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Zig-zagging across Central Europe: recent range extension, dispersal speed and larval hosts of *Aproceros leucopoda* (Hymenoptera, Argidae) in Germany

Stephan M. Blank[1], Thomas Köhler[2], Toralf Pfannenstill[3], Nadine Neuenfeldt[3], Bianka Zimmer[3], Ewald Jansen[4], Andreas Taeger[1], Andrew D. Liston[1]

1 *Senckenberg Deutsches Entomologisches Institut, Eberswalder Str. 90, 15374 Müncheberg, Germany* **2** *Beuth Hochschule für Technik Berlin, Fachbereich V – Life Sciences and Technology, Luxemburger Str. 10, 13353 Berlin, Germany* **3** *Landesamt für Ländliche Entwicklung, Landwirtschaft und Flurneuordnung (LELF), Müllroser Chaussee 54, 15236 Frankfurt/Oder, Germany* **4** *Alter Marktweg 8, 04319 Leipzig, Germany*

Corresponding authors: *Stephan M. Blank* (sblank@senckenberg.de); *Andrew D. Liston* (aliston@senckenberg.de)

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Abstract

Aproceros leucopoda, the zig-zag sawfly, an invasive pest of elms (*Ulmus* spp.), was found in two separate areas of Germany through July 2014, i.e., a northern area including the states of Berlin, Brandenburg, Mecklenburg-West Pomerania, Saxony and Saxony-Anhalt, and a southern area in Bavaria. A speed of self-dispersal of 45–90 km/yr has been calculated from earlier and present records. Observations of *A. leucopoda* in Belgium and the Netherlands during 2013, which are 360–610 km distant from records in Germany of that year, are interpreted as resulting from human-mediated jump dispersal. Larvae, feeding traces and cocoons were frequently found on the native elm species *U. minor* and *U. glabra*, whereas none could be detected on *U. laevis*. Other occurrences were often on Resista® elms, causing severe defoliation in a recent planting. New host plant records for *A. leucopoda* are: *U. minor* 'Webbiana', *U. minor* var. *suberosa* , and the Resista® cultivars *U.* 'New Horizon', *U.* 'Regal' and *U.* 'Rebona'. The future dispersal of *A. leucopoda* throughout most of Germany is expected, because at least *U. glabra* and *U. minor* are widespread in this country.

Keywords

Argidae, *Aproceros leucopoda*, zig-zag sawfly, invasive species, pest species, *Ulmus laevis*, *Ulmus* Resista® hybrids, distribution in Germany, self-dispersal, human-mediated jump dispersal

Introduction

The invasive zig-zag sawfly *Aproceros leucopoda* Takeuchi, 1939, is of East Asian origin and was first found in Europe in 2003 (Blank et al. 2010). Its larvae feed on elms (*Ulmus* spp.) and sometimes severely defoliate their hosts. By 2009, the known European distribution of *A. leucopoda* extended from eastern Ukraine to Austria and from Poland to Romania. Since then, it has also been found in northern Italy (Zandigiacomo et al. 2011), Slovenia (de Groot et al. 2012), Croatia (Matošević 2012), Moldova (Timuş et al. 2008, misidentified as *Arge* sp.) and widely in European Russia from Rostov-on-Don to Moscow (Artokhin et al. 2012, Anonymous 2013). In Germany, it had been recorded only from the extreme southeast of Bavaria (Kraus et al. 2012) but not from the eastern states close to the Polish border, although the records of *A. leucopoda* from Poland made in 2003 are amongst the first from Europe. In 2013, *A. leucopoda* was observed near northwestern Germany in Belgium (Boevé 2014) and in the Netherlands (Mol and Vonk 2013).

Aproceros leucopoda is classified in the Argidae, which comprise roughly 70 species in Europe and about 900 worldwide (Taeger et al. 2006, 2010). In Europe, a few species of *Arge* have been reported to occur as pests of ornamental plants and forest trees (e.g., Pschorn-Walcher 1982, Taeger et al. 1998). Outbreaks of *Arge pullata* (Zaddach, 1859) may occur on birch trees. When the trees grow in pastures, farm livestock can be poisoned after ingestion of larvae (Brummerstedt et al. 1987, Thamsborg et al. 1987, Kannan et al. 1988, Hara and Shinohara 2008). Similar to *Aproceros leucopoda* in its association with elms as the larval hosts, is *Arge captiva* (F. Smith, 1874) (Shinohara et al. 2009). It became an invasive pest after its accidental introduction to Kazakhstan, where the larvae have severely damaged Dwarf Elm trees (*U. pumila*) planted in the new capital Astana (Blank et al. 2011).

To effect an early warning, in 2011 *A. leucopoda* was placed on the EPPO Alert List, which displays information on pest organisms that possibly represent a risk to the European and Mediterranean EPPO member countries (EPPO 2014). The Federal Research Centre for Cultivated Plants of Germany assessed the phytosanitary risk attached to this invasive species as high (Schrader and Schröder 2013). As a result of the monitoring of *A. leucopoda* in Germany, we report here on the recent range extension into large areas of Germany, map the current distribution in this country and provide new information on host plant choice. The current distribution pattern is discussed and the speed of the range extension is estimated.

Methods

Since 2009, A.D. Liston [ADL] and S.M. Blank [SMB] have paid special attention to elms in eastern Brandenburg, in the expectation that *Aproceros leucopoda* would become established in this region. Searches were made for feeding traces, larvae, cocoons and imagines (Figs 1–2). These were described and illustrated in detail by Blank et al.

(2010). Following the first observations in eastern Brandenburg in May 2013, the frequency of searches was increased and the area in Germany that was searched was extended, covering initially Br [Berlin and Brandenburg], Ni [Lower Saxony, Niedersachsen], Sn [Saxony], St [Saxony-Anhalt] (abbreviations of the German states as used in the checklist of the sawflies of Germany, Blank et al. 2001). In early October 2013, SMB checked the western distribution of *A. leucopoda* while on a round-trip through By [Bavaria], BW [Baden-Wurttemberg], He [Hesse], Ni, NW [North Rhine-Westphalia] and SH [Schleswig-Holstein]. Observations of E. Jansen [EJ] during 2012–2013 primarily covered BW, Sn and St. T. Köhler [TK] contributed observations from Br and MV [Mecklenburg-West Pomerania] in 2013–2014, T. Pfannenstill [TP] and B. Zimmer [BZ] from southern Br in 2013–2014, and A. Taeger [AT] from St in 2014. Usually, presence and absence of *A. leucopoda* on a study site was noted by ADL, EJ, SMB, TK, but only presence was recorded by AT, BZ and TP. To determine presence or absence, elms on randomly chosen sites were screened for feeding traces, larvae, cocoons or imagines from late May to early October. The time spent searching for *A. leucopoda* depended on patch size of an individual elm stand, usually varying from 2–5 minutes for small bushes to 5–10 minutes for large trees. Usually, the number of signs of *A. leucopoda* was noted for a patch, but sometimes the search was stopped as soon as a single sign was detected. ADL, BZ, SMB and TK also determined the elm species or cultivar on the study site. The nomenclature of *Ulmus* taxa follows Mackenthun (2010). Unless attributed to other recorders, the observations were made by the authors. Voucher specimens of larvae and imagines from some localities as well as extensive photographic documentation of occurrences are held at the Senckenberg Deutsches Entomologisches Institut. Statistical analysis of the observation data follows Zöfel (1988).

As a contribution towards encouragement of 'citizen science', an attempt was made to mobilize additional potential observers by placing an illustrated description of *A. leucopoda* and its distinctive feeding traces in the German popular press, with an appeal that observations be reported to the Senckenberg Deutsches Entomologisches Institut in Müncheberg (Bartel 2013). Records sent by citizen scientists as photos or herbarium vouchers were collected and re-identified by ADL and SMB.

For the outbreak area in Schlieben, Brandenburg, N. Neuenfeldt and TP assessed the density of specimens hibernating in cocoons in the ground. Samples of soil and leaf litter were taken from below three elm trees in December 2013. Each sample was from a 5–10 cm deep plot of ca 0.40 m² area. Cocoons of *A. leucopoda* were extracted from a mixed sample of ca 1.8 kg soil and litter and stored outdoors in a tent until imagines emerged.

The distribution map was prepared from a draft map produced by Carto Fauna-Flora 1.2 (Barbier and Rasmont 1996), and subsequently enhanced with Adobe Photoshop® and Corel Draw®. Countries outside Germany with records of *A. leucopoda* are labelled with the international vehicle registration codes. German states are labelled with the acronyms explained above. Distribution data for *Ulmus glabra* and *U. minor* were obtained from FLORKART (BfN and NetPhyD 2013). Free use of these data for the purpose of scientific analyses is licensed under the provisions of Creative

 Only data sets with unambiguous identifications and observation dates later than 1979 were used to display the contemporary distribution of these elms, which have disappeared in some regions of Germany since 1980.

To estimate the speed of annual range extension it seems prudent to compare a number of estimates based on different hypothetical dispersal scenarios. Based on the known records, we measured the distance, *A*, between the earliest records from Hungary and Poland (Blank et al. 2010) and the most distant observation sites in Germany; *B*, between the closest neighbouring sites, where *A. leucopoda* was recorded within the period of a few years; *C*, the minimum and maximum distances between the records in Belgium (Boevé 2014) and the Netherlands (Mol and Vonk 2013) and the closest observation sites in Germany known in 2013. The annual dispersal speed was calculated from these distances and the related years of observation.

Results

Distribution of *A. leucopoda* in Germany

Through mid-July 2014 *Aproceros leucopoda* was recorded from the easterly German federal states of Berlin (recorded from 8 study sites), Brandenburg (39), Mecklenburg-West Pomerania (1), Saxony (5) and Saxony-Anhalt (2) and also from southeast Bavaria (5). These numbers also include data published by Kraus et al. (2012) and Sobczyk and Nuss (2014). At most localities, the presence of *A. leucopoda* was revealed by the conspicuous 'zig-zag' feeding traces (Fig. 1) made by the young larvae. However, older larvae or cocoons also drew attention to its presence, particularly later in the year. Only very few imagines were observed in the field, although several were reared from cocoons collected from the undersides of elm leaves.

The data on the presence and absence of *A. leucopoda* throughout Germany and in the neighbouring countries are mapped in Fig. 3. *Aproceros leucopoda* was not found on 140 study sites, which are distributed in the above mentioned as well as in more western federal states of Germany (Fig. 3, blue crosses). The record by Pimpl (2014) for the Erzgebirge in Saxony is based on a misidentification of *Cladius rufipes* Serville, 1823 (Tenthredinidae, re-identification by SMB). Currently, the following additional records for Germany exist (sorted by federal state and 'Landkreis', a subdivision of a German federal state):

Bavaria: Landkreis Deggendorf: Niederalteich NW 3 km, rest area 'Seebach' on highway A3, 48.788°N, 13.011°E, 315 m alt., 07.08.2013, 3 larvae and feeding traces, *Ulmus* sp. Landkreis Freyung-Grafenau: Irlesberg S 700 m, along federal highway B12, 48.720°N, 13.531°E, 425 m alt., 07.08.2013, 1 larva and feeding traces, *U. minor*. Landkreis Regensburg: Wörth SE, rest area 'Tiefenthal' on highway A3, 48.993°N, 12.420°E, 335 m alt., 07.08.2013, 1 larva and 5 feeding traces, *U.* sp.

Berlin: Friedrichshagen, environs of S-train station, 52.456°N, 13.625°E, 20.05.2013, numerous, partly late instar larvae, *U. glabra*; Kreuzberg, Columbiadamm,

Figure 1. Feeding traces, with young larvae of *Aproceros leucopoda*, on leaf of *Ulmus minor*, Forstbotanischer Garten in Eberswalde (Brandenburg). Photo: SDEI/Liston.

52.483°N, 13.401°E, 29.8.2013, feeding traces, *U.* 'New Horizon' (planted in 2007–2009); Lichterfelde, Botanic Garden, Arboretum, 52.453°N, 13.305°E, 24.07.2013, feeding traces, *U. davidiana* var. *japonica*, *U. minor* 'Webbiana' and *U.* sp. (not *U. laevis*); Lichterfelde, Botanic Garden, Balkan section, 52.453°N, 13.305°E, 24.07.2013, feeding traces, *U. minor* 'suberosa'; Pankow, Märchenweg, along Fließgraben, 52.576°N, 13.475°E, 10.08.2013, 1 feeding trace, *U. minor*; Pankow, Treskowstraße, 52.561°N, 13.429°E, 11.08.2013, 2 feeding traces, *U.* 'Rebona'; Wedding, intersection of Tegeler Straße and Lynarstraße, 52.540°N, 13.358°E, 24.07.2013, feeding traces, *U. pumila* var. *arborea*; Wedding, Utrechter Straße, 52.548°N, 13.355°E, 14.8.2013, feeding traces, *U. pumila* var. *arborea*.

Brandenburg: Landkreis Barnim: Biesenthal ESE, Grüntal, Feldgehölz, 52.740°N, 13.728°E, 16.07.2013, feeding traces, *U. minor*; Eberswalde, Forstbotanischer Garten, 52.825°N, 13.791°E, 30 m alt., 23.06.2013, 30 larvae, *U. minor*. Landkreis Dahme-Spreewald: Brusendorf NW, rest area 'Am Fichtenplan' on highway A10, 52.315°N, 13.497°E, 50 m alt., 07.08.2013, 3 feeding traces, *Ulmus* cultivar with smooth leaves, slender crown form. Landkreis Elbe-Elster: Kolochau, federal highway B87 in direction of Herzberg, 51.716°N, 13.281°E, 27.08.2013, numerous larvae, feeding traces and cocoons, massive infestation, *U.* 'Resista' cultivar; Schlieben in direction of Herzberg, bicycle path from Kolochau for 3 km length, 51.727°N, 13.312°E, 29.07.2013, 3 reared ♀, numerous

larvae, feeding traces and cocoons, massive infestation, *U.* 'New Horizon'. Stadtkreis Frankfurt/Oder: Frankfurt/Oder, Leipziger Straße, Südring Center, 52.328°N, 14.521°E, 05.09.2013, 2 cocoons and feeding traces, 1–5% damage observed on 39 of ca 100 *U.* 'Resista' trees. Landkreis Havelland: Märkisch Luch SW, 52.560°N, 12.602°E, 30 m alt., 10.08.2013, 1 eonymph, *U.* cultivar planted as alley along street; Tremmen, 52.533°N, 12.8167°E, 06.09.2013, weak infestation on *U.* 'New Horizon' (planted 2010) and *U.* 'Rebona' (planted 2009). Landkreis Märkisch-Oderland: Gabow N, 52.820°N, 14.071°E, 14.07.2013, 4 larvae, *U. minor*; Hoppegarten E, Berliner Chaussee, 52.496°N, 14.058°E, 20.05.2013, 15 leaves with feeding traces, 10 early instar larvae, *U. glabra*; Jahnsfelde, 52.507°N, 14.228°E, 19.05.2013, 6 leaves with feeding traces, 3 early instar larvae, *U. glabra*; Müncheberg, car-park of Netto supermarket, 52.506°N, 14.133°E, 18.07.2013, feeding traces, *U.* cultivar ('Columella'?); Müncheberg, railway station, 52.524°N, 14.102°E, 04.07.2013, 3 feeding traces, *U. glabra*; Müncheberg, Waschbanksee, 52.502°N, 14.139°E, 14.07.2013, 5 feeding traces, cultivated *U.* cultivar ('Sapporo Autumn Gold', 'New Horizon' or 'Rebona'?); same site, 15.07.2013, 2 larvae, cultivated *U.* sp.; Müncheberg, ZALF campus, 52.515°N, 14.115°E, 07.06.2013, 1♀ swept from *U. glabra*; same site, 04.07.2013, 2 larvae, *U. glabra*; same site, 20.06.2014, 4 larvae, *U. glabra*; Podelzig, entrance of road to railway station, 52.482°N, 14.538°E, 30.07.2013, 10 feeding traces, *U. minor*; Steinhöfel, alley, 52.400°N, 14.167°E, 30.08.2013, feeding traces, *U.* 'Resista' (planted ca 2008); Waldsieversdorf 2 km SW, road in direction of Rotes Luch, 52.523°N, 14.039°E, 14.08.2013, 1 feeding trace, *U. glabra*. Landkreis Oberhavel: Borgsdorf, S of church, 52.704°N, 13.248°E, 25.06.2014, feeding traces, *U. minor*; Borgsdorf, W of quarry pond, 52.704°N, 13.226°E, 25.06.2014, *U. glabra*; Liebenberg, Fichten, rest area of federal highway B167, 52.890°N, 13.267°E, 14.07.2013, 1 feeding trace, *U. glabra*; Oranienburg, Berliner Straße, 52.723°N, 13.250°E, 26.07.2013, feeding traces, *U. glabra*; Oranienburg, Berliner Straße, in front of Poliklinik, 52.742°N, 13.239°E, 23.07.2013, feeding traces, *U.* 'New Horizon'; Oranienburg, Holbeinstraße, 52.725°N, 13.248°E, 20.07.2013, 3 leaves with feeding traces, *U. minor* (2 m high shoots growing from roots); Oranienburg, Idenstraße, 52.771°N, 13.249°E, 23.07.2013, larva and several feeding traces, *U.* 'Regal'; Zehlendorf, W and S of clay pit, 52.799°N, 13.380°E, 20.07.2013, 1 cocoon, *U. minor* (*U. glabra* and *U. laevis* growing nearby not infested). Landkreis Oberspreewald-Lausitz: Calau SW 6 km, rest area on highway A13, 51.700°N, 13.899°E, 135 m alt., 01.08.2013, feeding traces, two *Ulmus* cultivars (possibly sorts of Resista due to the narrowly cone-shaped crown). Landkreis Oder-Spree: Beeskow, alley, 52.174°N, 14.247°E, 30.08.2013, feeding traces, *U.* 'Resista' (planted 2007); Fangschleuse, S of railway station, 52.402°N, 13.825°E, 20.05.2013, 2 leaves with feeding traces, *U. glabra*; Kagel, along road L 323, 52.467°N, 13.917°E, 04.09.2013, 2 young larvae and feeding traces, *U.* 'Resista' (planted 2010). Landkreis Teltow-Fläming: Ahrensdorf near Ludwigsfelde, 52.317°N, 13.200°E, 01.10.2013, feeding traces, *U.* 'Rebona', observed by K. Langner; Ahrensdorf, alley along street K 7220, 52.195°N, 13.172°E, 02.09.2013, heavy infestation, of 22 *Ulmus* trees (planted ca 2008), late instar larvae still present on 01.10.; Blankenfelde SW 4 km, rest area on highway A10, 52.308°N, 13.369°E, 30.06.2013, 4 feeding traces of early instar larvae, *U. glabra*; Dahlewitz, Friedhofsweg, 52.319°N, 13.436°E, 7.9.2013, feeding traces

on 2 leaves, *U. minor*; Löwendorf, Märtensmühle, 52.204°N, 13.184°E, 27.08.2013, larvae and feeding traces, *U.* sp.; Zossen-Neuhof, Cottbuser Straße, 52.144°N, 13.479°E, 29.08.2013, 2 feeding traces, *U.* sp. Landkreis Uckermark: Prenzlau, Seelübber Weg, 53.299°N, 13.879°E, 11.08.2013, 3 feeding traces, *U. glabra*; Schönermark, railway station, 53.106°N, 14.033°E, 11.08.2013, 2 feeding traces, *U. glabra*.

Mecklenburg-West Pomerania: Landkreis Mecklenburgische Seenplatte: Neustrelitz, intersection of Strelitzer Straße and Bürgerhorststraße, 53.357°N, 13.072°E, 27.08.2013, feeding traces, *U.* 'New Horizon'.

Saxony: Landkreis Leipzig: Leipzig, Leipziger Auen, Weiße Brücke, 51.303°N, 12.356°E, 125 m alt., 27.06.2014, 2 feeding traces, *U.* sp.; Leipzig-Rückmarsdorf, Bienitz, 51.353°N, 12.252°E, 120 m alt., 22.06.2014, 3 feeding traces, *U.* sp. Landkreis Meißen: Wildberg, 51.100°N, 13.588°E, 120 m alt., 01.08.2013, 2 larvae, *U.* sp. (*glabra* or *minor*). Landkreis Nordsachsen: Kathewitz, nature reserve 'Alte Elbe Kathewitz', 51.516°N, 13.111°E, 85 m alt., 22.07.2014, more than 50 *Ulmus* controlled, but only 2 feeding traces of early instar larvae found; Schkeuditz, nature reserve 'Luppeaue', 51.381°N, 12.252°E, 100 m alt, 13.06.2014, 1♀ and 2 feeding traces, *U.* sp.

Saxony-Anhalt: Landkreis Aschersleben-Staßfurt: Westeregeln, 51.960°N, 11.386°E, 06.07.2014, feeding traces, *U.* sp. Landkreis Saalkreis: Sietzsch E, rest area 'Kapellenberg' on highway A9, 51.492°N, 12.204°E, 110 m alt., 07.08.2013, 2 feeding traces, *U. minor*.

The altitudinal range of the 66 study sites in Germany where *A. leucopoda* was observed, varies from 20–425 m above sea level (elevation determined using Google Earth where no original data were available). 51 observations were made below 100 m altitude. These comprise most of the data from Berlin, Brandenburg, Mecklenburg-West Pomerania and Saxony-Anhalt. All five records from Bavaria were at over 300 m altitude. In Austria, *A. leucopoda* was found between 160–580 m altitude (Blank et al. 2010; E. Altenhofer, unpublished data).

The press release by Senckenberg, requesting observations of *A. leucopoda* from citizen scientists (Bartel 2013), was published in more than 300 print and online media primarily in Germany, but also in neighbouring German-speaking countries. During the following months, 23 persons responded by contacting ADL and SMB. Observations by three persons (among them TK and TP) were actually of *A. leucopoda*, whereas those of 20 persons related to other insects, plant species other than elms, or were ambiguous. As a result of the press release we were able to include 17 additional sites in this study, including the report of the severe outbreak in Schlieben and the most northern occurrence in Mecklenburg-West Pomerania, together with observations made on 13 elm species and cultivars, of which five were previously unrecorded as hosts.

Infestation of elm species and cultivars

At several localities all three *Ulmus* species which are autochthonous to Germany were present. Where *A. leucopoda* was found at such places, it was more abundant on *U. minor*

Table 1. Infestation of elm species, varieties and cultivars by *Aproceros leucopoda*: Number of study sites in Germany with [+] or without [–] larvae, larval feeding traces or cocoons attached to the tree. Observations from 2011–2014. Only unambiguously identified elm species, varieties and cultivars are listed. The cultivars 'New Horizon', 'Rebona' and 'Regal' belong to the 'Resista' series.

Species or sort of elm	+	–
Ulmus crassifolia		1
Ulmus davidiana var. *japonica*	1	
Ulmus glabra	12	36
Ulmus glabra 'Pendula'		1
Ulmus × *hollandica*		1
Ulmus laevis		21
Ulmus lamellosa		1
Ulmus minor	11	8
Ulmus minor var. *suberosa*	1	
Ulmus minor 'Webbiana'	1	
Ulmus minor 'Wredei'		1
Ulmus multinervis		1
Ulmus 'New Horizon'	5	
Ulmus parvifolia		1
Ulmus pumila var. *arborea*	2	2
Ulmus 'Rebona'	2	
Ulmus 'Regal'	1	2
Ulmus 'Resista'	6	2

than on *U. glabra*. Also the total number of observation sites with infestations on *U. minor* is significantly higher than that on *U. glabra* (chi-squared test, n = 71 records including varieties and cultivars [Table 1], $\chi^2 = 7.79$, $p < 0{,}01$). Despite careful searches of *U. laevis*, no feeding traces or larvae were found. A very few feeding traces were seen on a single elm labelled "*U. laevis*" in Berlin Botanic Garden growing near other specimens under the same name which bore no traces. However, the tree with the feeding traces possessed some characters which are not typical for *U. laevis*, so there is doubt about its identity.

Aproceros leucopoda was found on several occasions feeding on Resista® elms. These cultivars have not previously been recorded as hosts. No clear pattern of difference in abundance of *A. leucopoda* was observed amongst these cultivars, of which three were identified as *U.* 'New Horizon', *U.* 'Regal' and *U.* 'Rebona'. *Ulmus minor* 'Webbiana' and *U. minor* var. *suberosa* were recorded as new hosts for *A. leucopoda*, and *U. davidiana* var. *japonica* (previous records only from Japan) and *U. pumila* var. *arborea* (previous records only from Hungary) were confirmed as hosts (Table 1). No signs of feeding were found on *U. crassifolia*, *U. glabra* 'Pendula', *U. lamellosa*, *U.* × *hollandica*, *U. multinervis* and *U. parvifolia*, nor on *Zelkova* species (Ulmaceae) partly growing close to *Ulmus*.

At most localities, comparatively low population levels were found, with insignificant damage to the hosts. Elms at such localities were at the edges of woodland or within areas of human settlement, i.e., in more or less sheltered positions. Serious

Figure 2. Feeding damage caused by *Aproceros leucopoda* on planted *Ulmus* 'Resista' during an outbreak between Schlieben and Kolochau (Brandenburg). Photo: LELF/Pfannenstill.

defoliation has so far been recorded in Germany only at Schlieben (Brandenburg, Landkreis Elbe-Elster). Surrounded by open agricultural areas, 235 trees of *U.* 'New Horizon' were planted here as a three kilometre long avenue along a road and a bicycle path in 2012. The trees originated from a nursery in the state of Schleswig-Holstein. *Aproceros leucopoda* could neither be observed in this particular nursery (A. Frers, personal communication) nor at other sites in this state. This outbreak was first detected in 2013 but the infestation was much less severe in 2014. In 2013, damage was unevenly distributed within the plantation. Many trees suffered severe damage, ranging from partial defoliation of twigs to defoliation of most of the crown (Fig. 2). 35 solid-walled

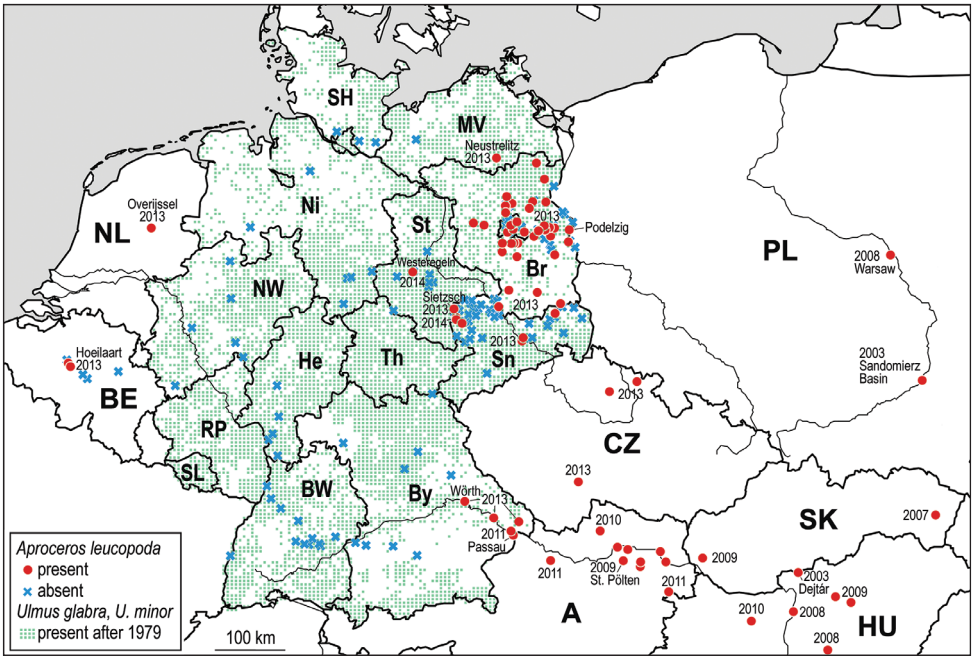

Figure 3. Distribution of *Aproceros leucopoda* in Germany, through 15.07.2014. Modified from Blank et al. (2009), including additional data for Austria (own data, Kraus et al. 2011), Belgium (Boevé 2013), the Czech Republic (own data, Jurášková et al. 2014), Germany (own data, Kraus et al. 2012, Pimpl 2014, Sobczyk and Nuss 2014), Hungary (Haris 2010) and the Netherlands (Mol and Vonk 2013). Distribution of *Ulmus glabra* and *U. minor* in Germany after BfN and NetPhyD (2013). German states are labelled with the abbreviations used in the checklist of the sawflies of Germany (Blank et al. 2001): Br – Brandenburg and Berlin, By – Bavaria, BW – Baden-Wurttemberg, He – Hesse, MV – Mecklenburg-West Pomerania, Ni – Lower Saxony (Niedersachsen), NW – North Rhine-Westphalia, RP – Rhineland-Palatinate, SH – Schleswig-Holstein, SL – Saarland, Sn – Saxony, St – Saxony-Anhalt, Th – Thuringia. Countries outside Germany where *A. leucopoda* is recorded are labelled with the international vehicle registration codes. Graphics: SDEI/Blank.

cocoons were separated from a mixed sample of soil and litter taken from below three elm trees. A density of ca 29 cocoons/m² for overwintering specimens is calculated for this outbreak site. In spring 2014, eight females emerged between April 8–25 under outdoor conditions. A less severe outbreak occurred in Frankfurt/Oder (Brandenburg) in 2013, where 1–5% defoliation was observed on 39 of ca 100 *U.* 'Resista' trees.

Dispersal distances and invasion speed of *Aproceros leucopoda*

In Europe *A. leucopoda* was first found in 2003 in the Sandomierz Basin of southeastern Poland and in Dejtár, northern Hungary (Blank et al. 2010). The following estimates of the invasion speed are based on the distances between presumed sources of subsequent

dispersal represented by the earliest recorded Hungarian and Polish localities and the sites most distant from these where *A. leucopoda* has been observed in Germany:

- Sandomierz Basin (2003) to the most western recorded site, Westeregeln in Saxony-Anhalt (2014): distance 740 km, invasion speed ca 70 km/yr;
- Sandomierz Basin (2003) to the most northern recorded site, Neustrelitz in Mecklenburg-West Pomerania (2013): distance 660 km, invasion speed ca 65 km/yr;
- Dejtár (2003) to the most southeastern recorded site, Passau in Bavaria (2011) (Kraus et al. 2012): distance 440 km, invasion speed ca 55 km/yr.

In the following cases the annual speed of invasion is calculated from the distance between the closest neighbouring sites, where *A. leucopoda* was recorded only a few years later:

- Warsaw in Poland (2008) (Blank et al. 2010) to the closest recorded German site, Podelzig in eastern Brandenburg (2013): distance 450 km, invasion speed ca 90 km/yr;
- St. Pölten in Austria (2009) (Blank et al. 2010) to the most southeastern recorded German site, Passau in Bavaria (2011): distance 170 km, invasion speed ca 85 km/yr;
- from the most southern recorded Bavarian site near Passau (2011) to the most northern recorded Bavarian site, near Wörth (2013): distance 90 km, invasion speed ca 45 km/yr.

In 2013 *A. leucopoda* was observed for the first time in Belgium (Boevé 2014) and the Netherlands (Mol and Vonk 2013). The following are the minimum and maximum distances between these sites and the closest German records known in 2013:

- Overijssel in the Netherlands to Sietzsch in Saxony-Anhalt, Germany: 360 km;
- Hoeilaart in Belgium to Wörth in Bavaria, Germany: 610 km.

Discussion and conclusions

Among the native elm species of Germany, *Aproceros leucopoda* clearly prefers *Ulmus glabra* and *U. minor* as larval hosts (Table 1), since no feeding has been observed on *U. laevis*. On a mixed stand of all three elm species in Lower Austria (Traismauer), *U. laevis* showed a very low infestation even during an outbreak of *A. leucopoda* (E. Altenhofer, personal observation). A number of additional elm species and cultivars must now be considered to be larval hosts. These were introduced to Germany as ornamental trees in horticulture, for afforestation, or planted in botanical gardens for scientific purposes. Feeding could not so far be observed on seven of the taxa listed in Table 1. However, in these cases, it would be premature to conclude that they are not potential hosts, because each of these species and cultivars was studied at only a single site.

Some of the Resista® hybrid elms now prove to be suitable hosts. These cultivars, of complex hybrid parentage, were created to meet the demand for elms which are resistant to the fungal diseases commonly referred to collectively as "Dutch elm disease". *Ulmus* 'New Horizon' and *U.* 'Regal' are at present respectively the most often and the second most often planted elms of this sort in Germany (Mackenthun 2010). They are usually planted in settings where they are highly visible to the public, such as along roads and in city parks. Aside from possible effects on the health of the affected trees, defoliation by *A. leucopoda* will impair their aesthetic value. That 'New Horizon' and 'Regal' are acceptable hosts to *A. leucopoda* is not surprising, because *U. pumila* and *U. japonica* figure prominently in the parentage of both (Mackenthun 2010). *Ulmus pumila* is known to be highly susceptible to attack by *A. leucopoda* (e.g., Wu 2006, Blank et al. 2010, Cao et al. 2011), whilst *U. japonica* is a known host in Japan (Blank et al. 2010) and recorded here for the first time as a host in Europe.

The range of *A. leucopoda* in Germany currently comprises two separate areas (Fig. 3). The northern one extends from southern Mecklenburg-West Pomerania in the north to central Saxony in the south and from central Saxony-Anhalt in the west to the Polish border in the east. The second, southern area covers part of southeast Bavaria. These two large areas of occurrence do not at present appear to be confluent. The distribution of *U. glabra*, one of the two preferred native elm species, covers the low mountain ranges of central Germany (BfN and NetPhyD 2013). Although autochthonous *U. glabra* and *U. minor* have disappeared in several regions (BfN and NetPhyD 2013), their combined, largely continuous distribution throughout Germany (Fig. 3) provides the opportunity for *A. leucopoda* to spread further into more westerly parts of the country.

The northern distribution area of *A. leucopoda* in Germany is mostly within the North German Plain, which in the south is delimited by the low mountain ranges of central Germany. Judging from available distribution data (Blank et al. 2010, Mol and Vonk 2013, Boevé 2014, Sobczyk and Nuss 2014, Juraskova et al. 2014, present data), *A. leucopoda* has been recorded only rarely above 400 m altitude in central Europe. From Austria into Bavaria, *A. leucopoda* has spread along the valley of the river Danube, where *A. leucopoda* was found at a maximum altitude of 580 m near Zwettel, Lower Austria (E. Altenhofer, personal communication). The Alps to the south and the Bohemian Massif to the north of the valley possibly work as barriers. Future observations may reveal whether the low mountain ranges of central Germany will slow down or restrict the dispersal of *A. leucopoda*, despite the general presence there of at least *U. glabra*.

Apart from range expansion through self-dispersal of imagines, it seems likely that individuals can sometimes be accidentally transported by human agency over much greater distances with road, rail, air and canal traffic (Blank et al. 2010). Trade by nurseries of infested plants throughout a wide geographic area might also have a significant impact, but we could not observe such an event involving *A. leucopoda*. The occurrences in Belgium (Boevé 2014) and in the Netherlands (Mol and Vonk 2013) seem likely to belong in the category of human-mediated jump dispersal (Suarez et al.

2001), because the gap of 360–610 km between these western records and the records in eastern Germany was unsuccessfully searched by us for signs of *A. leucopoda* in 2012 and 2013 (Fig. 3). Contrarily, the two observed distribution areas in Bavaria and in the northeastern German states should be explained by self-dispersal of *A. leucopoda* originating from the neighbouring countries Austria, Poland and possibly the Czech Republic, although human-mediated jump dispersal cannot be ruled out as a component within self-dispersal. Records made during consecutive years in Austria indicate a stepwise spread in a westerly direction (Fig. 3). Although comparable data from western Poland are missing, we suppose that self-dispersal also took place here, because the speeds of annual dispersal calculated from the distance between the Polish and the eastern German records (65–90 km/yr) are similar to speeds calculated from Austrian, Hungarian and Bavarian records (45–85 km/yr). The common distribution area of the preferred native larval hosts, *U. glabra* and *U. minor*, is more or less continuous from Germany to Hungary and to Poland (Meusel et al. 1965, BfN and NetPhyD 2013), which has facilitated the self-dispersal of *A. leucopoda* in a westerly direction.

The 2013 observations from southeastern Bavaria indicate an apparently limited speed of range extension (45 km/yr) in that area since *A. leucopoda* was first recorded near Passau in 2011 (Kraus et al. 2012), although the total of study sites in Bavaria is comparatively low. Contrastingly, range expansion into northeastern Germany seems to have been both more rapid and extensive. At the majority of German localities, a low number of feeding traces made by young larvae were often the only signs that the species was present, perhaps indicating that colonisation had recently taken place. The inconspicuous damage may also have been a reason for the low number of replies by citizen scientists in response to our press release in 2013 (Bartel 2013). If the spread of *A. leucopoda* into eastern Germany is nevertheless assumed to have depended purely on natural dispersal of imagines, the distance (ca 220 km) between the most westerly recorded locality (Westeregeln) and the Polish border (Podelzig) indicates that the first female may already have arrived in northeastern Germany two to five years before 2013.

Very little is known about the dispersal ability of sawflies and horntails (Hymenoptera 'Symphyta') in general, or the time scales and distances associated with the spread of individual species undergoing range expansion. The speed of annual range expansion resulting from self-dispersal of 45–90 km/yr estimated here for *A. leucopoda* lies within the range known for a few sawflies and for other insects. *Nematus oligospilus* Förster, 1854 (Tenthredinidae), a sawfly species invasive to New Zealand with larvae feeding on willow, extended its range through the North Island at 300 km/yr (Charles and Allan 2000; ca 165 km/yr measured as a straight line). In South America Ovruski and Fidalgo (1991) observed a range expansion of 300 km/yr also for *N. desantisi* D.R. Smith, 1983, which might be conspecific with *N. oligospilus* from New Zealand (Koch and Smith 2000). Ovruski and Fidalgo (1991) supposed passive transport to be a possible component of the dispersal. *Gilpinia hercyniae* (Hartig, 1837) (Diprionidae) is invasive to the Nearctic, where its larvae damage spruce trees (*Picea* spp.). The speed of range expansion in Canada is given as 50 km/yr (CABI 2014). The average speed for *Sirex noctilio* Fabricius, 1793 (Siricidae), a woodwasp invasive in South America, has

been estimated as 30–50 km/yr (Yemshanov et al. 2009). Smith (1996) summarized distribution data for the invasive Asian woodwasp *Eriotremex formosanus* (Matsumura, 1912), which in the United States was first observed in southern Georgia and in northern Florida in 1974. *E. formosana* was found 15 years later in southeastern Virginia, about 740 km distant from these earliest sites (ca 50 km/yr) and 16 years later in eastern Texas, 990 km distant (ca 60 km/yr). However, *S. noctilio* and *E. formosanus* differ greatly from the *Aproceros*, *Gilpinia* and *Nematus* species in several ways, e.g., in the large body and the larval feeding habit inside solid wood. *Sirex noctilio* reproduces sexually and usually produces at most one generation per year (Eichhorn 1982), whereas *E. formosanus* is apparently parthenogenetic in the US and supposedly has two generations per year, based on phenological data (Smith 1996). Compared to the range expansion of 30–60 km/yr resulting from self-dispersal of these woodwasps, not even the highest estimated speed of 90 km/yr for *A. leucopoda* seems excessive, because several life traits of *A. leucopoda* promote rapid dispersal: it reproduces parthenogenetically, has up to four generations per year, and the larvae are external feeders on leaves (Blank et al. 2010), which appear more nutritious than wood infested by fungi. Among insects other than Hymenoptera, Brown et al. (2008) calculated an invasion speed of 58–145 km/yr for *Harmonia axyridis* (Pallas, 1771) (Coleoptera, Coccinellidae) in Europe. The considerably higher speed of 500 km/yr estimated for this species in South Africa (Stals 2010) probably includes jump-dispersal events. The speed of range expansion in *Cameraria ohridella* Deschka & Dimić, 1986 (Lepidoptera, Gracilariidae) in central and western Europe was estimated to be 60–70 km/yr based on the dates of first observations in European countries (Šerfová and Laštůvka 2001), although these authors also cite much lower speeds for other moths. For *C. ohridella* both active dispersal and passive transport by wind and man were considered to play a role.

The rapid range expansion of *A. leucopoda* throughout Europe predicted by Blank et al. (2010) is evidently taking place, and likely to progress. Although occurrences in Germany have so far seldom resulted in severe defoliation, this may only be because population levels still have not peaked. The considerable differences in climate between the European territories which it has already colonised, together with the altitudinal range inhabited by the species, suggest that it should easily be able to spread through most of Europe where elms grow (Meusel et al. 1965). Whether it is possible in the long-term to exclude it from territories such as the British Isles or Scandinavia, which may be adequately protected by the sea from self-dispersal events, remains to be seen.

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