

Research article

Regional trends and preliminary results on the local expansion rate in the invasive garden ant, *Lasius neglectus* (Hymenoptera, Formicidae)

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Abstract. The expansion process of the invasive garden ant, *Lasius neglectus* in Europe and Asia is described in terms of: a) local expansion through colony growing measured on four supercolonies (Seva, Debrecen, Buda Castle and Budatétény) from two distant and climatically different countries (Spain, Hungary), and b) regional expansion, using data from all published and several new non-native localities. Short, local distance processes (few meters to 89 m year⁻¹), as colony budding, are two to five orders of magnitude smaller than long regional distances (ten km to >1000 km). This suggests direct human intervention in the invasive spread. The regional trend also shows that the invasive garden ant has been quickly and steadily increasing the number of non native localities (77) and countries (14) it has reached during the last 30 years.

Keywords: *Lasius neglectus*, expansion rate, Hungary, Spain, tramp ants.

Introduction

Biological invaders are accepted as important agents of global change (Elton, 1958; Lodge, 1993; Vitousek et al., 1996), and this, with much help from human transport and trade (di Castri, 1989; Jenkins, 1996; Mack et al., 2000). An important component in the biology of invaders is their expansion rate (Hastings, 1996), and pattern, with its characterization admittedly a difficult task (Suarez et al.,

2001). Suarez et al. (2001) provide a useful model to describe, at different spatial and temporal scales, the expansion pattern in the Argentine ant (*Linepithema humile*) and two different processes have been proposed. The first, a local process, implies colony budding and produces much shorter distances –by three orders of magnitude– than the regional processes that involve small colony fragments unintentionally brought around by humans. This dual model of expansion is probably a general rule in tramp ants (Suarez et al., 2001; Holway et al., 2002).

The biological profile of the invasive garden ant, *Lasius neglectus* van Loon, Boomsma and Andrásfalvy 1990, specially its unicoloniality, has produced a recent upsurge of interest in the species. Its biology is strikingly convergent with the Argentine's, albeit the species is much less studied: high polygyny level (Boomsma et al., 1990; Espadaler et al., 2004), unicoloniality and reduced intraspecific aggression (Cremer, pers. comm.; Steiner et al. 2004; pers. obs.), strong interspecific aggression (Steiner et al., 2004; Cremer et al., 2006), prevalence of nest mating and budding as a dispersal mechanism (Boomsma et al., 1990; Espadaler and Rey, 2001), small size in comparison with its relatives (van Loon et al., 1990; Seifert, 1992), worker sterility and a proclivity for the human environment (Passera, 1994; Espadaler and Rey, 2001). Interestingly, two other general characteristics of ant invaders –easy migration, short lived queens– are still to be demonstrated in *L. neglectus*.

The qualifier “rapid” has been used to describe the range expansion of the invasive garden ant, *Lasius neglectus* (Seifert, 2000), but this needs a quantitative

Table 1. Locality, climatic characteristics, date of early records and surface estimations of four supercolonies used to estimate local expansion rate in *Lasius neglectus*.

Supercolony	Locality and characteristics					First record	First surface estimate	Surface at present (ha)
	Country and detailed location	Original habitat	Climate	Annual temp. °C	Annual rainfall (mm)			
A Budatétény 47.31°N, 19.00°E	N-Hungary type locality	Urban garden	Subcontinental with weak Mediterranean influence	10.4	516	1973 (1)	400ha in 1988	>3600
B Debrecen 47.52°N, 21.62°E	Botanical Garden at University of Debrecen	Urban garden	Subcontinental with weak Mediterranean influence	9.9	566	1997 (2)	1.5ha in 1998	> 4
C Buda Castle 47.29°N, 19.02°E	N-Hungary: District I Budapest	Urban garden	Subcontinental with weak Mediterranean influence	10.4	516	1988 (1)	0.005 in 1988	> 10
D Seva 41.80°N, 2.26°E	NE Spain El Muntanyà	Suburban gardens	Mediterranean	11.5	775	1985 (3)	14 ha in 1999	> 17

1: van Loon et al. (1990); 2: Tartally (2000a); 3: Espadaler and Rey (2001).

assessment, both at a local scale in a given supercolony, and at regional or continental scale. Documenting the – seemingly – initial stage in the spread of this ant is important as it may help in understanding the spread dynamics of pest ants. Here we present the analysis of the local expansion rate, at a short time scale (<20 years) in four supercolonies of the invasive garden ant from two distant and climatically different countries. In addition, and for a complete data set of all known non-native localities for this species, a summary of data on a larger spatial (continental Europe, West and Central Asia) and time scale, using the first date of detection at each locality is also presented. We show that the local expansion rate is 2–5 orders of magnitude smaller than long distance jump-dispersal distances and that the invasive garden ant is, as already correctly stated by Seifert (2000), rapidly expanding its range.

Materials and methods

Data on local expansion rate are from four supercolonies (Table 1). The three from Hungary are at a similar altitude (120–140 m a.s.l.) and that from Spain is at 650 m a.s.l.

Local pattern of expansion

This is the rate of spread at the invasion front. Due to the different circumstances of the different colonies (e.g. climate; size; proportion of vegetation and human buildings; available maps; date of first detection), different methodologies have been applied to the measuring of the expansion rate. However, the final results are expressed in the same units (m year⁻¹) and are, thus, comparable. Details follow.

Linear method using transects

This method was applied for two colonies from Hungary.

Budatétény supercolony. The map of van Loon et al. (1990: their Fig. 1) was used for giving the borders in 1988. Six radial transects were designated from the centre through six identifiable points an up to the recent borders (details available from A.T.). The presence of *L. neglectus* on these six transects was mapped using a map of Budapest (scale 1: 30000; reprint 2005) in August 2005. The presence of *L. neglectus* workers and/or nests (by turning over stones, disrupt the cortex of trees and digging the soil if no entrance was visible) was checked on and around paths, trees and bushes. The distances were read from the map with a ruler.

Debrecen supercolony. Since only an unpublished dendrological map of the Botanical Garden of the University of Debrecen (scale 1: 500; from 1997) was available as a detailed map we also worked with transects in this case. Four transects were designated from the crossroads in the middle of the supercolony to the observatory (O), to the well (W), to the entrance (E) and to the lake (L) (see details in Tartally, 2006). In September (when most worker pupae had hatched but the ants were still active) in 1998, 2000, 2002 and 2005 the presence of *L. neglectus* workers and/or nests was checked with the same methods as in the Budatétény supercolony.

Circular model

Seva supercolony. A map of the area occupied had been completed in 1999. From then, and up to 2006, on each year, in May, a detailed map (scale 1: 4000) has been updated after colony hibernation, when the ants are already intensively foraging. This was done by checking the limits of the previous year and noting newly infested areas. Roads, sideways, and non-urbanized lots were checked for the presence of ants, usually by following cracks in the concrete. If ants were present those fissures were covered with soil or debris. Small herbs or mosses growing in cracks were also checked with a pickaxe. Private properties were also inspected for ants foraging on trees and in flowerpots. Hedges in the limits of lots were searched too, as a majority was made using *Prunus laurocerasus*, a plant with extrafloral nectaries in the leaves, regularly visited by *L. neglectus*. The newly infested area added each year was directly measured on the maps. The expansion rate for the Seva colony was estimated as follows. The colony limits are irregular (see: Espadaler et al., 2004: Fig. 1) and expansion is not uniform in all

directions. An annual rate of expansion was deduced from the area added each year (1999 to 2006; seven measures), modelled as a uniform circular growth over the area of the previous year. Thus, for the initial estimation in 1999 of 14.49 ha (a model circle of 214.8 m radius) and the increase of 0.72 ha noted in 2000, the equivalent expansion rate would have been 5.27 m (a model circle of 220.07 m). A mean expansion rate year⁻¹ for the seven-year period was obtained.

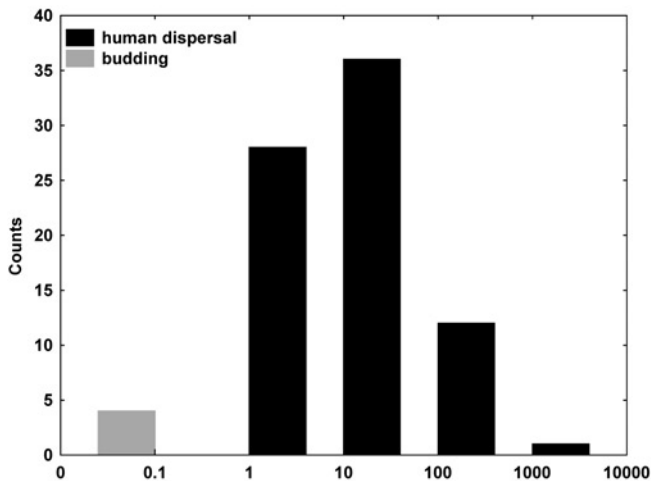


Figure 1. Distribution of yearly local dispersal distances (grey) and long-dispersal events (black). Local rates through colony budding were determined directly from four colonies (Budatétény and Buda Castle, Hungary, 17 years; Debrecen, Hungary, seven years; Seva, Spain, seven years). Long distance dispersal was noted as distances between nearest neighbour localities. Data exclusively from populations out of Turkey. X-units are km.

Buda Castle supercolony. The area of this colony was mapped thoroughly on August 2005 with the same methods (but without designating transects) as at the Budatétény supercolony. According to van Loon et al. (1990) we assume that the area of this supercolony was maximum 0.005ha in 1988 because “Workers were found in massive numbers on only one tree and around decorative potted laurel trees...” (van Loon et al., 1990: 359).

Regional pattern of expansion

Using the same rationale as Suarez et al. (2001), one measure was taken to describe the long distance jump-dispersal process: minimum distances (nearest neighbour model) between localities out of Turkey were measured as straight line on country road maps or on a Reader’s Digest Atlas of the World (scale 1: 2000000; reprint 1989). Localities from Turkey were not used as doubts remain over the specific identity of many Turkish populations. Unequal spatial sampling or detection could lead to overestimate jump-dispersal distances. That is a potential flaw with our data and we cannot dismiss this possibility. In effect, it is known that not all populations of this species outside its native range have developed up to reach a pest status (Rey and Espadaler, 2005). In those situations, no special warning signal has emerged and many such populations may exist but remain unnoticed within Europe and Asia (the large gap between Iran and Kyrgyzstan is probably an artefact of a lack of sampling, see also Schultz and Seifert, 2005). Regrettably, the scarcity of ant identification experts in some European and especially in Asian countries may be an additional, inherent difficulty towards a comprehensive invasion history of the invasive garden ant.

A comparison between local expansion rate and regional expansion rate was done by a direct consideration of the order of magnitude. Using the year of collection of *L. neglectus* in all known localities,

histograms of observations (Y-axis: counts) were constructed –both for individual data and for data grouped in 9-year classes –with Statistica (StatSoft, 2003). We looked for a pattern in the relation between time (years elapsed from first available date –1973; without data from Turkey) and cumulative number of: a) countries, and b) localities, with an exponential regression.

Results

Local expansion rate Budatétény colony

The mean expansion for each of the six transects was 123 m year⁻¹, 134 m year⁻¹, 63 m year⁻¹, 86 m year⁻¹, 84 m year⁻¹ and 40 m year⁻¹. The mean for 17 years of local expansion by budding is 89 m year⁻¹. *L. neglectus* workers/nests were observed also within the area given by van Loon et al. (1990: Fig. 1) along each transect.

Local expansion rate Debrecen colony

Gradual increase in four transects for three periods between 1998 and 2005 is indicated in Table 2. The mean for those seven years of local expansion by budding in the transects is 13 m year⁻¹.

Table 2. Local expansion rate of the supercolony of *Lasius neglectus* (Debrecen, Hungary).

Year	Transect O (m)	Transect W (m)	Transect E (m)	Transect L (m)	Mean increase (m)
1998	45	25	73	60	
2000	56	57	88	113	27.75
2002	83	96	133	145	35.75
2005	109	109	N.A.	179	24.33

N.A. non available because of constructions built between 2003 and 2005.

Local expansion rate Buda Castle colony

Absolute increase from 1988 (ca. 50 m²) to 2005 is estimated as 102450 m². Under the assumption of the circular model (see Methods section) the local expansion rate is 10.6 m year⁻¹.

Local expansion rate Seva colony

Gradual increase for every year from 1999 to 2006 is indicated in Table 3. The mean \pm s.d. for seven years of local expansion by budding, and assuming a circular model (see Methods sections) is 2.75 \pm 1.5 m year⁻¹.

Table 3. Local expansion rate of the supercolony of *Lasius neglectus* (Seva, Spain).

Year	Area occupied (ha)	Increase (ha)	Expansion rate	Circular model ^a
1999	14.4976		1	
2000	15.2180	0.7203	1.049	5.27
2001	15.4540	0.2359	1.015	1.69
2002	15.9635	0.5095	1.032	3.62
2003	16.5313	0.5677	1.035	3.97
2004	16.8197	0.2884	1.017	1.99
2005	17.0472	0.2275	1.013	1.56
2006	17.2250	0.1778	1.010	1.21
Mean (s.d.)		0.389 (0.208)	1.024 (0.014)	2.75 (1.53)

^a linear distance expansion (m), assuming a circular shape for the colony.

Regional pattern of expansion

The mean \pm s.d. nearest neighbour distance for the 77 non-native localities is 88 ± 273 km (median 20 km; range 2–2300 km) with an extreme for the isolate locality in the Canary Islands. Using the nearest neighbour model, the distance distribution, both from the local and the long-distance processes, shows a remarkable bimodal pattern, with local processes two to five orders of magnitude smaller than long distances (Fig. 1). Table 4 lists the first collecting date for all known non-native localities. The first available date (1973; Budapest) is only thirty-four years ago. Outside from Turkey –the supposed centre of origin (Seifert, 2000)– seventy-seven localities are known. It is perhaps safe to interpret broadly that they have been reached during those 34 years, with a rate of roughly two new localities year⁻¹ and the detection of the ant in a new country every two years. More than one supercolony fragment may be known for a given locality and they are well separated by large, unoccupied zones, without connections between them: in Barcelona (15 fragments), Bishkek (5), Budapest (16), Sant Cugat (25), Warszawa (5) (Czechowska and Czechowski, 2003; Tartally et al., 2004; Espadaler and Bernal, 2005; Schultz and Seifert, 2005; Cs. Nagy, unpubl. data) although data usually refer to a single fragment or sample. The distribution of individual data shows a regular increase over time. By grouping dates in wider classes some buffering of the inherently haphazard nature of those particular data may be attained. The general impression of a steady increase of newly discovered localities is also apparent (Fig. 3). There is a strong linear correlation ($r^2 = 0.78$; $p < 0.001$) between the number of localities and countries (Fig. 3) indicating there is no undue weighting from any country.

Discussion

Data on ant local expansion rates are scarce. For the much studied Argentine ant, the range of spread by budding is from 0 to 270 m year⁻¹ ($n=47$ sites) and a mean maximum rate of 154 ± 21 m year⁻¹ (Suarez et al., 2001). For the crazy ant, *Anoplolepis gracilipes*, in the Seychelles Islands, local expansion rates vary from 36 to 402 m year⁻¹ ($n=5$ sites; Haines and Haines, 1978; Gerlach, 2004) and for *Wasmannia auropunctata* from 15 m year⁻¹ in Florida (Spencer, 1941) to 170 to 500 m year⁻¹ in Santa Cruz Island (Galápagos), depending on precipitation (Lubin, 1984; Lubin, 1985). Data for *L. neglectus* indicate a shorter rate (range 1.2–134 m year⁻¹; four populations overall mean: 28.8 m year⁻¹) although our sample size ($n=4$ sites) is too small to be conclusive for *L. neglectus*. Local expansion rates from other localities are needed. Notwithstanding, the circumstance of lack of observations of easily released migratory behaviour by *L. neglectus* may indicate an interesting difference in the biological profile between this species and the Argentine ant, whose easy dispersal has been noticed since the earliest studies (Newell and Barber, 1913). No published information is available on the feeding habits of *L. neglectus* in its native range and the heavy dependence of *L. neglectus* on tree aphids outside of its native range is perhaps a constraint that limits its freedom to move far from trees. Notwithstanding, this could be a very partial interpretation. In effect, the main introduction sites (botanical gardens, city parks, institutes of plant protection research) usually have many or at least some trees on their areas. *L. neglectus* is there because it was introduced to these sites and not because the sites have trees. *L. neglectus* could be a food generalist as there was a very large supercolony in grassland without trees at the dam site of the reservoir 5 km east of Tiflis. These ants used root aphids (B.S., pers. obs.). The problem with this supercolony was that a human could not easily become aware of the ants without turning stones and careful inspection of the grasses. In parks one will note them easily but not in urban or semiurban grasslands where the ants remain more hidden and do not directly affect human interests. Absence of suitable nesting microhabitat might also prevent the ants from expansion. Compared with the Argentine ant, which has most chambers and tunnels concentrated just beneath the surface (Halley et al., 2005), nesting habits seem to be more exigent in *L. neglectus*. This ant digs relatively deep, well defined and long-lasting galleries, up to 30 cm deep (X.E., pers. obs.), thus probably investing more energy in nest construction and maintenance than Argentine ants. Moreover, *L. neglectus* populations throughout Europe show complete hibernation in winter in contrast to the less marked activity arrest in populations of the Argentine ant (pers. observ.) which means that colonies of this last species may be able to develop for longer time during the year. If the absence of easy migration is confirmed for *L. neglectus*, then the

Table 4. Ordered localities by date (year) of collection. Locality, country and source for all presently known *Lasius neglectus* localities out of Turkey (n=77).

Year	Locality	Country	Source
1973	Budapest	Hungary	van Loon et al., 1990
1974	Pizunda	Georgia	Seifert, 2000
1978	Ghent	Belgium	Dekoninck et al., 2002
1981	Gif-sur-Yvette	France	J.S. Pedersen (pers. comm.)
1983	Rhodos city	Greece	Seifert, 2000
1984	Albena	Bulgaria	Seifert, 2000
1984	Sotchi	Georgia	Seifert, 2000
1985	Tiflis	Georgia	Seifert, 2000
1985	Tiflis – 5 km E	Georgia	Seifert, 2000
1985	Seva	Spain	Espadaler and Rey, 2001
1986	Paris	France	Jolivet, 1986 (as <i>L. alienus</i>)
1987	Orange	France	Seifert, 2000
1988	Athens	Greece	Seifert, 2000
1990	Barcelona	Spain	Espadaler, 1999
1993	Matadepera	Spain	Espadaler and Rey, 2001
1995	Port Leucate	France	Seifert, 2000
1995	Toulouse	France	Seifert, 2000
1995	Epta Piges, in Rhodes	Greece	B. Seifert (unpubl.)
1995	Kolybia, in Rhodes	Greece	Seifert, 2000
1995 (1)	Warszawa	Poland	Czechowska and Czechowski, 1999
1996	Baile Herculeane	Romania	Markó, 1998
1997	Jena	Germany	Seifert, 2000
1997	Debrecen	Hungary	Tartally, 2000a,b
1997	Volterra	Italy	Seifert, 2000
1997	Bellaterra	Spain	Espadaler, 1999
1998	Érd	Hungary	Tartally, 2000b
1998	Bishkek (=Frunze)	Kyrgyzstan	Seifert, 2000
1998	Tash Kумыr	Kyrgyzstan	Seifert, 2000
1999	Tahi	Hungary	Tartally, 2000b
1999	Dschalal-Abad	Kyrgyzstan	Schultz and Seifert, 2005
1999	Kara Suu	Kyrgyzstan	Schultz and Seifert, 2005
1999	Les Planes	Spain	Espadaler and Rey, 2001
1999	Sant Cugat	Spain	Espadaler and Rey, 2001
1999	Taradell	Spain	Espadaler and Rey, 2001
2000	Montpellier	France	Marlier et al., 2002
2002	St. Aubin de Médoc	France	C. Galkowski (in lit.)
2002	Barberà	Spain	Rey and Espadaler, 2005
2002	Cerdanyola	Spain	Rey and Espadaler, 2005
2002	Icod, in Tenerife	Spain	Espadaler and Bernal, 2003
2002	Ripollet	Spain	Rey and Espadaler, 2005
2002	Oberhaus	Germany	P. Sturm (pers. comm.)
2003	Llissà de Vall	Spain	Rey and Espadaler, 2005
2004	Saint Sever	France	C. Galkowski (in lit.)
2004	Vigoulet-Auzil	France	B. Seifert (unpubl.)
2004	Batken	Kyrgyzstan	Schultz and Seifert, 2005

Table 4. Ordered localities by date (year) of collection. Locality, country and source for all presently known *Lasius neglectus* localities out of Turkey (n=77). (Continued)

Year	Locality	Country	Source
2004	Burgöndü	Kyrgyzstan	Schultz and Seifert, 2005
2004	Eski-Nookat	Kyrgyzstan	Schultz and Seifert, 2005
2004	Karasnaja Maja	Kyrgyzstan	Schultz and Seifert, 2005
2004	Koshkor-Ata	Kyrgyzstan	Schultz and Seifert, 2005
2004	Kyzyl-Kyya	Kyrgyzstan	Schultz and Seifert, 2005
2004	Osh	Kyrgyzstan	Schultz and Seifert, 2005
2004	river Isfayran Say, Austay	Kyrgyzstan	Schultz and Seifert, 2005
2004	Bucharest	Romania	V. Bernal (pers. comm.)
2004	Orsova	Romania	K. S. Petersen (pers. comm.)
2004	Iselnita	Romania	K. S. Petersen (pers. comm.)
2004	Dubova	Romania	K. S. Petersen (pers. comm.)
2004	Drobeta-Turnu Severin	Romania	K. S. Petersen (pers. comm.)
2004	Vanju mara	Romania	K. S. Petersen (pers. comm.)
2004	Rogova	Romania	K. S. Petersen (pers. comm.)
2004	Bhot	Bulgaria	K. S. Petersen (pers. comm.)
2004	Balcik	Bulgaria	K. S. Petersen (pers. comm.)
2004	Kronevo	Bulgaria	K. S. Petersen (pers. comm.)
2004	Varna municipality	Bulgaria	K. S. Petersen (pers. comm.)
2004	Kavarna	Bulgaria	K. S. Petersen (pers. comm.)
2004	Tolbuhin	Bulgaria	K. S. Petersen (pers. comm.)
2004	Senokos	Bulgaria	K. S. Petersen (pers. comm.)
2004	river Aksu, Jordan	Uzbekistan	Schultz and Seifert, 2005
2005	Gorgan	Iran	B. Seifert (unpubl.)
2005	Amol	Iran	B. Seifert (unpubl.)
2005	Abpari forest	Iran	B. Seifert (unpubl.)
2005	Astaneh Ashrafieh	Iran	B. Seifert (unpubl.)
2005	Babolsar	Iran	B. Seifert (unpubl.)
2005	Sentfores	Spain	R. Vila (pers. comm.)
2005	Piera	Spain	R. Vila (pers. comm.)
2005	Begues	Spain	F. García (pers. comm.)
2006	Narbonne Plage	France	J.-L. Marrou (pers. comm.)
2006	L'Escala	Spain	Herraiz and Espadaler, 2007

The date of 1995 has been used as a conservative option following the comment in Czechowska and Czechowski (2003: 198) that "...*L. neglectus* appeared at the beginning of the 1990s at the latest".

expansion rate through budding measured in the four studied supercolonies (in the order of few to several tens of m year⁻¹) could be accurate for the species. Clearly, field behavioural observations are needed to address interspecific aggression and colony migration in *L. neglectus* (Holway and Suarez, 1999). Also, precise knowledge of when budding events occur, whether in summer, after mating, or before entering in hibernation or in early spring, after hibernation, is lacking.

Another mechanism of dispersal is also possible. If we consider the multiple fragments detected in localities like Barcelona (15 fragments), Bishkek (5), Budapest (16),

Sant Cugat (25), Warszawa (5), how are they to be interpreted? If they are not connected, the budding and here defined local expansion process, can not be the main driving factor. A different process, a short distance human mediated introduction and expansion after long distance human mediated introduction (transport of plant pot with nests from one to another garden in the same city; see also van Loon et al., 1990: 359) could explain that pattern of unconnected nests. This possibility should be investigated by checking the genetic relationship between nearby isolated colonies and by aggression tests. It is worth mention here that Steiner et al. (2004) showed already

that all intraspecific pairings of *L. neglectus* from Budapest resulted in non-aggressive behaviour.

The usual mechanism of dispersal in ants is through mating flights (Hölldobler and Wilson, 1990). In *L. neglectus* no mating flight has ever been detected (van Loon et al., 1990; Espadaler and Rey, 2001, but see Seifert (2000) and Schultz and Seifert (2005) for an intriguing case of winged sexuals trapped in a spider web at house wall in a garden in Bishkek). Therefore, the scale of regional processes, in the range of a few tens or up to two thousand km, points directly towards human intervention. The population from the Canary Islands is an obvious example of unintentional transport by humans. A similar conclusion had been reached in reference to the Argentine ant invasion in USA by Suarez et al. (2000) and recently in New Zealand (Ward et al., 2005). To explain the regional trend in time, indicated by collection dates, several possibilities should be considered: 1. There is an ongoing human mediated spread of the ant, even if the recent inflation in the number of localities discovered –from the year 2000 on– is accounted for by regions where myrmecologist do their work (e.g. all the populations around Barcelona) (Fig. 3). In effect, before the year 2000 the increasing trend is also apparent. 2. It reflects the well known lag phase in invasive organisms; see ant examples for this lag-phase in O'Dowd et al. (2003) or Steiner et al. (2006). 3. A combination of both processes (we favour this last possibility). Distribution data are still too scarce and biology of *L. neglectus* (e.g. intrinsic rate of growth in the field) is too poorly known for a proper assessment of the three possibilities. To be completely explained, each invasion example has to include some local and historical components. In a sense, every episode of invasion is unique, even within a given species (Grosholz, 1996; Byers et al., 2002); then, the different invading populations of *L. neglectus* in its non-native range may be in rather distinct phases of the expansion process and, depending on local circumstances (specially the climate, management and urbanization processes), they will remain in an arrested state or will slowly gain terrain as local ecology and perturbation allow. It is worth noting that *L. neglectus* is the only known invasive ant with real cold-hardiness (Seifert, 2000; Schultz and Seifert, 2005) and potential to expand farther north. Hence, data presented here may not apply to other populations, known or unknown, which deserve specific study.

The examination of the spreading of the myrmecophilous isopod, *Platyarthrus schoblii*, could be interesting for tracing the way of introduction of *L. neglectus* into different localities because this species is often introduced together with *L. neglectus* but its native area is better known (Tartally et al., 2004). It is to be noted that native, local myrmecophiles may be also accepted by *L. neglectus* (Dekoninck et al., 2007).

Data we present here are based on the current status of *L. neglectus* and are, thus, in no sense predictive. Arguments using this last aspect remain necessarily speculative: detection date does not equal date of arrival

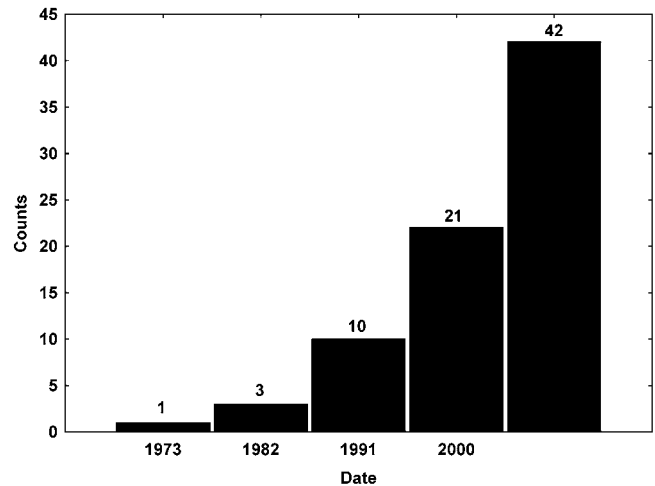


Figure 2. Collection dates for known localities of *Lasius neglectus*, (non-native) grouped in 9-year wide classes. Data for each column pertain exclusively to the corresponding 9-year class, but for the last class that includes only six years. Figures show frequency.

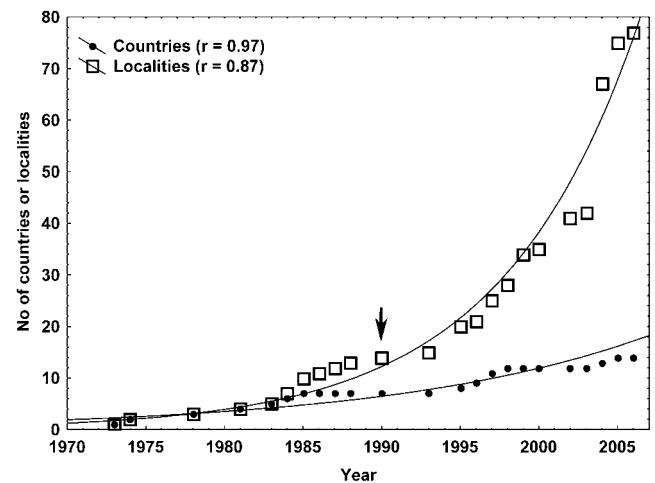


Figure 3. Relationship between the cumulative number of known countries and localities and time (year of collection) for non-native populations. Arrow indicates year of formal description.

due to the usual lag-phase present in invaders (Hastings, 1996; Williamson, 1996), itself a multifactor and variable effect (Mack et al., 2000; Crooks, 2005), and is also reflecting very much the recent sampling effort. Furthermore, although the rate of discovery of new localities has increased over time, it has been shown that the discovery rate can increase even when there is no increase in either the introduction rate or the sampling rate (Costello and Solow, 2003). It is worth noting that this species was practically ignored for about 10 years after its description and Seifert (1992) synonymised it with *L. turcicus* (as *Lasius turcicus polygynous* form) in an influential work. Thus, an average myrmecologist could not have probably realized if they had seen *L. neglectus* in the 1990 s. The next publications in which the species is noted were those of Seifert (1996), Markó (1998), Czechowska and Cze-

chowski (1999), Espadaler (1999), Espadaler and Rey (2001), Seifert (2000) and Tartally (2000a,b), in which it was treated again at specific level, where it has remained since.

The cumulative number of known localities and countries across time were found to be strongly correlated. We suggest this indicates a true pattern, at the two scales (country, locality) and not a mere correlation due to location of myrmecologists or to the nesting of localities within countries. Data for a fourth of the collection sites predate 1990, when *L. neglectus* was formally described from Budapest (van Loon et al., 1990) and a trend is already apparent (first 3 columns Fig. 2). Private or public collections are again (Dekoninck et al., 2002; Schlick-Steiner et al., 2003; Suarez and Tsutsui, 2004) shown to be a useful resource in tracing back collection dates, allowing a more precise tracking of the dispersal process. A thorough search in historical archives of commercial and horticultural relationships between the Company of Fruit and Agricultural Development in Budatétény (type locality; van Loon et al., 1990) and external sources of plants, especially from Turkey, would perhaps yield interesting and more specific hints as to when or how *L. neglectus* reached Budapest.

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