

Worldwide spread of the Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae)

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Abstract

The Argentine ant, *Linepithema humile* (MAYR, 1868), originally from subtropical South America, is an important pest in many parts of the world. To evaluate its worldwide distribution and potential for further spread, we mapped records of *L. humile* from > 2100 sites. Because several South and Central American *Linepithema* species have been often misidentified as *L. humile*, we excluded all unconfirmed South and Central American records. We documented the earliest known *L. humile* records for 95 geographic areas (countries, island groups, major islands, and US states), including several for which we found no previously published records. We could not confirm any *L. humile* records from several South and Central American countries with published reports.

Most records of *L. humile* come from the subtropics, particularly from regions with Mediterranean-like climates (i.e., warm dry summers and cool moist winters), including its native range in South America and exotic populations in California, the Mediterranean, southern Africa, Australia, New Zealand, and Japan. In more humid subtropical areas, such as the southeast US, *L. humile* rarely dominates outside urban areas. In tropical latitudes, *L. humile* dominates only at higher elevations, most notably in Hawaii. In temperate areas, *L. humile* is almost exclusively an indoor pest.

Linepithema humile has already spread to most subtropical lowland regions with Mediterranean-like climates, but is not known yet from most tropical highland areas with suitable climates. In the past, *L. humile* probably arrived in tropical regions by sea accompanying human commerce and had to survive coastal lowland conditions before spreading to higher, cooler elevations. Nowadays air travel allows *L. humile* to stowaway in cargo delivered almost anywhere in the world. Therefore, a wider spread of this pest is expected in the future.

Key words: Biogeography, biological invasion, exotic species, Formicidae, invasive species.

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Introduction

Several exotic ant species are known to have substantial ecological impacts. When these species invade, they can disrupt the indigenous invertebrate fauna and transform the native biotic community. Among the most destructive invasive ants are the red imported fire ant, *Solenopsis invicta* BUREN, 1972 (ALLEN & al. 2004), the little fire ant, *Wasmannia auropunctata* (ROGER, 1863) (WETTERER & PORTER 2003), the long-legged ant *Anoplolepis gracilipes* (SMITH, 1857) (WETTERER 2005), the African big-headed ant, *Pheidole megacephala* (FABRICIUS, 1793) (WETTERER 2007), and the Argentine ant, *Linepithema humile* (MAYR, 1868) (VEGA & RUST 2001).

Linepithema humile (Figs. 1 - 4) has negative impacts on many other animals, both vertebrates and invertebrates (e.g., VEGA & RUST 2001, WETTERER & al. 2001, SUAREZ

& al. 2005). In addition, *L. humile* can be a significant agricultural pest, enhancing populations of Hemiptera (VEGA & RUST 2001). Hemiptera cause damage by sapping plants of nutrients and increasing the occurrence of diseases, including viral and fungal infections.

Linepithema humile is native to the Paran  River drainage area of subtropical Argentina, Brazil, Paraguay, and Uruguay, which has a Mediterranean-like climate, i.e., warm dry summers and cool moist winters (WILD 2004). It has become a major pest in many areas around the world with similar climates. Recently, several papers have examined the worldwide spread of *L. humile* and predicted its potential distribution based on current and future climate estimates (SUAREZ & al. 2001, HARTLEY & LESTER 2003, ROURA-PASCUAL & al. 2004, HARTLEY & al. 2006, WARD



Figs. 1 - 4: *Linepithema humile*. (1) head of worker from Entre Rios, Argentina (specimen ID = CASENT0106983); (2) lateral view of the same worker; (3) dorsal view of the same worker; (4) worker tending a scale insect in California (photos by A.L. Wild).

2007). In the present paper, we have documented more fully the historic spread and current worldwide distribution of *L. humile*, and corrected some errors in the literature.

Methods

We documented the range of *L. humile* using both published and unpublished records. Antbase.org and the FORMIS bibliography were essential resources for finding relevant published papers. We obtained unpublished site records from the collections of American Museum of Natural History (AMNH), Archbold Biological Station (ABS), the Natural History Museum, London (BMNH), the California Academy of Science (CAS), the Field Museum (FM), the Florida State Arthropod collection (FSAC), the Los Angeles Museum of Natural History (LACM), the Museum of Comparative Zoology (MCZ), the Museo Civico di Storia Naturale "Giacomo Doria" (MSNG), the Museu de Zoologia da Universidade de São Paulo (MZSP), the Naturhistorisches Museum Wien (NMW), the Oxford University, Museum of Natural History (OUNH), the Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ), the Smithsonian Institute (SI), the University of Arizona Museum (UAM), and the University of Minnesota Museum (UMM), and from on-line databases of the Australian National Insect Collection, the California Academy of Science,

Fauna Europaea, the Global Diversity Information Facility, Landcare Research, the Essig Museum, the Pacific Basin Information Node, and the Nebraska State Insect Records (NSIR). We received unpublished site records from E. Bodson (Belgium), J. Delabie (Brazil, Chile, Tunisia), R. Guillem (Gibraltar, Morocco), G. Heller (Canary Islands, Italy, France, Spain), M. Lush (Spain), and P. Pellitteri (Wisconsin). We also included our own unpublished specimen records.

If a site record listed a geographic region rather than a "point locale," and we had no other record for this region, we used the coordinates of the capital or largest town within the region or, in the case of small islands and natural areas, the center of the region. Often, if one reference had many sites less than 10 - 20 km apart (e.g., HUDDLESTON & FLUKER 1968), we did not plot every site. We did not map records of *L. humile* on boats or intercepted in transit by quarantine inspectors, though it is possible that we included some quarantine records that were not labeled as such.

Because WILD (2007) found many *L. humile* records from South and Central America were misidentifications of other *Linepithema* species (e.g., *Linepithema dispertitum* (FOREL, 1885), *Linepithema iniquum* (MAYR, 1870), and *Linepithema neotropicum* WILD, 2007), we excluded all South and Central American records not confirmed by

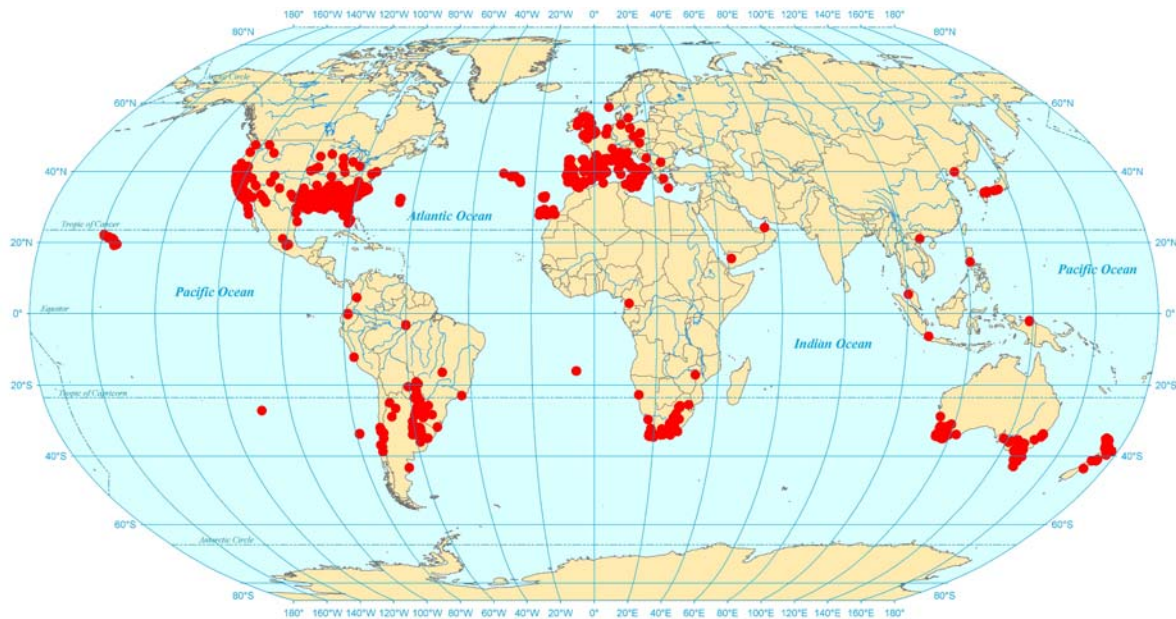


Fig. 5: Worldwide distribution of *Linepithema humile*.

WILD (2007). In contrast, the only other *Linepithema* species that WILD (2007) recorded from outside South and Central America were a few *L. iniquum* records from Belgium (two records), Germany (one record), Ireland (one record), and Massachusetts (one record). We therefore mapped all other *L. humile* records outside South and Central America assuming that they were fairly reliable.

Results

We plotted records of *L. humile* from > 2100 sites around the world (Fig. 5). These records of *L. humile* came from 95 different geographic areas (i.e., countries, island groups, major islands, and US states), including several for which we found no previously published records: Tunisia, Idaho, Nebraska, Pennsylvania, and Wisconsin (Tabs. 1 - 6).

We could not confirm any *L. humile* records from several South and Central American countries with published reports: Costa Rica, El Salvador, Guyana, Surinam, and Venezuela. WILD (2007) found that many published records of *L. humile* from South and Central America were actually based on misidentification of other species: e.g., Costa Rica (PERFECTO & SNELLING 1995; all records = *L. neotropicum*), Venezuela (ROURA-PASCUAL & al. 2004; only record = *L. iniquum*), and El Salvador (ROURA-PASCUAL & al. 2004; only record = *L. dispertitum*). We could not find any specimens confirming published *L. humile* records from Surinam and Guyana (DÜRR 1952).

We excluded unconfirmed *L. humile* records from other South and Central American countries, including several that predate our earliest confirmed records from those countries: Brazil (e.g., VON IHERING 1894), Colombia (e.g., FOREL 1912), Chile (e.g., NEWELL & BARBER 1913), Mexico (e.g., CARPENTER 1902), and Peru (e.g., DALE 1974).

Discussion

Originally from subtropical South America, *Linepithema humile* began its spread to the greater Mediterranean region in the 19th century. The earliest known specimen of *L. humile*, predating even the type specimens collected in

Tab. 1: Earliest confirmed records of *Linepithema humile* from South and Central America. See text for acronyms. * = see text for earlier unconfirmed published records.

| Native range | Earliest confirmed record |
|--------------|--|
| Argentina | 1866 (MAYR 1868) |
| Uruguay | 1885 (collector unknown; NMW): Montevideo |
| Paraguay | 1896 (G. Boggiani; MSNG): Puerto 14 de Mayo |
| Brazil | 1914* (BORGMEIER 1928 as <i>Iridomyrmex riograndensis</i> BORGMEIER, 1928) |
| Exotic range | |
| Chile | 1965* (A. München; MZSP): Temuco |
| Mexico | 1965* (N. Krauss; BMNH): Mexico City |
| Colombia | 1973* (W.P. Mackay; pers. coll.): Armenia |
| Peru | 1982* (P. Majlut; MZSP): Los Condores |
| Ecuador | 2002 (M.F. Salvador; QCAZ): Quito |

Argentina in 1866 (MAYR 1868), was collected on the Atlantic island of Madeira between 1847 and 1858 (WETTERER & al. 2006). In the 19th century, Madeira was a hub for commerce between Portugal and its colonies in South America, and collection records suggest that *L. humile* may have first spread through the greater Mediterranean region via Madeira and Portugal (WETTERER & WETTERER 2006, WETTERER & al. 2006). All of the earliest records from continental Europe (1890 - 1896) come from Portugal (SCHMITZ 1897, MARTINS 1907, COUTINHO 1929). Some 50 years after first being collected in Madeira, and 20 years after being recorded in Portugal, *L. humile* began appearing in other parts of the greater Mediterranean region (Tab. 2). By the 1920s, *L. humile* had been collected in two other

Tab. 2: Earliest known records of *Linepithema humile* from the greater Mediterranean region and on Atlantic islands. See text for acronyms. + = no previously published records.

| | Earliest record |
|------------------|--|
| Madeira | ≤ 1858 (WETTERER & al. 2006) |
| Portugal | 1890 (MARTINS 1907) |
| Italy | 1902 (SILVESTRI 1922) |
| France | ~ 1906 (MARCHAL 1917) |
| Canary Islands | 1909 (STITZ 1916) |
| Spain | 1916 (FRISQUE 1935) |
| Bosnia | 1916 (FRISQUE 1935) |
| Azores | ≤ 1921 (CHOPARD 1921) |
| Monaco | ≤ 1921 (CHOPARD 1921) |
| Algeria | 1923 (FRISQUE 1935) |
| Sicily | 1926 (H. Donisthorpe, BMNH): Palermo |
| Bermuda | 1949 (BENNETT & HUGHES 1959) |
| Balearic Islands | 1953 (GÓMEZ & ESPADALER 2006) |
| Morocco | 1956 (WETTERER & al. 2006) |
| Greece | ≤ 1967 (BERNARD 1968) |
| Corsica | ≤ 1967 (BERNARD 1968) |
| Malta | ≤ 1968 (BARONI URBANI 1968) |
| Sardinia | ≤ 1974 (CASEVITZ-WEULERSSE 1974) |
| St Helena | 2002 (WETTERER & al. 2007) |
| Bulgaria | ≤ 2004 (RADCHENKO 2004) |
| Crete | ≤ 2004 (RADCHENKO 2004) |
| Gibraltar | ≤ 2004 (RADCHENKO 2004) |
| + Tunisia | ≤ 2005 (J. Delabie, pers comm.): Hammamet |

North Atlantic archipelagos (Canary Islands and Azores) and from numerous sites in southwestern Europe (Spain, southern France, and Italy). Later, *L. humile* began to turn up in coastal North Africa and the central Mediterranean (Tab. 2, Fig. 5). *Linepithema humile* arrived in Bermuda in the 1940's, and is now the most-dominant ant species there (WETTERER & WETTERER 2004).

Shortly after appearing in southern Europe, *L. humile* began to be reported as an indoor pest in northern Europe (Tab. 3, Fig. 5). The earliest of these records came from Belfast, Northern Ireland, where CARPENTER (1902) reported an enormous *L. humile* population living under the floors and in the walls of a home. The highest latitude records come from Sandnes, Norway (58.85° N), where GÓMEZ & al. (2005) reported *L. humile* living in two apartments. Greenhouse records of *L. humile* are common from many parts of Europe. Because *L. humile* can live anywhere that humans live, there is no limit to the latitude where indoor populations of this species may be found.

Tab. 3: Earliest known records of *Linepithema humile* from western, northern and central Europe.

| | Earliest record |
|--------------------|---------------------------|
| Ireland (Northern) | 1899 (CARPENTER 1902) |
| Germany | 1901 (STITZ 1939) |
| Belgium | 1911 (BONDROIT 1911) |
| Scotland | 1912 (DONISTHORPE 1927) |
| Poland | ≤ 1915 (PAX 1915) |
| England | 1915 (DONISTHORPE 1916) |
| Ireland (Eire) | ≤ 1921 (CHOPARD 1921) |
| Guernsey | ≤ 1927 (DONISTHORPE 1927) |
| Czech Republic | ≤ 1947 (NOVÁK 1947) |
| Austria | 1952 (HÖLZEL 1966) |
| Switzerland | 1980 (KUTTER 1981) |
| Sweden | ≤ 1995 (DOUWES 1995) |
| Netherlands | ≤ 2002 (VIERBERGEN 2003) |
| Norway | 2004 (GÓMEZ & al. 2005) |

Linepithema humile arrived in the US in the late 19th century, where it was first noted in New Orleans (TITUS 1905). It was soon found in subtropical sites across the Southeast US and California (Tab. 4, Fig. 5). *Linepithema humile* now dominates at many urban and riparian sites in California, and has indoor and greenhouse records scattered across temperate parts of the US (Tab. 4, Fig. 5), e.g., in the Desert Dome Exhibit of the Henry Doorly Zoo in Omaha, Nebraska (2003; NSIR).

In South and Central America, *L. humile* has extended its range into temperate and tropical regions (Tab. 1, Fig. 5), though it is not known as a dominant species in any of these areas. Many tropical records are from highland areas, e.g., around Mexico City (WILD 2004). Most records from areas with climates less hospitable to *L. humile* may come from indoor populations.

Linepithema humile has also been reported from subtropical areas of southern Africa and southern Australia with Mediterranean-like climates (Tab. 5, Fig. 5), where it has long been a major widespread pest (CLARK 1941, DÜRR 1952). More recently, *L. humile* has begun to spread across subtropical parts of Oceania and Asia, and a few other subtropical locales (Tab. 5).

In tropical Oceania, *L. humile* is known primarily from Hawaii (Tab. 6, Fig. 5). COLE & al. (1992) studied the impact of *L. humile* in the highlands of Maui, where it reaches elevations up to 2880 m. WETTERER & al. (1998) found *L. humile* were common on the dry western slope of Mauna Kea volcano on the Big Island up to 1680 - 2020 m elevation, but densities quickly dropped off in the cooler areas above this elevation (maximum elevation 2640 m). *Linepithema humile* also has records from other tropical locales (e.g., Indonesia, Cameroon, and Zimbabwe), though these may be indoor records.

Tab. 4: Earliest known records of *Linepithema humile* from US states. See text for acronyms. + = no previously published records.

| | Earliest record |
|----------------|--|
| Louisiana | 1891 (TITUS 1905) |
| Mississippi | 1904 (TITUS 1905) |
| California | 1905 (SMITH 1936) |
| Illinois | 1906 (SMITH 1936) |
| Alabama | 1913 (NEWELL & BARBER 1913) |
| Texas | 1914 (NEWELL 1914) |
| Florida | 1914 (WHEELER 1932) |
| Arkansas | 1915 (BARBER 1916) |
| Georgia | 1915 (BARBER 1916) |
| North Carolina | 1915 (BARBER 1916) |
| South Carolina | 1915 (BARBER 1916) |
| Tennessee | 1915 (BARBER 1916) |
| Arizona | 1922 (collector unknown, UAM): Douglas |
| South Dakota | 1924 (H.C. Severin, MCZ): Brookings |
| Maryland | ≤ 1931 (SMITH 1936) |
| Missouri | ≤ 1933 (SMITH 1936) |
| Virginia | ≤ 1936 (SMITH 1936) |
| Washington | 1938 (R. Gregg, FM): Spokane |
| Minnesota | 1941 (collector unknown, UMM): St. Paul |
| Oregon | ≤ 1942 (MALLIS 1942) |
| Nevada | 1953 (LA RIVERS 1968) |
| Utah | ≤ 1982 (ALLRED 1982) |
| + Nebraska | 1983 (A. Tosco, NSIR): Omaha |
| Oklahoma | 1992 (ALBRECHT 1995) |
| Ohio | ≤ 1993 (ARNETT 1993 in COOVERT 2005) |
| + Pennsylvania | 1993 (KING & GREEN 1994): Philadelphia |
| Michigan | ≤ 1998 (GULMAHAMAD 1998) |
| New Mexico | ≤ 2002 (MACKAY & MACKAY 2002) |
| + Idaho | ≤ 2005 (Ventana, SI): Sierra |
| Indiana | ≤ 2005 (ROBINSON 2005) |
| + Wisconsin | ≤ 2006 (P. Pellitteri, pers. comm.): Fond du Lac |

Future spread

Linepithema humile has already spread to most subtropical lowland areas around the world with Mediterranean-like climates, where we would expect its impact would be

Tab. 5: Earliest known records of *Linepithema humile* from subtropical parts of sub-Saharan Africa, Asia, Australia, and Oceania. See text for acronyms.

| | Earliest record |
|----------------------|--|
| South Africa | 1893 (LOUNSBURY 1909) |
| Lesotho | 1908 (Wroughton, SI): Maseru |
| Juan Fernandez | 1920 (collector unknown, LACM): site unknown |
| Australia | ~ 1931 (CLARK 1941) |
| Namibia | 1982 (A.C. Marsh, BMNH): Swakopmund |
| Easter Island | 1987 (G. Pauley, SI): Hanga Roa |
| New Zealand | 1990 (GREEN 1990) |
| Japan | 1993 (SUGIYAMA 2000) |
| United Arab Emirates | 1995 (COLLINGWOOD & al. 1997) |
| North Korea | ≤ 2005 (RADCHENKO 2005) |

Tab. 6: Earliest known records of *Linepithema humile* from the Old World tropics. See text for acronyms.

| | Earliest record |
|-------------|--------------------------------------|
| Hawaii | 1916 (FRISQUE 1935) |
| Indonesia | 1944 (DONISTHORPE 1950) |
| Cameroon | 1979 (D. Jackson, BMNH): Nkoemvom |
| Zimbabwe | 1986 (FERRER 2000) |
| Yemen | 1998 (COLLINGWOOD & VAN HARTEN 2001) |
| Philippines | 1999 (DAFF 2001) |
| Malaysia | ≤ 2000 (NA & LEE 2001) |
| Vietnam | ≤ 2005 (RADCHENKO 2005) |

the greatest. Within these areas, many populations are still expanding (e.g., Santa Cruz Island, California, WETTERER & al. 2001; Japan, OKAUE & al. 2007; New Zealand, WARD & al. 2005). In some areas, however, populations have declined. For example, on the island of Madeira, *L. humile* was once a serious pest, but now it is relatively uncommon, except in the semi-arid eastern regions (WETTERER & al. 2006).

Despite BYTINSKI-SALZ's (1952) prediction that *L. humile* "must be expected to penetrate the Eastern Mediterranean soon," *L. humile* has not yet been reported east of Crete. *Linepithema humile* also has not yet been reported from regions of southern China and central Africa that have appropriate Mediterranean-like climates (ROURA-PASCUAL & al. 2004, HARTLEY & al. 2006). Although *L. humile* will likely spread to other subtropical areas as well (ROURA-PASCUAL & al. 2004, HARTLEY & al. 2006), it is unlikely to dominate in more humid areas. The importance of aridity in determining the dominance of *L. humile* is well illustrated on a fine grain scale in the Madeira archipelago, where

L. humile is common in the dry eastern parts, but relatively rare in wetter areas (WETTERER & al. 2006). *Linepithema humile* once was a significant pest across much of the humid southeastern US, but is now largely restricted to urban areas (e.g., see BUCZKOWSKI & al. 2004).

Linepithema humile is still largely unknown from tropical highland areas that have suitable climates that might allow it to dominate. Until recently, most exotic ant species invading tropical regions probably arrived by sea accompanying human commerce. These invaders had to survive under lowland tropical conditions before spreading to other locales. This may explain why relatively few ant species have invaded the cooler highland areas (REIMER 1994). WILSON & TAYLOR (1967) noted that populations of *L. humile* in Hawaii were often associated with army camps and bivouacs, and concluded that colonies probably were being transported inadvertently with army supplies and equipment. Nowadays, air travel allows exotic ants to stow-away in cargo delivered almost anywhere. The latitudinal range of *L. humile* may also increase globally as a result of climate change (ROURA-PASCUAL & al. 2004).

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Zusammenfassung

Die Argentinische Ameise, *Linepithema humile* (MAYR, 1868), mit Ursprung im subtropischen Südamerika, ist in vielen Teilen der Erde ein bedeutsamer Lästling. Um die weltweite Verbreitung und das Potenzial für weitere Ausbreitung zu bewerten, haben wir Nachweise von *L. humile* von > 2100 Fundorten gesammelt. Da mehrere süd- und mittelamerikanische *Linepithema*-Arten oft fälschlicherweise als *L. humile* bestimmt wurden, haben wir alle unbestätigten Nachweise aus Süd- und Mittelamerika ausgeschlossen. Wir dokumentierten die frühesten bekannten Nachweise von *L. humile* für 95 geographische Gebiete (Länder, Inselgruppen, große Inseln und US-Bundesstaaten), einschließlich einiger, für die wir keine bisher veröffentlichten Nachweise gefunden haben. Für einige süd- und mittelamerikanische Länder konnten wir keinen der veröffentlichten Berichte von Vorkommen von *L. humile* bestätigen.

Die meisten Nachweise von *L. humile* stammen aus den Subtropen, insbesondere aus Regionen mit mediterranem Klima (warm-trockene Sommer und kühl-feuchte Winter), einschließlich dem ursprünglichen Verbreitungsgebiet in Südamerika und exotische Populationen in Kalifornien, dem Mittelmeerbereich, dem südlichen Afrika, sowie in Aus-

tralien, Neuseeland und Japan. In humideren subtropischen Gebieten, wie dem Südosten der Vereinigten Staaten, dominiert *L. humile* nur selten außerhalb urbaner Bereiche. In tropischen Gebieten dominiert *L. humile* nur in Höhenlagen, mit Hawaii als prominentem Beispiel. In temperaten Gebieten ist *L. humile* fast ausschließlich ein Lästling in Gebäuden.

Linepithema humile hat bereits die meisten subtropischen Gebiete mit Tieflage und mediterranem Klima erreicht, ist aber bisher für die meisten tropischen Gebiete mit Höhenlage und geeignetem Klima nicht nachgewiesen. In der Vergangenheit hat *L. humile* tropische Regionen wahrscheinlich am Seeweg in Folge menschlicher Handelsaktivitäten erreicht und musste die Tieflandbedingungen der Küste überleben, um sich anschließend in kühlere Höhenlagen ausbreiten zu können. Heute ermöglicht die Luftfahrt *L. humile*, als blinde Passagiere in Frachtgut an nahezu jeden Punkt der Erde zu gelangen. Deshalb ist eine fortschreitende Ausbreitung des Lästlings für die Zukunft zu erwarten.

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