Our conclusion conflicts with that of Van Goethem et al. (1984), who did sense an increased incidence over this period.

Van Goethem et al. (1984) provided qualitative comments on the habitat of *D. invadens*. It was more synanthropic than *D. reticulatum*, and could predominate over that species in such habitats, whereas it was less common on canal banks. It seemed to be absent from the interior of woods, especially coniferous woods, but it was rare even in poplar plantations.

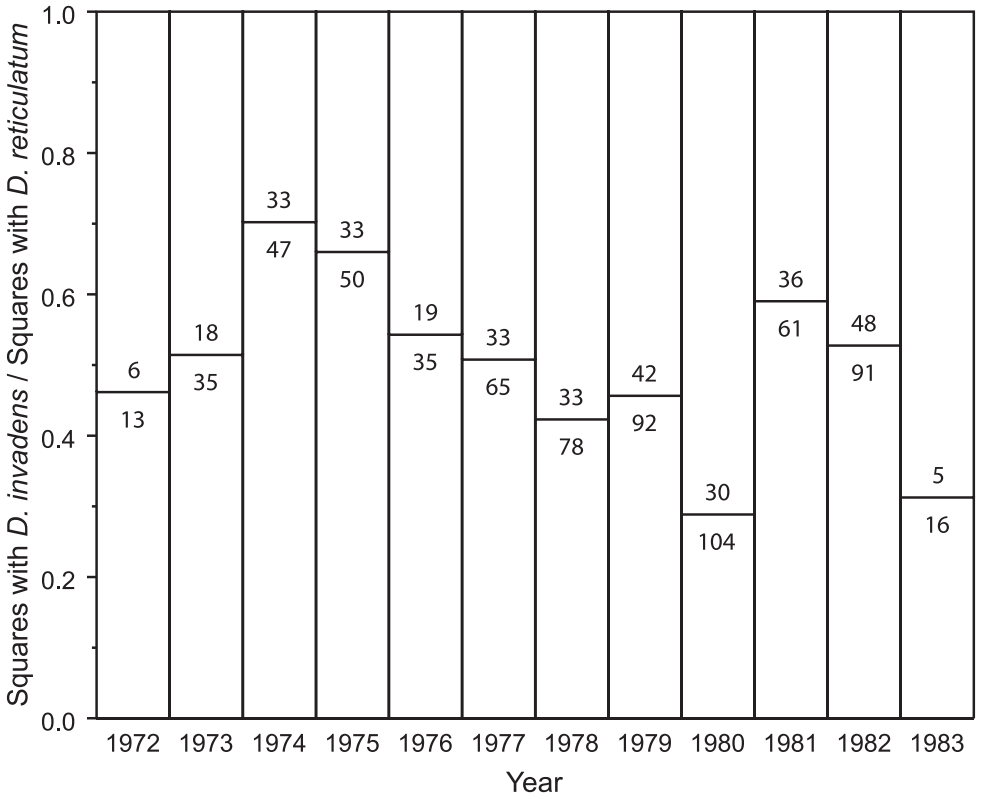

Figure 3. *Deroceras invadens* did not get easier to find in Belgium 1972–83. Ratio of the number of Belgian 10 km grid squares in which *D. invadens* was found to those in which *D. reticulatum* was found, for each year reported by Van Goethem et al. (1984). Numbers above and below the line are the counts for *D. invadens* and *D. reticulatum* respectively.

Netherlands

The first finding was in 1969 in Domburg at the southwest tip of the country (Gittenberger et al. 1970). By 1982 it was recorded from five provinces across the south of the country (de Winter 1984), and already in 1984 de Winter estimated that he had found it in a third of gardens and similar habitats examined. A distribution map prepared in 2005 (Atlasproject Nederlandse Mollusken; http://www.anemoon.org/anm/voorlopige-kaarten, accessed 5.vi.13) shows it spread over the whole country, including even the Wadden island of Terschelling (Mienis 2003), although mapping of the Netherlands is much less complete than for the British Isles or Belgium. This map shows *D. invadens* as recorded in 50 5 km squares between 1990 and 2005, compared with 199 squares for *D. reticulatum*. The ratio of these numbers is somewhat lower than in Britain, Ireland or Belgium (0.25 vs. 0.44, 0.38 and 0.65), which might partly reflect the lesser sampling intensity in the Netherlands: if each square is sampled rarely the ratio reflects the chance of encountering *D. invadens* at an individual collecting site, rather than somewhere in the whole grid square.

Three intensive local surveys from the south of the Netherlands confirm the broad pattern. In Zuid-Holland, Boesveld (2005a) found *D. invadens* in 34 5 km squares, compared with 80 for *D. reticulatum* (ratio = 0.42). For 1 km squares, the corresponding figures are 48 and 129 (ratio = 0.37). In Noord-Brabant, Boesveld (2005b) found *D. invadens* in 9 of the 118 1 km squares visited, and *D. reticulatum* in 36 (ratio = 0.25). Both studies pointed out that they had undersampled urban areas, where *D. invadens* is commoner. Along the coast of Zeeland (Boesveld 2005c), *D. invadens* occurred in 22 out of the 79 1 km squares visited compared with 38 for *D. reticulatum* (ratio = 0.58).

Luxembourg

There are four 1997–98 records of *D. invadens* provided by Weitmann and Groh in the database of the Musée d'histoire naturelle Luxembourg (accessed via http://data.gbif.org/species/5190777 Sept. 2012).

Germany

Falkner (1979) documents several cases in the 1970s of *D. invadens* turning up in Munich on purchased lettuce, endive and strawberries, mostly imported from Italy. The first findings outdoors in Germany were in 1977 and 1978 in and near Munich (Falkner 1979). Analysing the subsequent spread is complicated because, although Germany is well supplied with malacologists, recording schemes have been organised, if at all, at the level of the 16 states (Bundesländer). The following paragraphs deal with each state in turn, in order of the first appearance of *D. invadens* in each, except that the states that were part of East Germany until 1990 are considered in a second paragraph (Berlin is listed with West Germany). The first published occurrence in the former East Germany postdated by a year the opening of the border between East and West Germany (Bössneck 1994), but by this time *D. invadens* had not been recorded either in 6 of the 11 West German states. Moreover, the notebooks of the late V. Herdam, indicate East German occurrences in Berlin in 1982 and in Brandenburg in 1985 (E. Hackenberg pers. comm.; Table 2); it is hard to judge how reliable these records are.

Bavaria: first found in 1977 (see above). North Rhine Westphalia: first found in 1979, at several sites near Cologne (Schnell and Schnell 1981); a thorough survey of Cologne between 1990 and 1994 located it at 15 sites throughout the city, compared with 49 for *D. reticulatum* (ratio = 0.31: Tappert 1996). Baden–Württemberg: first found in 1982, from several distant sites (Schmid 1997). Schleswig–Holstein: first found by 1983 (Wiese 1983); the 1991 atlas (Wiese 1991) showed it in 2 10 km squares, compared with 21 for *D. reticulatum* (post-1960 records; ratio = 0.10). Hesse: W. Hohorst collected *D. invadens* in Frankfurt am Main in 1985 (Table 2); in a 2010–11 survey in Frankfurt am Main, *D. invadens* was recorded from 11 of 22 sites, compared with 5 for *D. reticulatum* (ratio = 2.2; Kappes et al. 2012). Rhineland Palatinate: first found in 1994, in Jockgrim (Schmid 1997). Lower Saxony: first found in 1998 on the island of Baltrum; other records in Lill (2001) indicate that by 2001 it occurred throughout the state, sometimes at high densities, but restricted to synanthropic sites. Hamburg: first found in greenhouses in 1998 and outdoors in 2000 (Glöer and Haus-

dorf 2001). Bremen: first found 2001 (Lill 2001). Berlin: we know of no published record, but note Herdam's 1982 record mentioned above, and we collected it ourselves from a garden in Steglitz in 2001 (Table 2). Saarland: we know of no record.

Saxony: first found in 1990, in Limbach near Reichenbach (Bössneck 1994), and in 1991 at the other end of the state, in Görlitz (Reise and Backeljau 1994). Thuringia: first found in 1993, in Erfurt (Bössneck 1994); rather few sites (c. 5) have turned up since (U. Bössneck, pers. comm. 28.i.14). Mecklenburg–Vorpommern: first found in 1998; by 2006 it had been recorded in 10 5 km squares, always at synanthropic sites (64 squares contained *D. reticulatum*: ratio = 0.16; Zettler et al. 2006). Saxony–Anhalt: Unruh (2001) stated that it had been part of the outdoor fauna for years but by 2012 it was recorded from only 4 10 km squares (compared with c. 55 with post-1990 records for *D. reticulatum*: ratio = 0.07; Körnig et al. 2013). Brandenburg: we know of no published record beside our own from 2004, in Senzig at the edge of the Berlin conurbation (Reise et al. 2011), but note Herdam's 1985 record mentioned above.

A 2000–12 survey covering a broad area of northwest Germany, extending also into the Benelux countries, found that the mean density of *D. invadens* slightly exceeded that of *D. reticulatum* in gardens and in early successional woodland (Kappes and Schilthuizen 2014) but not in grassland or mature woodlands. The ranking of habitats in decreasing order of mean density of *D . invadens* was: gardens (0.68 m^{-2}), early successional woodland, mesic open, floodplain forest, wet open, wet deciduous forest, deciduous forest, scree forest, conifer; in the later three types the density was very low or absent.

In conclusion, *D. invadens* is now widely distributed in Germany and can be a common synanthrope in the west, but it took decades to turn up in many states and is still uncommon in many areas. The other invading *Deroceras*, *D. sturanyi*, is often commoner (e.g., Zettler et al. 2006, Körnig et al. 2013) although not in the northwest (Kappes and Schilthuizen 2014). There is little indication of *D. invadens* colonising more natural habitats.

Switzerland

The first record was in Basle near the German border in 1982 (Falkner 1982), the next not until 1991 (Turner et al. 1998). By 2011 *D. invadens* had still been recorded from only eight 5 km squares (around Basle, Bern, Lucerne and Zürich, so only from the lowlands in the northern half of the country: Boschi 2011). This compares with records of *D. reticulatum* from 350 squares since 1951 (Boschi 2011; ratio = 0.02). However, an independent study in 2007–09 (Fabian et al. 2012) found *D. invadens* to be one of the three commonest slugs in wildflower strips edging arable fields south of Lake Neuchâtel; perhaps the mapping had tended to overlook such occurrences in mundane agricultural landscapes.

Austria

The first record was in or before 1977 from a market garden in Maissau (NE Austria; Reischütz 1977, 1980). A 1986 atlas (Reischütz 1986) shows *D. invadens* in 9 10 km

squares, all in the eastern quarter of the country, centred on Vienna. However, *D. invadens* had been collected already in 1979 from Lienz (SSW corner of Austria: Kofler 1986), and in the north also the species has since been found further to the west (1990 in Schiebbs: Ressl 2005; 1999 in Braunau am Inn: collected F. Seidl, Table 2; 2009 in Linz, 2011 in Wels: Aescht and Bisenberger 2011). In 2013 we found the species still further west, in Innsbruck (Table 2).

A 1992 survey of greenhouses around Vienna found *D. invadens* in 3 out of 10 establishments (the same as for *D. reticulatum*; *D. laeve* occurred in 6: Leiss and Reischutz 1996).

Czech Republic

A specimen collected in Ostrava in 1996 was identified as *D. invadens* only in 2003 (Horsák and Dvořák 2003). By that time there was a further 2002 record from a greenhouse in Sušice. Horsák and Dvořák (2003) believed that it was liable to have been widely overlooked elsewhere, but the latest review (Horsák et al. 2013a) provides no further records. We have recently (2014) found the species at two sites within the town of Hrádek nad Nisou, close to the German and Polish borders (Table 2).

Slovakia

Deroceras invadens is known only from greenhouses of the botanical garden in Bratislava where it was first found in 2003 (Dvořák et al. 2003; Horsák et al. 2013a).

Poland

The only record of which we are aware is from 2001 from the botanical garden and adjacent areas in Wrocław (SW Poland: Wiktor 2001a, 2004). The population was still extant in 2013 (A. Wiktor and HR pers. obs.).

Lithuania

Deroceras invadens had been reported from the botanic garden in Kaunas (Skujienė G 2013 Invasive slugs in Lithuania: results, problems and perspectives of the investigations. Abstract booklet of "Slugs and snails as invasive species, a meeting of the IOBC/WPRS slugs and snails subgroup, Bergen, Norway 25–27 September 2013", p. 11). However, Skujienė kindly lent us the specimen on which this record was based and it proved to have been misidentified.

Hungary

Deroceras invadens was listed as present in Hungary in the guide book by Kerney et al. (1983). However, the more authoritative lists of Wiktor and Szigethy (1983) and Pintér and Suara (2004) do not include this species.

Romania

Grossu (1969) retracted the earlier claim that *D. invadens* occurred in Romania (Grossu and Lupu 1965).

Bulgaria

Wiktor (2000) mentioned a population in the Piryn mountains of Bulgaria that he assigned to *D. panormitanum*. At that time the confounding of *D. panormitanum* and *D. invadens* meant that the genitalia of the species were considered very variable. Now we reject this identification; for example, the sarcobelum is strongly flattened in these Bulgarian slugs, which is utterly untypical of *D. invadens*, or of *D. panormitanum* s.s.

Greece

Wiktor (2001b) reported "*Deroceras* cf. *panormitanum*" at "scattered localities" in Greece; he considered the 202 specimens from many sites to be all one species but was tentative in placing them in this taxon. However, specimens fitting this description from Crete proved to be an undescribed species (Reise et al. 2011). We have now checked the anatomy of five Greek samples in the Museum of Natural History, Wrocław University (from Mount Lampeia in the Erymanthos mountains, Cape Sounion south of Athens, the island of Skyros, the Kallicratis plateau in SW Crete, Heraklion in Crete) and one sample in the Naturalis Biodiversity Centre, Leiden (RMNH.MOL 329848 from the island of Lefkada), all labelled by Wiktor as *D. panormitanum*. In the light of the recent taxonomic revision (Reise et al. 2011), our opinion is that none of these are *D. invadens* or *D. panormitanum* s.s., so we concluded that probably all Greek records of *D. invadens* should be considered unreliable.

However, recently Rowson et al. (2014a) have published a finding of *D. invadens* from Lake Kournas in Crete reliably identified by a COI gene sequence (Genbank KF894343; R. Anderson pers. comm. 15.iv.2014). Anderson had found the species in a patch of disturbed scrubland in May 2011 and 2012. Crete has been fairly well sampled for slugs without this species being noted elsewhere, so a recent introduction seems likeliest.

Denmark

The first specimens were already collected in 1937, outdoors in a park in Odense. But their identity was not recognised until the mid 1950s when further specimens turned up at seven different cemeteries in another part of Denmark (northern end of Jutland: Lohmander 1959). We have found no more recent information.

See below for records from the Faroe Islands.

Sweden

The first findings date from 1957 to 1959, when *D. invadens* was found in six greenhouses well spread over the country (even up in Bysek at 65°N; Waldén 1960). However, subsequently the species remained rare in greenhouses or even declined (Proschwitz 1991). Outside greenhouses, occurrences also remained "extremely rare" before 1980, but by 2002 *D. invadens* was rapidly establishing itself, perhaps as a result of milder winters (Proschwitz 2002). It is now recorded outdoors from the provinces of Skåne, Halland, Småland, Västergötland, Dalsland, Uppland, Värmland and the Baltic islands of Öland and Gotland, with records denser in the south but extending as far north as Uppsala (59.8°N: Proschwitz 2009, 2010).

Norway

The first find was in about 1967 from a greenhouse in a botanic garden in Bergen (Olsen 2002). Outdoors, *D. invadens* was first found in 1983–84 at four synanthropic sites along the mild Atlantic coast, as far north as Møre og Romsdal (c. 62°N: notebooks of H.W. Waldén, cited in http://databank.artsdatabanken.no/FremmedArt2012/N79713 accessed July 2013). By 2002 it was considered common outdoors in cultural habitats (Olsen 2002), and it is spreading to more natural habitats (Sneli et al. 2006).

Finland

Brander and Kantee (1961) reported *D. invadens* from Finland, without stating the date of discovery. Valovirta (1967) made clear that it was known only from the greenhouses of southern Finland. We are not aware of more recent information.

Portugal

Seixas (1978) was the first to report *D. invadens*, from near Lisbon in 1977. Rodríguez et al. (1993) reported three further localities in the northern half of Portugal from 1983–85 (out of 55 sites visited across Portugal, 40 of which yielded *D. reticulatum*: ratio = 0.05).

See below for records from Madeira and the Azores. The indications of *D. panormitanum* s.s., together with *D. invadens*, on both these archipelagos suggest that it would be worthwhile rechecking specimens from mainland Portugal.

Spain

The first published record of *D. invadens* was from Bilbao (north coast) in 1980 (Gómez et al. 1981). However, Castillejo (1983) had identified material collected as early as 1974 from northeast Spain; over the period 1974–80 *D. invadens* had been found in 16 10 km squares in Galicia (compared with 36 for *D. reticulatum*: ratio = 0.44; records added over the next decade changed this to 20:50 = 0.40: Castillejo and Rodríguez 1991). Later mapping (Castillejo 1997) indicates a distribution along the wet northern coast, with one record in the southern foothills of the Pyrenees ENE of Huesca and some around Valencia (middle of east coast). The species is rarer in the east than in the northwest: in the east-coast province of Castellon, Borredà and Collado (1996) found *D. invadens* in 2 out of 105 locations sampled in 1990–92, compared with 61 for *D. reticulatum* (2 vs 38 10 km squares occupied by each species: ratio = 0.05). Similarly in the neighbouring east-coast province of Valencia, *D. invadens* occurred in 2 out of 69 localities sampled in 1990 and *D. reticulatum* in 34 (2 vs 27 10 km squares: ratio = 0.07; Borredà et al. 1990). Two of our own findings (Table 2) extend the range to the northeast (Bàscara = first record for Catalonia) and further south of the Pyrenees (Tudela). There remains a dearth of records from the drier middle and south of the country. Survey work in Castilla–La Mancha (central Spain) 2003–07, located only one site for *D. invadens* compared with about 101 for *D. reticulatum* (Bragado et al. 2010).

The first record for the Balearic Islands was 2001 from Majorca, where *D. invadens* has since been found in several other localities (Beckmann 2007). There are also

records from Ibiza in 2001 (under pots in garden centre: Anderson 2003) and from Menorca in 2002 (hedgerows and/or woods: Anderson 2004).

Castillejo (1998) emphasised that *D. invadens* is restricted to synanthropic habitats in mainland Spain, especially gardens, whereas Altonaga et al. (1994) listed wet meadows and beside streams. In northwest Spain it occurs in arable fields and permanent cattle-grazed pasture, in both of which it is sometimes the commonest slug (Iglesias et al. 2001, 2003; Cordoba et al. 2011).

See below for records from the Canary Islands.

Africa

Egypt

A 2005–07 survey in Asyut Governate (along the Nile, upstream of Cairo) found *D. invadens* in 15 out of 38 gardens and farms (Obuid-Allah et. al. 2008; 8 sites contained *D. reticulatum*: ratio = 4.75). This was the first report from Egypt, probably partly because the authors sent some specimens abroad to be identified.

South Africa

Deroceras invadens was recorded from several widely separated sites in Cape Province (George, Wilderness, Cape Town) in 1963–65 (Altena 1966). Now (Herbert 2010), it is also known from the Eastern Cape and from Guateng, including Pretoria, which, at 25.7°S, has a humid subtropical climate (cf. the mediterranean climate of the Cape). Although most records are from gardens it has been found also in indigenous forest on Table Mountain and near Somerset East (at the former already in 1965: Altena 1966, Herbert 2010). Herbert's (2010) distribution maps show 10 dots for *D. invadens* compared with 16 for *D. reticulatum* (ratio = 0.63), the major difference being that only *D. reticulatum* has been reported from the region west of Durban.

See below for records from Marion Island.

Kenya

A specimen was intercepted arriving in the USA on cut flowers (*Astrantia*) from Kenya (04.viii.12, USDA 110834). One area in Kenya where *Astrantia* is grown commercially for export is at Kipipiri, at an altitude of 2300–3000 m. Such altitudes may well provide a suitable habitat for *D. invadens*.

Asia and Australasia

Sri Lanka

Two publications report the presence of *D. invadens* in Sri Lanka (Kumburegama and Ranawana 2001, Bambaradeniya 2002) and this information has been repeated in secondary sources. However, a later review paper including some of the same authors,

but in conjunction with European experts, did not list the species (Naggs et al. 2003). The explanation is that the original reports were erroneous (N.P.S. Kumburegama, pers. comm. 21.viii.13).

Australia

Altena and Smith (1975) were the first to identify *D. invadens* in Australia. The earliest collection date of the specimens they identified was 1967, although in 1964 specimens had been intercepted arriving in New Zealand on plants from Australia (Barker 1979). However, a sample in the Museum Victoria from near Melbourne was collected in 1936 (collection no. F174271; HR confirmed identity). Previous to 1975, the species had been misidentified as *D. laeve* and *D. reticulatum*. Because they had never encountered specimens of *D. laeve* from Australia, Altena and Smith (1975) suggested that *Limax queenslandicus* Hedley, 1888, which had been synonymised with *D. laeve* soon after its description, might have been *D. invadens*. Reise et al. (2011) argued strongly against this; they showed that *D. laeve* was present in Queensland in the nineteenth century and that the identification of *L. queenslandicus* as *D. laeve* was reliable.

Deroceras invadens has been reported widely from Australia (Altena and Smith 1975, Smith 1992a, Stanisic et al. 2010, Atlas of Living Australia http://bie.ala.org.au/species/Deroceras+panormitanum accessed 21.vii.13). However, we have borrowed some of the material in the Australian museums on which these records were based and found that much of it is misidentified *D. laeve*. As in North America, *D. laeve* in Australia often grows larger than in Europe, which might have misled originally. Altena and Smith (1975) did not encounter *D. laeve*, but did not dissect material from outside Victoria that they assumed to be *D. invadens*. The belief that *D. laeve* was rare in Australia and, for instance, did not occur at all in Queensland (Stanisic et al. 2010) must have inhibited routine dissection. The latest Australian guidebook gives general coloration and paleness around the pneumostome as characters to distinguish *D. laeve* and *D. invadens* (Stanisic et al. 2010); these are certainly not reliable characters in Europe and may well explain misidentifications in Australia.

We can confirm the occurrence of *D. invadens* in Victoria, New South Wales, Tasmania, South Australia and Western Australia (Table 2). There is no reliable evidence of *D. invadens* in Queensland. We have examined 14 lots covering a wide geographic range in Queensland from the New South Wales border as far north as 16° (10 labelled as *D. panormitanum* from the Queensland Museum, one similarly labelled from the Museum Victoria, and 3 others). All were *D. laeve*. The northernmost confirmed records of *D. invadens* in New South Wales are 30.4°S (Table 2).

Already in the 1975, *D. invadens* was described as "one of the commonest and most wide-spread of introduced slugs", "a pest both of pasture plants and those of suburban gardens", occurring "in only slightly disturbed native bushland as well as wholly modified habitats" (Altena and Smith 1975). More recent surveys found it to be the commonest introduced mollusc in native grassland in southeast Australia (Holland

et al. 2007), and to occur also around the edges of ponds and swamps (Stanisic et al. 2010). It is found in some arable fields (Nash et al. 2007). The frequent misidentifications of *D. laeve* as *D. invadens* might have coloured these claims, but we can confirm its presence in gardens, agricultural habitats, and rough grassland.

See below for erroneous records from Lord Howe Island and Norfolk Island.

New Zealand

Barker (1979) published the first records of *D. invadens* from New Zealand, including specimens collected in 1974. Barker (1979, 1999) concluded that earlier widespread records of *D. laeve* must have referred to *D. invadens*, because he found that *D. laeve* had a restricted distribution in New Zealand. For instance, Suter (1913, p. 1071) described *D. laeve* as cosmopolitan, and already in 1891 Musson mentioned that *D. laeve* occurred. An occurrence at either of these dates would predate the first records of *D. invadens* anywhere in the world. The argument mirrors that for an early occurrence in Australia, which we criticised above, but we find it more compelling in the case of New Zealand: New Zealand has been more thoroughly surveyed, the distribution of *D. laeve* was more restricted at the time of these reliable surveys, and, unlike in Australia, there are no extant specimens of *D. laeve* collected before the late 1950s.

Barker (1999) described the habitat of *D. invadens* in New Zealand thus; "a slug of moist habitats found in gardens, parks, and pastures, on arable land, stream banks, and roadsides, and in greatly disturbed areas of native forest". It is "frequently found in roadside margins adjacent to forest, often kilometres from any cultivated areas", "ubiquitous where there is improved grassland and cultivated plants", "often the most abundant species in humid glasshouses and wet field situations", and "an important pest of cultivated plants" (Barker 1982, 1992). In one old pasture, 39% of slugs were *D. invadens* (= 14 m^{-2}, cf. 16 m^{-2} *D. reticulatum*; Barker 1990). Although most often recorded in the Auckland area of North Island, *D. invadens* also occurs widely around the coast of South Island and on Stewart Island (Barker 1999).

See below for records from Raoul Island and the Chatham Islands.

Americas

United States of America

Pilsbry (1948) described *D. invadens* as widespread in the Bay Area of California (the environs of San Francisco) by 1940; habitats he listed were a park, nurseries, a lawn and a ranch. Subsequently it has been recognised further south, in Monterey County (Lange 1944, Pilsbry 1948) and in Los Angeles (Roth and Sadeghian 2003). It also occurs further north, in Oregon and Washington: Burke (2013) described it as common in urban and suburban areas of the Pacific Northwest from California to southern British Columbia and Pearce et al. (2013) described it as well established in Olympia and Tacoma (Washington State). Table 2 includes further records from this region.

With this firm foothold , one would expect the species to have become widely distributed in the USA, because some large horticultural firms grow plants in the benign climate of the Pacific Northwest and then ship nationally. However, compared with Europe, North America has far fewer experts able to identify slugs, especially those requiring dissection. Also problematic is that *D. laeve* in North America often grows larger than in Europe so that *D. invadens* is readily mistaken for it unless specimens are dissected (Reise et al. 2006). It is not a healthy sign that all the records of *D. invadens* from the USA outside of the west coast are our own!

In 1998 we found *D. invadens* in Washington DC, under bushes in a park, the first outdoor record in eastern North America (Reise et al. 2006). Our surveys of synanthropic habitats in Colorado and Utah in 2004 and 2006 respectively (JMCH and HR, unpublished; see Table 2) turned up *D. invadens* in several garden centres and in the watered plantings in city centres (e.g. Park City; Memory Grove Park, Salt Lake City: Reise et al. 2011), but also in unwatered parts of a city park (Cheesman Park, Denver), along the banks of a drainage ditch (university campus, Fort Collins) and beside a stream in a ski resort (Snowbird).

The only other records from the eastern USA of which we are aware are from two sites in Kentucky (specimens in Florida Museum of Natural History, catalogue numbers 43778 and 44718, details available via http://data.gbif.org/species/5190777 accessed 24.iii.14). However, we have dissected one animal from each sample and they were not *D. invadens*.

Canada

The first Canadian records are from greenhouses in two cities in Quebec Province in 1966 (Chichester and Getz 1969). This thorough survey of 770 sites (although only 25 greenhouses, nurseries or gardens) in the northeast of the USA and southeast of Canada failed to find the species elsewhere, whereas *D. reticulatum* and other European slugs were frequently encountered. The first outdoor records are from the other side of the continent on the UBC campus in Vancouver in 1974 (Rollo and Wellington 1975). *Deroceras invadens* is nowadays present at other sites in Greater Vancouver and around Victoria on Vancouver Island (Forsyth et al. 2001, Forsyth 2004, http://linnet.geog.ubc.ca/efauna/Atlas/Atlas.aspx?sciname=Deroceras%20invadens; Table 2). We also found it in 2013 in a garden centre in Kamloops, in the drier interior of British Columbia (Table 2). On the Atlantic coast, *D. invadens* was found in 2012 on rough ground adjacent to gardens in St John's, Newfoundland (Forsyth 2014; confirmed by HR); the maritime influence there ameliorates winter temperatures.

Identifications of *D. invadens* from a garden in Edmonton, Alberta and from orchards by Osoyoos Lake, British Columbia, (Neckheim 2013, 2014) were not based on dissection (C.M. Neckheim pers. comm. 02.x.13), so should be regarded as unconfirmed; winters in Edmonton are more extreme than in any area where the species is known with certainty (see Discussion). A 1994 record from wild habitat near Kingston, Ontario (Grimm et al. 2009) is also best considered as unconfirmed because of other misidentifications by the collector (Forsyth 2013).

Mexico

We have confirmed the identification of specimens of *D. invadens* collected by A.S.H. Breure in 1974 at 3000 m in the Desierto de los Leones National Park, above Mexico City (Table 2). The gardens of the nearby convent might have been the original point of introduction but these slugs were collected in the surrounding pine and oak woodland (A.S.H. Breure 1974, pers. comm. 27.ix.13). At this altitude the climate is cool and damp. Although the specimens were correctly identified by Altena and deposited in the Naturalis Biodiversity Centre, Leiden, the record was not published so that *D. invadens* is missing from a recent national checklist (Thompson 2008).

Costa Rica

In 2006, we found ten specimens under rocks in a small wood near Tierra Blanca, Provincia Cartago (USDA 131032; Table 2). The altitude was 2060 m. The only *Deroceras* species listed from Costa Rica by Barrientos (2003) was *D. laeve*.

Panamá

In July 2007, a specimen of *D. invadens* was found on a leaf imported into the USA from Panamá (USDA 131034). In July 2009, three further specimens were found on *Allium* imported into the USA from Panamá (USDA 131033). Note that Panamá connects Costa Rica to Colombia, countries for which the presence of *D. invadens* has been confirmed on the ground.

Colombia

Two specimens of *D. invadens* in the Field Museum Chicago (JK-198690, identity confirmed by HR) were collected by the University of Oxford expedition to Colombia in September 1975. There are no further locality data but in this month the expedition was both near Nazaret (Guajira state) and in the capital Bogotá (Knappett et al. 1976).

Deroceras invadens was next found in 2000 at two rural sites near Bogotá in a garden and a flower plantation (Hausdorf 2002). It was considered a serious horticultural pest. Although the localities are less than 5°N, the altitude (> 2600 m) makes the climate oceanic (subtropical highland). Until Hausdorf's visit, the species had apparently not been recognised by local researchers, so that it may be more widespread. However, *D. invadens* was not found at 6 of the 8 sites where Hausdorf's survey found *D. reticulatum* (ratio = 0.25).

Cut flowers imported into the USA from Colombia in March 2008 contained *D. invadens* (USDA 131036).

Ecuador

In April 2012, L. Manangón collected a specimen "on alder" near Bolivar, Provincia Carchi (USDA 110614: Table 2). Although this is only 56 km north of the equator, the altitude of 2600 m meliorates the climate (cf. the localities in Colombia, 600 km away along the chain of the Andes). Earlier, in August 2004, an individual of *D. invadens* had been intercepted on cut flowers imported into the USA from Ecuador (USDA 131035).

Peru

The only *Deroceras* species listed from Peru by Ramírez et al. (2003) were *D. laeve* and *D. reticulatum*. However, in March 2012, an individual of *D. invadens* was intercepted on lettuce imported into the USA from Peru (USDA 110831). Peru connects Ecuador and Chile, countries for which the presence of *D. invadens* has been confirmed on the ground.

Chile

Letelier et al. (2003) reported *D. invadens* as present in southern Chile. We can add three later records of our own from central Chile in, and within 70 km of, the capital Santiago (Table 2). At these latitudes, the species occurs at low altitudes.

See below for a record from the Juan Fernández Islands. The presence of *D. invadens* there in 1962 suggests that it was probably present in mainland Chile by this time.

Argentina

Gutiérrez Gregoric et al. (2013) reported the occurrence of *D. invadens* in Argentina without providing the date of first discovery. However, the online catalogue of the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (http://datos.sndb.mincyt.gob.ar/portal/occurrences/search.htm?c[0].s=0&c[0].p=0&c[0].o=Deroceras+panormitanum) indicates that much of the material was collected in 2010 and 2011 in well vegetated valleys at the eastern edge of the Andes around the shores of lake Nahuel Huapi (770 m a.s.l.), and 94 km south in El Bolsón (310 m a.s.l.). A further site is a little to the east on a cultivated estate in the arid Patagonian steppe. The map in Gutiérrez Gregoric et al. (2013) indicates a further locality near the city of Neuquen 300 km to the northeast of Nahuel Huapi. So the range in Argentina is sizeable and Gutiérrez Gregoric et al. (2013) stated that localities include both urban areas and national parks.

Brazil

Barker (1999) listed two samples of *D. invadens* that he examined, from a park in the city of Porto Alegre and from a state park 70 km outside the city, both collected in 1991. These determinations should be considered reliable because Barker was familiar with *D. invadens* in New Zealand. However, recent species lists from the same state (Agudo-Padrón 2009) and from all Brazil (Simone 2006, Agudo-Padrón and Lenhard 2010) do not mention this species. They do list *D. laeve*, which seems likely to have masked the presence of *D. invadens* from local malacologists.

Recently (27.ii.14) a specimen of *D. invadens* was intercepted arriving in the USA on cabbage from a ship's stores that had been loaded in Brazil (USDA 140148).

Oceanic Islands

Faroe Islands (Denmark)

This sizeable archipelago (1400 km^2, population 50,000) lies between Scotland and Iceland at 62°N, having a maritime subarctic climate. In 1970, McMillan (1972) found *D. invadens* to be frequent in waste ground to the west of the capital Tórshavn.

Madeira (Portugal)

The first record of *D. invadens* is from 1980 (Rähle 1992). Based on fieldwork from 1980 to 1986, Rähle (1992) concluded that it was widespread but rare and restricted to synanthropic sites on the main island. Seddon (2008) provided more records, but the species had still not been recorded from Porto Santo or other minor islands. Whereas Rähle knew it from 7 sites compared with 10 for *D. reticulatum* (ratio = 0.7), Seddon's distribution maps show 21 dots for *D. invadens* and 11 for *D. reticulatum*. However, Seddon's data may have confounded occurrences of *D. invadens* with those of *Deroceras lombricoides* (Morelet, 1845): Seddon has no records of the latter species, whereas Rähle found it to be the commonest *Deroceras*.

Rähle's (1992) illustrations indicate that he found *D. invadens* rather than *D. panormitanum* s.s. We have also confirmed the identity of samples in the Stuttgart State Museum of Natural History from 6 localities (collected 1980–85) and of samples in the Naturalis Biodiversity Centre, Leiden, from a further 11 localities (collected 1987–88). However, we collected *D. panormitanum* s.s. from the south of Madeira in 2006 and again eight years later just 0.7 km away (USDA 131030, USDA 140106: Table 2); the localities lie <2.5 km from one where *D. invadens* was found in 1988.

Azores (Portugal)

Waldén (1960) mentions the first finding of *D. invadens* in the Azores by a 1957 expedition (see Backhuys 1975, p. 22). However, Backhuys' (1975) team of collectors did not find this species during their extensive fieldwork in 1969, in contrast to numerous records for other slugs, including *D. laeve* (reported as always aphallic, so not a misidentification). Backhuys (1975) reported a single later finding in 1974 from a synanthropic habitat on São Miguel. In dramatic contrast, single-island surveys 13–20 years later showed the species to have become widespread (e.g., present at 5 out of 29 sampling stations on São Miguel in 1987, 8/21 stations on Flores in 1989, 5/17 stations on Santa Maria in 1990, 2/9 stations on São Jorge in 1992, 3/18 stations on Faial in 1993: de Winter 1988; Martins et al. 1990, 1991, 1993; Cunha et al. 1994). By 2010 the species was known from all of the nine main islands except Terceira (Cunha, Rodrigues and Martin 2010).

A slug intercepted arriving in the USA from the Azores on a taro root in March 2008 was *D. panormitanum* s.s. (USDA 110434). So we checked specimens collected by J. Wieringa from four sites on São Miguel in 1987 (Naturalis Biodiversity Centre, Leiden: collection numbers 329842–329845). They were *D. invadens*, as was another U.S. interception from the Azores (USDA 131029, Dec. 2008). Probably, as on Madeira, both species occur.

Canary Islands (Spain)

The first records of *D. invadens* are from the island of La Palma in 1947 (Altena 1950). In the 1980s Alonso et al. (1986) found it to be commoner there than *D. reticulatum* (12 vs 2 localities, 8 vs 1 5 km squares) and to range in altitude from 60 to 1800 m. On the island of Tenerife, Altena (1950) failed to find *D. invadens* in 1947 and extensive sampling in 1982–85 located it at only one site (Alonso et al. 1986), but by 2007 it was widespread in native laurel forests (Kappes et al. 2009). The species was also present on Gran Canaria by 1984 (M. Ibáñez, pers. comm. 16.ix.13, Table 2).

Tristan da Cunha (UK)
This lies in the middle of the South Atlantic (37.1°S), 2816 km from South Africa, with a population of under 300. The climate is temperate. Preece's (2001) survey in 1982–83 found *D. invadens* not only on the main island of Tristan da Cunha but also on Inaccessible Island 40 km away. The latter had been inhabited rarely, and not since 1938 (Anon. 2011). Seabirds abound, so possibly they could have dispersed slugs from Tristan da Cunha.

Raoul Island (New Zealand)
This lies 29.3°S in the South Pacific, 1100 km NNE of New Zealand's North Island. The climate is subtropical. *Deroceras invadens* was found in 1973 in forest litter (Barker 1999). At this time there was a small farm on the island as well as a meteorological station, although resupply was infrequent.

Chatham Islands (New Zealand)
These lie 44°S in the South Pacific, 680 km from New Zealand. The climate is temperate and they have a sizeable agricultural community and frequent transport links. *Deroceras invadens* was found in 1976 in pasture on the main island and nearby Pitt Island (Barker 1979).

Marion Island (South Africa)
This is a subantarctic island (46.9°S, 290 km^2) with a cool oceanic climate, unpopulated except for research stations; South Africa lies 1730 km to the northwest. *Deroceras invadens* was first reported in 1972, under timber and in damp mossy habitat beside the base hut; a thorough survey in 1965–66 had not reported it (Smith 1992b). By 1976–77 it occurred in further habitats but had not spread far, and by the early 1990s it was much more abundant but still known only within several hundred metres of the base (Smith 1992b, Chown et al. 2002). Further dispersal around the rest of the island over inhospitable terrain is thought to have been facilitated by its habit of sitting under wooden boxes lying on the ground, which helicopters then carried to other huts (Chown et al. 2002). The species has now spread right around the island but the cold restricts it to land under about 200 m (Lee et al. 2009). It is most abundant near the coast.

Juan Fernández Islands (Chile)
In the Field Museum Chicago and the Museum of Natural History, Wrocław University are specimens of *D. invadens* collected in 1962 from Robinsón Crusoe Island, formerly Más a Tierra (identities confirmed by HR; Field Museum catalogue number = 198633). This Pacific island is 48 km^2 in area, and lies 600 km west of mainland Chile, with a mediterranean climate and a population in 1999 of over 500. The slugs were collected in a ravine in the Valle de Lord Anson, which rises from the main village.

Errors and Absences
Lord Howe Island and Norfolk Island are small (15 and 35 km^2) but well populated Pacific islands, belonging to Australia although 570 and 1400 km east from the Australian mainland. Online records from the Australian Museum (http://ozcan.ala.org.

au accessed 08.iii.2013) indicated that *D. invadens* was collected on Lord Howe Island in 2000 (single record) and on Norfolk Island in 1999 and 2002 (6 records, most from the largest patch of woodland but two from the opposite side of the island). We have borrowed the specimen from Lord Howe Island and two from Norfolk Island (one from each year); one from each island were *D. laeve* and the third specimen was not identifiable. Given the high rate of similar misidentifications of other Australian material (including from this museum; see above), we consider that there is no reliable evidence of *D. invadens* occurring on either island.

Specimens in the Natural History Museum London labelled as *D. caruanae* from São Tomé in the Gulf of Guinea (collected 1993 by A. Gascoigne from Lagoa Amelia and Tras-os-Montes; BMNH 19991797, 19991798) turned out to be *D. laeve* (dissection by HR); these records appear not to have been published or put online.

It may also be helpful to list some oceanic islands where *D. invadens* has not been found even though the climate might be suitable and recent surveys have been extensive and informed enough to have probably revealed the species were it well established: Iceland (Sumner 2007), Bermuda (Bieler and Slapcinsky 2000), Cape Verde Islands (Groh 2012), Mascarene Islands (Griffiths and Florens 2006), Hawaii (Cowie 1997, Hayes et al. 2012), Samoan Islands (http://pbs.bishopmuseum.org/samoasnail/query.asp, updated 2003), Pitcairn (Preece 1995), Rarotonga (Brook 2010), Fiji Islands (Brodie and Barker 2011), Easter Island (Boyko and Cordeiro 2001). Of these ten island groups, all but the Samoan Islands have been colonised by *D. laeve*, and five have *D. reticulatum* also.

Figure 4. The global distribution of *D. invadens* related to climate. **A** Each symbol represents presence of *D. invadens* on a grid of one degree of latitude and longitude; exceptions are small oceanic islands (single symbol for each island group) and when records specify only a region which overlaps the grid lines (California, N Norway, Öland, and interceptions; a single symbol is marked in a representative "square"). Green cross = records only from greenhouse or garden centre; orange or magenta square = any other record (including garden or park); magenta indicates that at least one record has been confirmed to be *D. invadens* rather than *D. panormitanum* s.s.; circled i = only evidence of presence is interception on produce exported from that country. Swedish records in Waldén (2007) are taken to be from greenhouses. In regions where there has been taxonomic confusion (Italy, Balkans, Australia), we have excluded records not verified by ourselves (exceptions are a COI sequence from Crete, and data in Barker (1992) and Altena & Smith (1975) confirmed by dissection) **B** The squares in A are replaced by black dots, and these are superimposed on a map of the most relevant Köppen climate categories, as modified and interpolated by Peel et al. (2007). Cb + Cc = temperate with warm or cold summer (T_h < 22 °C, 0 °C < T_c < 18 °C). Ca = temperate with hot summer (T_h > 22 °C, 0 °C < T_c < 18 °C). Da + Db = cold winter, with hot or warm summer (T_c < 0 °C, T_h > 22 °C or $N_{T>10} \geq 4$). BSk = cold steppe ($5\,P_T < P < 10\,P_T$, T_m < 18 °C). T_h = temperature of hottest month, T_c = temperature of coldest month, T_m = mean annual temperature, $N_{T>10}$ = number of months when temperature is above 10 °C, P = annual precipitation, P_T = constant set by T_m and timing of precipitation **C** The squares in A are replaced by black dots, and these are superimposed on a map indicating winter temperature. For each calendar month, the mean of the daily minimum temperature was calculated, this was averaged over years, and the lowest value amongst the calendar months used (Hijmans et al. 2005; http://www.worldclim.org/ accessed 01.x.2013). Maps created in QGIS 2.0.1 (QGIS Development Team 2013) using outlines from Natural Earth.

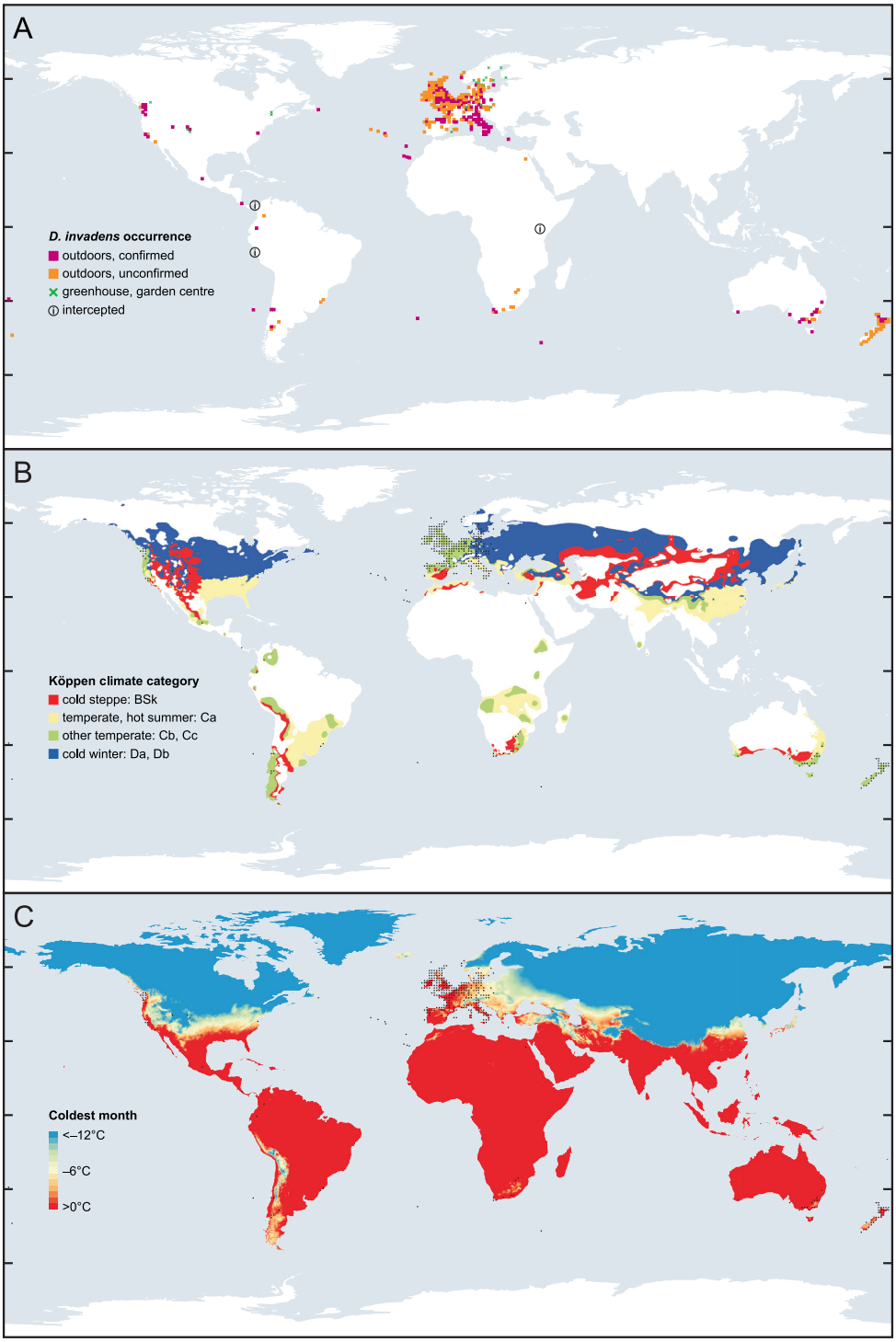
A
D. invadens occurrence
outdoors, confirmed
outdoors, unconfirmed
greenhouse, garden centre
intercepted
B
Köppen climate category
cold steppe: BSk
temperate, hot summer: Ca
other temperate: Cb, Cc
cold winter: Da, Db
C
Coldest month
<–12°C
–6°C
>0°C

Table 2. Findings that significantly extend the range of *D. invadens* or *D. panormitanum* s.s. We exclude records published or available online in museum catalogues and Genbank. Identifications have been confirmed anatomically by HR except for those of Herdam; his notebooks show a sketch of the genitalia, but it is unclear if this is based on these East German specimens.

Locality	Habitat	Latitude, Longitude	Collection date	Collector	Collection, catalogue number
D. invadens					
Hotel Garden Beach, Strada Panoramica Villasimius, Castiadas, Sardinia, ITALY	Unrecorded	c. 39.195°N, 009.561°E	20.vi.2013	S. Schnurrenberger	SMNG p17942
SAN MARINO	Under bushes in town square, automatic irrigation	43.9371°N, 012.4461°E	14.iii.2013	JMCH	SMNG p17943
SAN MARINO	Olive grove	43.9486°N, 012.4454°E	16.iii.2012	JMCH	SMNG p17944
Above Av. de la Porte Neuve, Monaco-Ville, MONACO	Under bushes in park, automatic irrigation	43.7316°N, 007.4222°E	16.viii.2012	HR, JMCH	SMNG p17945
Tierpark, Berlin, GERMANY	Unrecorded	52.50°N, 013.53°E	1982	V. Herdam	not preserved
Forstbotanischer Garten, Eberswalde, Brandenburg, GERMANY	Unrecorded	52.83°N, 013.79°E	1985	V. Herdam	not preserved
Palmengarten, Frankfurt am Main, Hesse, GERMANY	Outdoors in alpine garden	c. 50.12°N, 008.65°E	21.x.1985	W. Hohorst	Hohorst collection in Senckenberg Museum für Naturkunde Frankfurt
Lentzeallee 94, Berlin, GERMANY	Suburban garden	52.469°N, 013.303°E	29.vii.2001	HR	SMNG p10289
Senzig, Brandenburg, GERMANY	Suburban garden	52.286°N, 013.6590°E	10.x.2004	HR	SMNG p14038
Enknachleiten, Braunau am Inn, AUSTRIA	Unrecorded	48.25°N, 013.03°E	5.iii.1999	F. Seidl	Museum of Natural History, Wrocław University
Innsbruck, AUSTRIA	Track beside allotments	47.2680°N, 11.4178°E	12.iii.2013	JMCH	SMNG p17946
Hrádek nad Nisou, CZECH REPUBLIC	Suburban backyards	50.85593°N, 14.84409°E, 50.85089°N, 14.84398°E	3.vi.2014	JMCH	SMNG p18006, p18007
Bàscara, Catalonia, SPAIN	Beside spring	42.16107°N, 002.90988°E	24.viii.2012	JMCH, HR	SMNG p17947
Tudela, Navarra, SPAIN	On mudbank in canalised stream	42.06353°N, 001.60082°E	29.viii.2012	JMCH	SMNG p17948
Armidale, NSW, AUSTRALIA	Native grass pasture and scrub	30.4339°S, 151.6750°E	19.ix.2012	M.A. Nash	SMNG p17986
Nashdale, NSW, AUSTRALIA	Vineyard	33.2962°S, 149.0209°E	18.ix.2012	MA. Nash	SMNG p17987

Locality	Habitat	Latitude, Longitude	Collection date	Collector	Collection, catalogue number
Wallendbeen, NSW, AUSTRALIA	Canola/wheat field	34.4987°S, 148.0509°E	06.x.2012	M.A. Nash	SMNG p17988
Yass, NSW, AUSTRALIA	Wheat stubble	34.7690°S, 149.1600°E	06.x.2012	M.A. Nash	SMNG p17989
Mangoplah, NSW, AUSTRALIA	Canola field	35.4516°S, 147.2631°E	12.vii.2012	M.A. Nash	SMNG p17990
Stony Creek, Victoria, AUSTRALIA	Vegetable garden	38.59°S, 146.06°E	18.viii.2013	G.M. Barker	SMNG p17991
Mortlake, Victoria, AUSTRALIA	Canola field	38.0221°S, 142.7569°E	16.vi.2004	M.A. Nash	SMNG p17992
Dudley Peninsular, Kangaroo Is., SA, AUSTRALIA	Cliff top	35.7328°S, 138.0036°E	19.v.1985	J. & F. Aslin, D. Adams	Field Museum Chicago 215867
Porongurup, WA, AUSTRALIA	Wooded area in national park	c. 34.676°S, 117.869°E	18.vi.1979	A. Solem, F. & J. Aslin	Field Museum Chicago 204582
Bothwell, Tasmania, AUSTRALIA	Wheat field	42.3849°S, 147.0307°E	28. vii.2013	M.A. Nash	SMNG p17993
Port Townsend, WA, USA	Town centre	48.1158°N, 122.7546°W	16.x.2001	HR, JMCH	SMNG p17949
Heart O' the Hills, S. of Port Angeles, WA, USA	Forest in National Park, near camp site	48.040°N, 123.428°W	17.x.2001	HR, JMCH	SMNG p17950
Priest Point Park, Olympia, WA, USA	Flower beds in park	47.0693°N, 122.8940°W	18.x.2001	HR, JMCH	SMNG p17951
Sunset Lake, Carnahan, OR USA	Street margins, front gardens	46.100°N, 123.930°W	3.x.2001	HR, JMCH	SMNG p17952
Oswego Lake, Portland, OR, USA	Beside stream	45.4103°N, 122.6637°W	3.x.2001	HR, JMCH	SMNG p17953
Phellan Gardens, 4955 Austin Bluffs Parkway, Colorado Springs, CO, USA	Greenhouse in garden centre	38.9033°N, 104.7397°W	23.vi.2004	JMCH	SMNG p17954
Arapahoe Acres Nursery, 9010 S. Santa Fe Drive, Littleton, CO, USA	Large garden centre	39.5539°N, 105.0350°W	24.vi.2004	JMCH	SMNG p17955
Cheesman Park, Denver, CO, USA	Suburban park, backing onto gardens	39.730°N, 104.964°W	21.vi.2004	JMCH	SMNG p17956
Paulino Gardens, 6300 N. Broadway, Denver, CO, USA	Large garden centre	39.8097°N, 104.9856°W	24.vi.2004	JMCH	SMNG p17957
Country Fair Garden Center, 2190 S Colorado Boulevard, Denver, CO, USA	Small urban garden centre	39.6769°N, 104.9400°W	24.vi.2004	JMCH	SMNG p17958
Fossil Creek Nursery, 7029 S. College Av., Fort Collins, CO, USA	Large garden centre	40.4894°N, 105.0787°W	26.vi.2004	JMCH	SMNG p17959
Arthur Ditch, Colorado State University, Fort Collins, CO, USA	Drainage ditch	40.574°N, 105.087°W	vii.2004	JMCH	SMNG p17960

Locality	Habitat	Latitude, Longitude	Collection date	Collector	Collection, catalogue number
Western Garden Center, 550 S 600 E Salt Lake City, UT, USA	Garden centre	40.7578°N, 111.8740°W	11.viii.2006	JMCH	SMNG p17961
J & L Garden Center, 620 N 500 W, Bountiful, UT, USA	Garden centre	40.8962°N, 111.8905°W	18.viii.2006	JMCH	SMNG p17962
Park City, UT, USA	Gardens, urban street margins; 2150 m a.s.l.	40.6438°N, 111.4952°W	18.viii.2006	JMCH	SMNG p17963
Snowbird Resort, Little Cottonwood Canyon, UT, USA	Beside stream; 2460 m a.s.l.	40.5805°N, 111.6560°W	13–16. viii.2006	JMCH	SMNG p17964
Crescent Beach, White Rock, BC, CANADA	Gardens abutting beach	c. 49.054°N, 122.886°W	14.x.2001	HR, JMCH	SMNG p17965
End of 92A Av., Langley, BC, CANADA	Cedar forest beside creek	49.1706°N, 122.6523°W	3.viii.2013	JMCH	SMNG p17966
Flume Rd, Robert's Creek, BC, CANADA	Roadside ditch	49.43085°N, 123.6654°W	6.viii.2013	JMCH	SMNG p17967
Lyons Garden Centre, Salish Road at Halston Av., Kamloops, BC, CANADA	Garden centre	50.7100°N, 120.3340°W	23.vii.2013	JMCH, RG & TJ Forsyth, HR	SMNG p17968
Desierto de los Leones NP, Distrito Federal, MEXICO	Oak forest with sparse pines; 3000 m a.s.l.	19.31°N, 099.31°W	27.vii.1974	A.S.H. Breure	RMNH.MOL.329841
Tierra Blanca, Provincia Cartago, COSTA RICA	Under rocks, small wood in agricultural landscape, 2060 m a.s.l.	09.9103°N, 083.8826°W	17.ix.2006	DGR	USDA 131032
Boliva, Provincia Carchi, ECUADOR	On alder, 2600 m a.s.l.	00.507°N, 077.900°W	18.iv.2012	L. Manangón	USDA 110614
Vivero Limache, Comuna Limache, Provincia de Quillota, CHILE	In leaf litter, outdoors in nursery, 110 m a.s.l.	33.005°S, 071.235°W	14.iii.2008	DGR	USDA 110169
Jardin Japonés, Cerro San Cristóbal, Santiago, CHILE	In leaf litter, in urban park, 670 m a.s.l.	33.4134°S, 070.6143°W	12.iii.2008	DGR	USDA 110153
Granja Educativo de Lonquén, Comuna Talagante, CHILE	In leaf litter, outdoors in nursery, 350 m a.s.l.	33.710°S, 070.873°W	12.iii.2008	DGR	USDA 110158
Osorio, near Teror, Gran Canaria Island, CANARY ISLANDS	Agricultural area	c. 28.07°N, 015.54°W	1984	M. Ibáñez	SMNG p17969
***D. panormitanum* s.s.**					
Bordighera, Liguria, ITALY	Fallen leaves in concrete culvert.	43.7853°N, 007.6826°E	16.viii.2012	JMCH, HR	SMNG p17970
Below Cabo Girão, Municipo Cãmara de Lobos, MADEIRA	Under boulders along road	32.659°N, 017.008°W	1.i.2006	DGR	USDA 131030
Cabo Girão, Municipo Cãmara de Lobos, MADEIRA	Under rocks along road	32.6571°N, 017.0018°W	23.xii.2013	DGR	USDA 140106

Discussion

Habitat

In Europe much of the area occupied by *D. invadens* counts as temperate according to the Köppen climate scale (Fig. 4B). This holds also for much of its range outside of Europe. Further areas of the world having this climate category, such as the southern USA and much of China and Japan, would be worth checking further for the presence of *D. invadens*, and should consider themselves at risk of invasion. Moreover, the presence of *D. invadens* in such regions as Austria and Newfoundland demonstrates that it can exist in areas with somewhat colder winters than allowed under Köppen's temperate categories (C), whereas its presence in eastern Spain shows that it can extend into drier climates classed as steppe (BS). Conversely, even around the Mediterranean, *D. invadens* does not occupy all the region classed as temperate. Inevitably, the criteria of the Köppen scale do not exactly match the critical factors defining the species' niche.

Cold seems to be one critical factor. In the laboratory, *D. invadens* collected from Marion Island was unable to survive brief temperatures lower than –6.4 °C, or, on a longer time scale, temperatures lower than about –3 °C on average. This neatly explained its altitudinal range on that island (Lee et al. 2009). Moreover, the gradual decline in density with altitude is explicable by a gradual reduction in performance with decreasing temperatures (Lee et al. 2009). Analogously, the slowness to penetrate Eastern Europe perhaps has as much to do with the cold winters as the restrictions on east–west trade until 1990. Temperatures experienced by slugs in winter depend on snow cover and how deep the slugs burrow underground, but weather stations normally measure only air temperature. In Europe, the coldest locations for which *D. invadens* has been recorded outdoors are Ultuna near Uppsala in Sweden (winter minimum air temperature averaged over last 20 years = –22 °C; coldest over same period = –29 °C), Södra Fjöle in Sweden (–22 °C and –28 °C for these statistics), and Ostrava in the Czech Republic (–19 °C and –27 °C: Klein Tank et al. 2002, http://www.ecad.eu accessed 25.ix.13). For Wrocław, we know the species has survived the last 12 winters, in three of which air temperatures dropped to –22 °C. Figure 4C suggests that winter temperatures could well block further expansion eastwards from Wrocław or northwards from Uppsala, but there does seem an opportunity for further expansion elsewhere, for instance along the Baltic coast of Poland, into Hungary, or onto Iceland. Proschwitz (2010) has suggested that in Sweden the ameliorating climate is associated with the recent range extension, and the same process could occur in eastern Europe.

In North America, three sites in Colorado and Utah where *D. invadens* has been found away from garden centres and plantings of annual bedding plants (Table 2) reach temperatures similarly cold as the extremes in Europe: for Fort Collins, winter minimum temperature over last 20 years averaged –22 °C with a minimum of –28 °C; for both Denver and Snowbird these statistics are –22 °C and –27 °C (http://ccc.atmos.colostate.edu/sum_form.html; http://climate.usurf.usu.edu).

At the other extreme, too much heat is probably not a restriction per se, since the species occurs in Egypt, for instance. Meyer and Cowie (2010) proposed that the occasional extremes of a temperate climate preadapt some invasive molluscs to be able to cope with the high temperatures of the tropics. However, heat may be associated with drought, at least seasonally. In such regions the automatic watering systems in use in intensive agriculture and in horticulture (particularly prevalent in prosperous countries) facilitate the survival and spread of *D. invadens*. Maybe these artificial habitats will provide a route for *D. invadens* to colonise naturally damp areas within steppe habitats.

In Central and South America, *D. invadens* occurs within the tropics but the accurately localised records are all from higher altitudes. This may be because higher altitudes tend to be cooler and have different precipitation patterns, or because such climatic differences have encouraged urbanisation or types of agriculture that favour the species. Higher altitudes would seem the likeliest place to search for *D. invadens* in other areas of the tropics, including Africa and India.

Deroceras invadens is typically associated with disturbed habitats, especially gardens, and is often easiest to find under discarded rubbish. It is one of the few molluscs to occur in the most urban sites, by surviving in the soil of flowerpots (Horsák et al. 2013b). Greenhouses and consistently watered nurseries suit it, and it occurs in some arable fields (e.g. England, N Spain, Switzerland, Australia), but is a significant pest more rarely than *D. reticulatum*. Although reported to avoid grassland in Britain (Dirzo 1980), *D. invadens* occupies that habitat in New Zealand and Australia (Barker 1982, Holland et al. 2007). Outside of the probable natural range of the species (Italy), the species has spread to natural habitats not only in western Europe (e.g. Britain, Ireland and France, although not in Germany) but also in Australia, South Africa and the Canary Islands. It seems likely that dispersal into gardens is often rapid, but that the spread into and across agricultural and natural habitats is a slower process and not inevitable. This could explain the positive association with population density even in long colonised countries such as Britain, Ireland and Belgium.

Deroceras invadens can become one of the most frequently encountered slugs, typically about half as frequent as *D. reticulatum*, but at some sites even commoner (e.g. Manchester gardens, British commercial greenhouses, Frankfurt am Main, Egypt). In the laboratory we have observed that *D. invadens* can mature a month faster than *D. reticulatum*, which may give it an advantage when growing seasons are short owing to either climate or agricultural activities.

Geographical range

Deroceras invadens is widespread over most of the western half of Europe. However, there are still areas within this region where it is scarce. In some cases this is probably because of climate (cold in Scandinavia, summer drought in central Spain), in other areas it might merely be because of a lack of time to spread there (e.g. Suffolk, Alsace). The species has yet to spread far in eastern Europe and is still much more thinly spread

in Germany and Austria than in Belgium or Great Britain, for instance. Currently the most eastern outdoor records in Europe are the Baltic coast of Sweden, Wrocław in Poland and Ostrava in the Czech Republic; further east, at least in Lithuania, Latvia and the Ukraine, there is sufficient current interest in slugs that *D. invadens* would probably have been recorded had it become well established (Skujienė 2002, Gural-Sverlova et al. 2009, Rudzīte et al. 2010). The species also appears largely absent from the eastern Mediterranean (except for one record from Crete and some from along the Nile in Egypt in agricultural habitats). The Balkans and Turkey are a centre of diversity of *Deroceras*, so maybe competition with local species is a factor limiting the spread here. But this diversity also makes it harder for malacologists to spot a new arrival. The absence of *D. invadens* from Asia is striking, but have malacologists there been looking critically at their alien *Deroceras* species?

The species has long been known from the Pacific Northwest of America, and also occurs sporadically elsewhere in the USA and Canada. The pronounced scarcity of records in the east compared with the west is untypical of other introduced European slugs. The reason could be that much of the east has an unsuitable climate for *D. invadens*; perhaps in areas southern enough to for the winters not to be too cold, the summers are too hot and dry (Fig. 4B). But surely there is enough artificial irrigation often to overcome this restriction. Or, supposing that *D. invadens* has spread to America much later than most other introduced slugs, perhaps its distribution remains more biased towards the original site of introduction. However, the pattern could also be an artefact: our hunch is that *D. invadens* is at least somewhat more widely spread in the east than currently recognised, but has been frequently misidentified as *D. laeve*. This confusion had no doubt hidden its occurrence in Central and South America; the records assembled here are sparse but imply that *D. invadens* is widespread.

Elsewhere in the southern hemisphere, the species has been present, maybe for a long time, in the former British colonies of South Africa, Australia and New Zealand. In this context, the indication from interceptions that it may be present in Kenya is not surprising. It has also colonised a number of remote oceanic islands; the maritime influence on their climates is probably favourable, and perhaps also their depauperate faunas have left a niche vacant.

The range of *D. invadens* is impressive (Fig. 4), and current records probably still significantly underestimate it. However, it should be recognised that there are a number of other European slugs that are ahead of it in the extent of their non-native range. Besides *D. laeve* and *D. reticulatum*, one can list at least *Lehmannia valentiana* (Müller, 1774), *Limacus flavus* (Linnaeus, 1758), and *Milax gagates* (Draparnaud, 1801) (Herbert 2010). Although these species have spread at different rates, the process is continuing, so it remains to be seen whether the ranges that they eventually occupy will differ significantly.

The similar species *D. panormitanum* s.s. from Sicily and Malta has also been introduced elsewhere, but much more rarely than *D. invadens*: the only such records are from one site in northern Italy, one in Wales, two adjacent sites on Madeira and an interception from the Azores (Tables 1, 2). Although both species are probably native

on Sicily, we never collected them together there (JMCH & HR unpublished), so the species might tend to exclude each other. We did collect them together from the same culvert in northern Italy (Table 2), but two subsequent visits to the site yielded only *D. panormitanum* s.s.

Spread

Deroceras invadens has been directly observed arriving from abroad on salads, vegetables, flowers, roots, and tiles (Falkner 1979 and USDA records). Such vectors need not be representative of the processes responsible for spread within a country, which surely must often be via garden plants, considering how frequently the species has been found in nurseries and garden centres. At both scales it seems unnecessary to invoke dispersal on bird's feet or plumage, for which there is conspicuously little direct evidence for any slug (Pearce et al. 2012); birds are a parsimonious explanation only perhaps for colonisation of uninhabited islands (e.g. to Inaccessible Island from Tristan da Cunha).

We hoped that our review of the literature would illuminate the rate and pattern of these dispersal processes, but mostly it is hard to be sure that the apparent rate of spread is actually not the spread of awareness that this novel species is worth distinguishing from others. That is particularly a problem with a slug species that requires dissection for reliable identification. In several cases (e.g. Britain, France, New Zealand) the species was probably widespread before anyone was aware of its presence; presumably at a more local level the distribution continued to grow denser, but usually there are no follow-up surveys once someone has claimed the first record. What is really required is an initial survey reporting absences of the species, then comparable repeat surveys of the same places in subsequent years; this has rarely, if ever, been done.

There is nevertheless good evidence of a spread within one or two decades through the Azores and Tenerife. The German data are also probably reliable and representative in suggesting a time scale of one to two decades to extend over a larger country, but it is far from the case that every suitable garden or even district has been colonised within that time. Puzzling gaps in the present distribution elsewhere (e.g. Suffolk in England, Alsace in France) suggest that "filling in" can take decades longer. It is difficult to make quantitative comparisons between species, especially because the delay in spotting a new arrival depends on the ease of recognising the species, but *D. invadens* probably has spread a little slower than three other terrestrial molluscs that have also invaded much of Europe within the last century, the slugs *Boettgerilla pallens* Simroth, 1912 and *Arion vulgaris* (Moquin-Tandon, 1855) and the snail *Hygromia cinctella* (Draparnaud, 1801) (Reise et al. 2000, Beckmann and Kobialka 2008, Kozłowski and Kozłowski 2011). Quite probably when *D. invadens* first arrived in England and France, the more local pattern of trade at that time led to a slower spread than has occurred in more recently colonised European countries, but the quality of the data is insufficient to test this. One also expects the spread to be slower in countries with

a hostile climate, which might explain the dearth of additional records in Poland, Slovakia and the Czech Republic. Similarly, the rate of spread in Sweden may reflect recent climate amelioration as much as the dispersal process (Proschwitz 2002). Marion Island is a special case, but is revealing in demonstrating the reliance on man for long-distance dispersal within the island, in contrast to the slow initial penetration of the natural habitat by natural means. Here and elsewhere, it is an interesting open question whether the spread accelerated following a period of genetic adaptation to the local environment. The climatic diversity of its non-native range would make *D. invadens* an appealing subject on which to test whether such adaptations have evolved.

One would expect uniparental reproduction to facilitate colonisation if adventitious human-mediated transport sometimes introduces a single slug at a time. Foltz et al. (1984) observed that self-fertilising slug species had been significantly more successful in colonising eastern North America, with *D. invadens* one of the species fitting this pattern (outcrossing and absent). Subsequently *D. invadens* has been found in eastern North America, but paternity studies in our laboratory (Reise et al. unpublished) have shown that the species does sometimes self-fertilise, producing viable offspring, especially in the absence of a partner. Nevertheless, the intra-site polymorphisms that Foltz et al. (1984) observed in populations from the British Isles and France do not suggest that the species' spread through these regions was dependent on a succession of founder events involving self-fertilisation. In contrast, on the remote Marion Island, all 25 slugs sequenced had the same COI haplotype (Lee et al. 2009). In ongoing work, we are comparing patterns of genetic diversity elsewhere in its range.

Acknowledgements

We thank the following for generously providing specimens: Jon Ablett, Roy Anderson, Gary Barker, Robert Forsyth, Jochen Gerber, Miguel Ibáñez, Darryl Potter, Richard Preece, Ted von Proschwitz, Mandy Reid, Wolfgang Rähle, Chris Rowley, Ulrich Schneppat, Bettina and Michael Schlitt, Sabrina Schnurrenberger, Willem Sirgel, Grita Skujienė, John Slapcinsky, Adrian Sumner, Ton de Winter, and the staff of Agrocalidad in Ecuador. Michael Nash deserves special thanks for his collecting in Australia for us and we would also like to acknowledge the diligence of numerous agricultural inspectors at US ports. Further thanks to the following for providing literature or other information: Roy Anderson, Gary Barker, Kevin Bonham, Ulrich Bössneck, Bram Breure, Arthur Chater, Benjamin Gómez, Eva Hackenberg, Shalika Kumburegama, Jürgen Jungbluth, Henk Mienis, Fred Naggs, Adrian Norris, Tello Neckheim, Barna Páll-Gergely, Ben Rowson, Alejandra Rumi. Ben Rowson, Ton de Winter, Bernhard Hausdorf, and a fourth anonymous referee all provided thoughtful reviews of the submitted manuscript and we are also grateful to Gary Barker, Robert Forsyth, and Anne Ludwig for their comments on it. We thank Bettina Schlitt for cataloguing specimens. A collecting trip to Italy was supported by the Paul Ungerer Foundation.

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