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Allolobophoridella eiseni (Lumbricidae), a truly arboreal earthworm in the temperate region of Central Europe

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Abstract

In a long-term survey of the Strict Forest Reserves in Hesse (Central Germany) a faunistic inventory was conducted using a wide range of traps and hand sampling over a period of two years. Five of the six sites are beech forest types (dominating: *Fagus sylvatica*), and one is a floodplain oak forest (dominating: *Quercus robur*). Although no special research program was run for the earthworms, pitfall traps and eclectors at tree trunks and logs provided an unexpectedly high number (9 to 13) of species of earthworms. A comparison of data from pitfall traps and trunk eclectors shows that highly different sets of lumbricids do occur in both types. In the pitfall traps *Lumbricus rubellus* (22–43 % of adults) and *Dendrobaena octaedra* (10–16 % of adults) were dominant. In the trunk eclectors the community consisted mainly (60–83 %) of *Allolobophoridella eiseni*. In addition, *Dendrodrilus rubidus* (3–25 %) and *Dendrobaena octaedra* (6–16 %) were regularly found in these eclectors. Based on our findings *Allolobophoridella eiseni* is a regular element of the invertebrate fauna of forests, occurring both in decaying logs and predominantly at the bark of living and dead trees. Therefore, this species can be classified as predominantly corticolous. For the first time it could be proven that *Allolobophoridella eiseni* regularly climbs on trees, which it does surprisingly mainly in late-autumn and in the winter.

Keywords Corticolous | *Fagus sylvatica* | Germany | pitfall traps | Strict Forest Reserves | trunk eclectors

1. Introduction

In 1990 the Government of Hesse (Germany), in cooperation with the Senckenberg Institute, started a long-term survey of the fauna in Strict Forest Reserves (= Naturwaldreservate) of Hesse; these are forest areas that are allowed to mature without direct human influence. In order to achieve a complete-as-possible faunal inventory, many different sampling methods were applied (Dorow et al. 1992), among them pitfall traps and eclectors at standing and lying trees. Surprisingly, with these two methods a high number of earthworm species and individuals were collected, the dominant species being *Allolobophoridella eiseni* (Levinsen, 1884).

Allolobophoridella eiseni is widespread in western (including the United Kingdom), central and south-eastern Europe, north-western Africa (Omodeo et al. 2003), several Atlantic islands, four states of the USA (Arkansas, Oregon, Tennessee, Washington) (Reynolds 1995), New Zealand, Tasmania and South Africa (Sims & Gerard 1999, Blakemore 2008). Csuzdi & Zicsi (2003) classified it as a peregrine species with Atlantic origin.

Among the lumbricid earthworms of Central Europe, *Allolobophoridella eiseni* (Levinsen, 1884) is peculiar for various reasons. Firstly, its generic affiliation has been highly controversial. Originally described as *Lumbricus eiseni* (Levinsen 1884), it was later placed at certain times in *Allolobophora*, *Bimastus/Bimastos*, *Dendrobaena*, *Eisenia* and *Helodrilus* (in alphabetical order, for details see Csuzdi & Zicsi 2003). Finally, Mršić (1990) erected the new genus *Allolobophoridella* and designated *Lumbricus eiseni* as its type species.

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Secondly, and despite the fact that it has been found all over Germany (Lehmitz et al. 2014), it is rarely found when using the most common and already standardized methods to sample earthworms, i.e. hand-sorting of soil samples or extraction of earthworms from deeper soil layers by using chemicals such as formalin (ISO 2006). Graff (1953) and Bouché (1972) considered it a rare species in Germany and France, respectively. The classification as 'moderately common' and 'not endangered' in Germany (Lehmitz et al. 2016) is partly based on the data presented here.

And thirdly, the ecology of this species differs from that of almost all other earthworm species in Europe, since it does not prefer soil but aboveground habitats – a preference well-known from some tropical earthworms (e.g. Lee 1985, Fragoso & Rojas-Fragoso 1996), which are regularly found on trees, often in bromeliad rosettes, filled with canopy debris (Richardson et al. 2006), i.e. mineral particles and decaying organic matter.

Traditionally earthworms are classified into three ecological types (1) mineral dwellers (endogeics = endogées), (2) litter dwellers (epigeics = épigées) and (3) species living in vertical burrows (anecic = anéciques). This concept was developed independently by Lee (1959) and Bouché (1971), working on Pacific Islands and in France, respectively. Furthermore, Lee (1959) realized that a minority of earthworm species does not live in soil but actually aboveground, on or in trees; for these 'arboreal' species he erected further groups: species (1) living under the bark of standing trees or fallen logs, (2) living in rotting logs and (3) living at the bases of epiphytes and in leaf axils of understorey forest trees (for a summary see Lee 1985). Bouché (1972) made similar observations and defined – among others – one subgroup of epigeic earthworms as 'corticoles', i.e. those living below the bark of trees. In fact, he already mentioned *Allolobophoridella eiseni* (sub *Lumbricus*) as a typical example of this group. The concept of three ecological groups of earthworms became widely accepted, and further differences were conceptualized as subgroups, especially when referring to the tropics (Lavelle 1984): endogeics were subdivided based on feeding differences and epigeics were subdivided based on their vertical distribution. For those epigeic species living under the bark of trees or on trees the terms corticolous and arboreal are used (e.g. Lee 1985, Sims & Gerard 1999). However, both terms are often used interchangeable.

Based on the data presented in the present contribution, Lehmitz et al. (2014) classified *Allolobophoridella eiseni* (Levinsen, 1884) as being corticolous, but with the note 'often under bark of deadwood'. Only one further species – out of 46 in Germany – was classified in a similar way; this species, *Eisenia lucens* (Waga, 1857), seems to prefer 'fallen logs under bark'.

Here we present a comparison of the numbers and percentages of earthworms found in pitfall traps and eclectors at standing and lying trees in six Strict Forest Reserve sites of the federal state of Hesse. Even though abundances cannot be calculated, these data clearly show that *A. eiseni* is (1) a truly arboreal species and (2) more common in Germany than previously assumed.

2. Materials and methods

The data presented here were gained in six Strict Forest Reserves and their adjacent managed sites in Hesse, central Germany (Fig. 1). Five of the six sites are beech forests (dominating: *Fagus sylvatica*) in low mountain ranges, and one (Kinzigaue) is a lowland floodplain oak forest (dominating: *Quercus robur*) located in a flooding area of a brook.

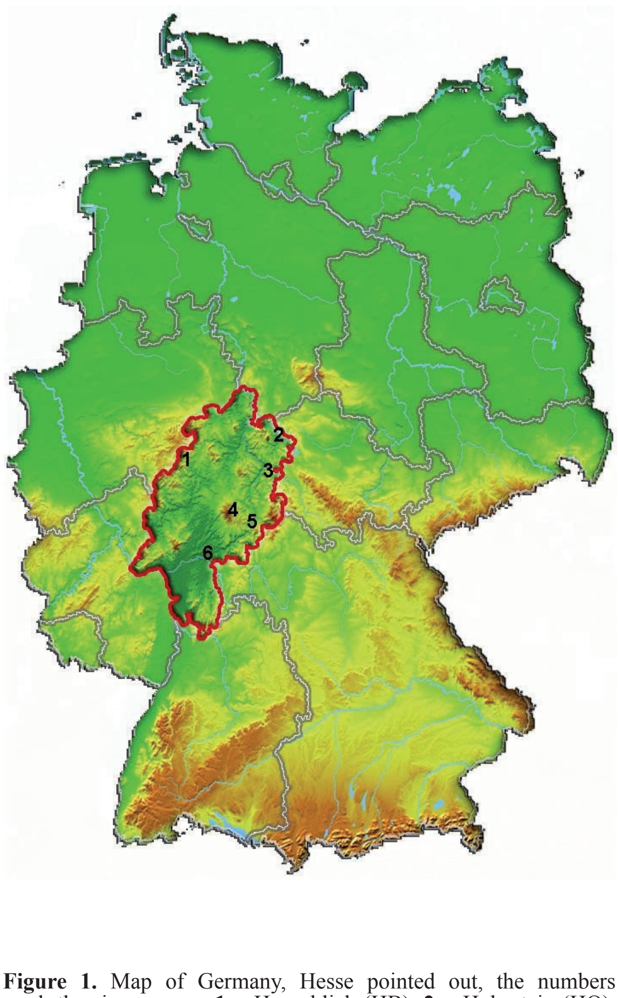

Figure 1. Map of Germany, Hesse pointed out, the numbers mark the six reserves: **1** = Hasenblick (HB), **2** = Hohestein (HO), **3** = Goldbachs- und Ziebachsrück (GZ), **4** = Niddahänge (NI), **5** = Schönbuche (SB), **6** = Kinzigaue (KI).

The fauna of the six Strict Forest Reserves and five adjacent managed sites in Hesse, Germany, was investigated over a period of two years (24 months) each, using diverse techniques: pitfall traps; different types of trunk eclectors on standing, lying, dead and living tree trunks, stumps, dead branches; blue, white and yellow pans; window traps. For details of the research concept see Dorow et al. (1992). Table 1 shows the numbers of trunk eclectors and pitfall traps in the reserves. Details on the study areas – beech forests in colline areas (300-690 m a.s.l.) except Kinzigaue, a lowland floodplain pedunculate oak-hornbeam-forest (110 m a.s.l.) – can be found in the following monographs: Goldbachs- und Ziebachsrück: Dorow et al. (2009, 2010), Hohestein: Flechtner et al. (2006), Dorow & Kopelke (2007), Kinzigaue: Blick et al. (2012, 2014), Niddahänge östlich Rudingshain: Flechtner et al. (1999, 2000), Schönbuche: Dorow et al. (2001, 2004), with special contributions on the earthworms (Römbke 1999, 2001, 2006, 2009, Römbke et al. 2012) The data on the earthworm fauna of the reserve Hasenblick and its adjacent managed site are not published yet. A brief overview of the reserves can be found online (IBV 2016).

The pitfall traps were constructed as follows: a 20 cm long plastic tube sunk in the ground with a 10 cm wide opening, leading via a plastic funnel into a collecting glass; the trap was covered with a metal roof against rain and leaf fall about 2 cm above the ground. The numbers of pitfall traps varied according to the vegetation structures present at each site.

There were different types of trunk eclectors:

Eclector at standing tree trunk: fyke-like trap-type that collects animals walking up a tree trunk; this type was used on living trees and on standing dead trees; the traps were placed in a height of 1.8–2.0 m (Fig. 2A,B).

Eclector at lying tree trunk: a combination of two different traps: (1) a 1 m long tube made of plastic and metal, fixed at the two sides with cloth to the trunk to collect animals that emerge from the trunk; (2) on both sides a cloth-collar attached to collect animals walking on the trunk surface. There are two sub-types: (1) trunks with only little contact to the ground (Fig. 3) and (2) trunks mostly lying on the ground (Fig. 4).

The ecletors could not be used on lying tree trunks in several managed sites, because there were no such trunks available. All eclectors had devices to collect species with positive as well as negative phototaxis (= negative and positive geotaxis, respectively).

Figure 2. Eclectors at standing trees.

Table 1. Research sites and number of trunk eclectors and pitfall traps. **GZ** = Goldbachs- und Ziebachsrück, **HB** = Hasenblick, **HO** = Hohestein, **KI** = Kinzigaue, **NI** = Niddahänge, **SB** = Schönbuche; **S** = strict reserve area (no forestry management), **M** = area with forestry management.

	GZ		HB		HO		KI	NI		SB	
Trap type	**S**	**M**	**S**	**M**	**S**	**M**	**S**	**S**	**M**	**S**	**M**
Eclector at living tree trunk	2	2	2	2	2	2	2	2	2	2	2
Eclector at standing dead tree trunk	2	2	2	2	2	2	2	2	2	2	
Eclector at dead tree trunk mostly lying on the ground	1		1	2	1		1	2	2	1	
Eclector at dead tree trunk with little contact to the ground	1		1		1		1	2		1	
Pitfall traps	27	29	54	33	24	21	36	27	25	18	19

All traps were run with a mixture of 70% alcohol + 99.5% glycerine in a 2:1 ratio as preserving fluid. For details see Dorow et al. (1992).

All samples were emptied once per month, except in winter where the traps where not emptied for four to five months (exposition time: December to March/April).

Figure 3. Eclector on trunk, lying only partly on the ground.

Figure 4. Eclector on trunk, lying mainly on the ground.

3. Results

3.1 Dominant earthworms in the three main trap types

Table 2 shows percentages of species finds in the different collecting devices. All in all we collected 1418 adult Lumbricidae in the trunk eclectors at standing trees, 294 in the trunk eclectors at lying trees and 865 in the pitfall traps. Trunk eclectors and pitfall traps showed different sets and percentages of lumbricids. In the trunk eclectors at standing and lying trees the community consisted predominantly (60–83%) of *Allolobophoridella eiseni*, with slightly higher percentages at standing trees compared to lying logs. This species was trapped at living beech trees (63%) and at standing dead beech trees (81%). Also *Dendrodrilus rubidus* reached percentages of 21–26% at the trunks in the beech forests, but not at the lying trunks in the floodplain oak forest. In contrast, *Dendrobaena octaedra* was collected in all eclectors and the pitfall traps with similar percentages (6–10%), except in the pitfall traps of the beech forests (16%). In the pitfall traps *Lumbricus rubellus* was by far the most abundant species (43% in the beech forests and 22% in the floodplain oak forest), followed by *Dendrobaena octaedra* in the beech forests (16%). In the oak forest *Allolobophoridella eiseni* reached a percentage of 20% in the pitfall traps, followed by *Lumbricus rubellus* and *Aporrectodea limicola* (the latter two being well known for their preferences of moist to wet places).

Dendrodrilus rubidus (21% in beech forests and 3% in the floodplain oak forest) as well as *Dendrobaena octaedra* (7% in beech forests and 9% in the floodplain oak forest) were also regularly found in trunk eclectors at standing trees, meaning that they are also able to climb up tree trunks (Tab. 2). The latter species was also abundant in pitfall traps (10–16% in both forest types), while the former one prefers clearly the drier beech stands.

3.2 Phenology of *Allolobophoridella eiseni*

In the following the total and mean numbers of *Allolobophoridella eiseni* in the three main trap types per month and per half year are presented (Tab. 3). In total, 1304 individuals of *Allolobophoridella eiseni* were caught in the three types of traps. Most of them (1011) were found in the traps on standing (living or dead) trees. But there were fewer traps on lying than on standing trees; due to the different trap types the absolute numbers cannot be compared directly. Therefore in Fig. 5 the relative numbers are used. In the traps on standing trees only one third of all *Allolobophoridella eiseni* specimens was found in the summer half year, while in the pitfall traps their number was almost six times higher in the summer than in the winter.

When looking at the numbers over the whole year the highest numbers were almost always found in the traps on standing trees, especially in the winter (Fig. 5). In addition, there was only one month (August) in which the numbers at the standing trees were lower than at the lying trees, but in this month the total number was the absolute minimum.

In general, only few *Allolobophoridella eiseni* were caught in the pitfall traps (103, of these 63 in the reserve Kinzigaue). Surprisingly, the highest number did occur in July, a month of usually low earthworm activity because of high temperatures and low soil moisture. In contrast, in the winter half year the numbers in the pitfall traps were small.

Table 2. Lumbricid species (in % of total number of adults) in the three main trap types (**TS** = trunk eclectors at standing trees, **TL** = trunk eclectors at lying trees, **PT** = pitfall traps on the ground) and shown separately for beech forests (**B**) and the floodplain oak forest (**O**).

	TS		**TL**		**PT**	
	B	**O**	**B**	**O**	**B**	**O**
Allolobophoridella eiseni (Levinsen, 1884)	70.8	83.1	59.5	75.5	7.4	19.6
Aporrectodea caliginosa (Savigny, 1826)	0.1				7.0	5.9
Aporrectodea handlirschi (Rosa, 1897)		1.7		1.1		0.9
Aporrectodea limicola (Michaelsen, 1890)					0.4	16.5
Aporrectodea longa (Ude, 1885)					0.2	
Aporrectodea rosea (Savigny, 1826)	0.1		0.5	1.1	0.6	1.9
Dendrobaena octaedra (Savigny, 1826)	6.5	8.5	8.0	8.5	16.2	9.9
Dendrodrilus rubidus (Savigny, 1826)	21.1	3.4	25.5	6.4	6.6	4.3
Eisenia fetida (Savigny, 1826)	0.1		2.0			
Eiseniella tetraedra (Savigny, 1826)					0.2	2.5
Helodrilus oculatus Hoffmeister, 1845	0.7				0.2	
Lumbricus castaneus (Savigny, 1826)			2.5	5.3	7.2	11.2
Lumbricus meliboeus Rosa, 1884					0.6	
Lumbricus rubellus Hoffmeister, 1843	0.4		1.5	2.1	42.9	21.7
Lumbricus terrestris Linnaeus, 1758			0.5		2.6	3.4
Octolasion cyaneum (Savigny, 1826)					4.4	2.2
Octolasion tyrtaeum (Savigny, 1826)					3.7	
Totals of adult Lumbricidae	**1359**	**59**	**200**	**94**	**543**	**322**

Table 3. Numbers of *Allolobophoridella eiseni* in the three main trap types (TS = trunk eclectors at standing trees, TL = trunk eclectors at lying trees, PT = pitfall traps on the ground) per month, in total, and as percentages of the total sum per half year

Month/Totals	**Standing**	**Lying**	**Pitfall**
V	91	19	13
VI	50	11	6
VII	53	28	34
VIII	7	16	12
IX	35	3	7
X	98	12	16
XI	248	59	9
XII-IV	429	42	6
Total	1011	190	103
V–X ‘summer’ (%)	33.0	46.8	85.4
XI–IV ‘winter’ (%)	67.0	53.2	14.6
Percentage of total sum	**100.0**	**100.0**	**100.0**

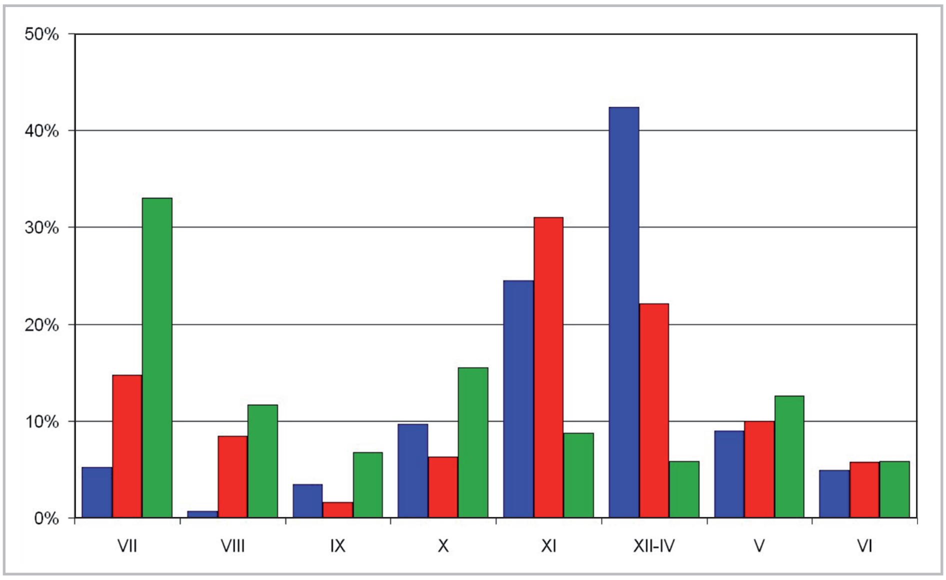

Figure 5. Relative numbers of *Allolobophoridella eiseni* in the three main trap types per month respectively in the winter period (months XII-IV; blue = eclectors at standing trees, red = eclectors at lying trees, green = pitfall traps).

4. Discussion

Based on these findings it can be stated that *Allolobophoridella eiseni* is a regular element of the invertebrate fauna of forests, which can be trapped predominantly at the bark on living trees, dead trees (including decaying logs) and less frequently (with exception of the moist oak forest) in pitfalls traps. Therefore, this species can be classified as predominantly arboricolous. For the first time it could be proven that *Allolobophoridella eiseni* regularly climbs on trees (Römbke et al. 2006) and is much more often caught in this habitat than in the litter layer, i.e. it is truly an arboreal species.

The occurrence, diversity and ecology of earthworms living on or at trees are not well-studied. Records from temperate regions are scarce, but Moeed & Meads (1983) mention that about 1 % of all invertebrates caught in up- and down-traps at trees in a New Zealand broadleaf/podocarp and a nearby hard beech forest were earthworms. No further details regarding the species are known, but fewer worms were caught in summer compared to winter. Actually, this behaviour is mainly described from tropical regions where arboreal earthworm species are found regularly (Lee 1985, James & Brown 2006, Richardson et al. 2006). According to Fragoso & Rojas-Fragoso (1996), there are two reasons why worms live on trees: either this behaviour is a temporal shift in order to avoid seasonal flooding of soils — e.g. in Amazonian lowland forests, such as the glossocolecid *Tuiba dianae* Righi, Ayres & Bittencourt 1976 (Adis & Bogen 1982: sub *Tairona tipema*) or the rhinodrilid *Andiorrhinus venezuelanus tarumanis* (Righi, Ayres & Bittencourt, 1976) (Adis & Righi 1989) — or it is a permanent response to acidity and low oxygen content of soils that occur in very wet tropical forests (Lee 1983). In any case the aboveground habitat has to be moist, meaning that such behaviour is often found in mountainous or cloud forests (e.g. James 2010). Further reasons are conceivable. For example Gaume et al. (2006) reported on a megascolecid earthworm species (*Perionyx pullus* Stephenson, 1920) that occurs together with at least four different ant species on the myrmecophytic understorey tree *Humboldtia brunosis* (Fabaceae) in the Western Ghats, India, but the nature of their interaction is not yet clear.

However, the factors given above do not fit well to the ecological conditions in temperate regions such as Central Europe: here, we assume that the availability of food as well as the protection gained on trees or in rotten wood is attractive for at least some litter-dwelling species, especially *Allolobophoridella eiseni*. The lack of competition with other lumbricids in this 'new' habitat might be another factor. Unfortunately, information on the climbing abilities of earthworms in general and of *Allolobophoridella eiseni* in particular is scarce. More or less anecdotal observations on earthworms climbing vertical objects have been reported. Probably the first example was given by Kuusinen (1962), who observed individuals of the epigeics *Eisenia fetida* and *Dendrodrilus subrubicunda* climbing up and down on house walls, especially during night rains after dry periods. The author explained this behaviour with oxygen deficiencies in the soil. Similar observations were regularly discussed on the internet, but always without detailed information on the species.

Epigeic species (at least the adults) at German acid forest sites have their activity minimum in the summer months when the litter layer is usually very dry (see Römbke 1985), e.g. *Dendrodrilus rubidus* and *Lumbricus rubellus*. In contrast, these worms are active in winter, provided that litter layer and the uppermost mineral soil layer are protected against freezing by a snow cover. This pattern was found in this study as well, at least when looking at the results of the traps on standing trees. The relatively high number in the August pitfall traps is caused by high numbers of individuals at the partly flooded site, which was probably still moist. Of course, the worms living on trees or deadwood cannot be protected by a snow cover, but they may gain protection against freezing on the tree by staying at specific sites where decaying organic matter is accumulated (e.g. in tree holes, bark pockets, phytotelmata, epiphyte-assemblages in natural habitats or in roof gutters in the urban environment).

Regarding the habitat preferences of *Allolobophoridella eiseni*, the literature accounts are varied. Zicsi (1965) mentions it as a typical example for the corticoles, i.e. species living below the bark of trees, for Austria. This is supported by Bouché (1972) for France . Csuzdi & Zicsi (2003) state, that all Hungarian individuals belonging to this species live solely under the bark of decaying logs. In contrast, Sims & Gerard (1999: 98) report that in Great Britain *Allolobophoridella eiseni* is found 'under moss and decaying leaves, [being] often the dominant earthworm in moorland, bog soils and by streams'. *Allolobophoridella eiseni* seems to be temperature-tolerant since it had been found not only in Central Europe but also quite far north, especially in wet acid moorlands of the Scottish islands. Similarly, Fender (1985), who found *Allolobophoridella eiseni* in coastal forests of the north-western United States (i.e. Oregon and Washington), states that 'these worms require cool, even temperatures, high rainfall, an acid medium, and high amounts of organic matter'. Omodeo et al. (2003) found *Allolobophoridella eiseni* at seven Algerian and two Moroccan sites (with one exception [grassland] always in forests) and classified it as being typically litter-dwelling but also as corticolous. In most of these studies, no information is provided which methods were used to collect *Allolobophoridella eiseni*.

Satchell (1955), referring to British forests, classified *Allolobophoridella eiseni* as an acid-tolerant species, with a preference of soil pH values of 3.7–4.7. Bouché (1972) classifies *Allolobophoridella eiseni* as an acidophilous species, i.e. preferring low soil pH-values. This statement is supported by Sims & Gerard (1999) who report occurrence in U.K. soils with a pH between 3.6 and 7.6. In contrast, most anecic and endogeic earthworm species prefer pH-ranges >4.5 (Graefe & Beylich 2003), meaning that *Allolobophoridella eiseni* is exceptional in tolerating acidic as well as neutral conditions. Satchell (1967) found correlations between the occurrence of *Allolobophoridella eiseni* and the oxidation-reduction potential, but mentions that such correlations are interfered with by other factors such as soil moisture or organic matter content. Höser (2013) considers *Allolobophoridella eiseni* a peregrine species belonging to the fauna of acid beech wood forests, referring to findings of Römbke (1985, 2009). In summary, it seems that *Allolobophoridella eiseni* is very tolerant in terms of several ecological factors. It has been found in very cool and wet (e.g. north-western USA) as well as in very warm and dry places (e.g. northern Africa). In addition its pH range of 3.6 to 7.6 is also relatively wide, like in most epigeic, acidotolerant lumbricid species.

Allolobophoridella eiseni was found already in the Hessian region Vogelsberg by Eggert (1982: sub *Bimastos eiseni*). In total, 23.6% of the earthworms found by him under the bark of living trees belonged to this species. In one case the species was caught at a height of about 2 m under moist moss on an apple tree. Römbke (1985: sub *Bimastos eiseni*) found just one individual of *Allolobophoridella eiseni* (out of a total of 1143 lumbricids) in the mineral soil of a moder beech forest in Baden-Württemberg (south-western Germany). In contrast, six out of 15 earthworms caught in head-boxes of ground-photo eclectors belonged to this species, indicating its ability to climb on smooth surfaces, since the collection box was located about 1 m above the litter layer – and the way up was not vertical but overhanging. Individuals of *Allolobophoridella eiseni* were found even in branch traps in the crowns of oaks in a Bavarian beech wood forest 15–22 m above ground (Goßner, pers. comm.). Interestingly, this site is also located in a low mountain range (520–535 m above sea level and with an annual precipitation of 750–800 mm). These results confirm that *Allolobophoridella eiseni* can be classified as a predominantly corticolous or arboreal species.

The feeding behaviour of worms is clearly correlated with their way of life (Lee 1985). Epigeics feed on litter and/or the attached microflora with little or no soil being ingested. Little specific information on the feeding habits of *Allolobophoridella eiseni* is available. Svendsen (1957) reports that in Scottish moors this species is more often found under cattle dung pads than in the remaining grassland, which may be caused by their high amount of protozoans and nematodes (Holter 1983). In the laboratory, *Allolobophoridella eiseni* also feeds on pine litter, accelerating the decomposition of the needles (Heungens 1969). The role of algae in the diet of earthworms is still not clear (Edwards 2004). Surely they will be digested when taken up together with soil, but no specific grazing behaviour of earthworms on algae has been reported so far. As a food source fungi are most important for epigeics while bacteria are of minor importance (Edwards & Fletcher 1988). Feeding of earthworms on soil algae has so far been reported only for endogeics and anecics, not epigeics (Piearce 1978; Schmidt et al. 2016). The detailed food spectrum and feeding behaviour of *Allolobophoridella eiseni* has to be investigated in further studies.

In summary, *Allolobophoridella eiseni* is not a rare species but a common member of the earthworm communities especially in moder beech (and oak) wood forests on acid soils in four German states located in northern, central and southern Germany. In Scottish heath and coniferous moor soils often only *Dendrobaena octaedra* and *Allolobophoridella eiseni* do occur. Probably *Allolobophoridella eiseni* has often been overlooked in studies in which earthworms were collected with traditional methods, focusing on soil and litter inhabiting species. In fact this species is probably an important part of the total invertebrate biomass at such habitats, at least up to about 20 meters above ground. However, its ecological role is difficult to quantify because pitfall traps as well as eclector traps do not sample earthworms per area but are activity-based. This means also that a direct comparison between the results of hand-sorting or chemical extraction from soil and the results of pitfall or eclector traps is not possible.

Thus, specific sampling programs focusing on those species inhabiting trees (i.e. not only *Allolobophoridella eiseni*) should be initiated in order to clarify the ecological role of these worms outside of the 'normal' habitat of earthworms. So far, examples for tree-dwelling earthworm species are mainly known from tropical sites (especially Latin America) but it seems possible that such behaviour has been simply overlooked in Europe so far due to a restriction to sampling methods which do not cover such habitats.

In detail, further research has to clarify the food spectrum of tree-dwelling earthworms, their migration behaviour and their interaction with other organisms in this very specific habitat. Similar work has, e. g., been done already for springtails (Shaw 2015). In fact, at a time where research on the interactions between below- and aboveground communities is a very hot research topic (Sutherland et al. 2013), species such as *Allolobophoridella eiseni* could play an important role in improving our understanding of the whole terrestrial ecosystem.

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6 References

Adis, J. & V. Bogen (1982): Reaction of Glossoscolecidae (Annelida, Oligochaeta) to flooding in a Central Amazonian Inundation forest. – Acta Amazonica **12**: 741–743.

Adis, J. & G. Righi (1989): Mass migration and life cycle adaptation – a survival strategy of terrestrial earthworms in Central Amazonian inundation forests. – Amazoniana **11**: 23–30.

Blakemore, R. J. (2008): British and Irish earthworms — a checklist of species updated from Sims & Gerard (1999) [http://www.annelida.net/earthworm/Britain&Ireland.pdf].

Blick, T., W. H. O. Dorow & J.-P. Kopelke (2012): Kinzigaue. Zoologische Untersuchungen 1999-2001, Teil 1. – Naturwaldreservate in Hessen **12**: 1–348 [http://www.senckenberg.de/root/index.php?page_id=16859].

Blick, T., W. H. O. Dorow & G. Köhler (2014): Kinzigaue. Zoologische Untersuchungen 1999-2001, Teil 2. – Naturwaldreservate in Hessen **13**: 1–238 [http://www.senckenberg.de/root/index.php?page_id=16859].

Bouché, M. B. (1971): Relations entre les structures spatiales et fonctionelles des écosystèmes illustrées par le role pédobiologique des vers de terre. – In: Pesson, P. (ed.): La vie dans les sols. – Gauthier-Villars, Paris: 187–209.

Bouché, M. B. (1972): Lombriciens de France. Écologie et systématique. – Annales de zoologie. Ecologie animale, hors série **72**(2): 1–671.

Bouché, M. B. (1977): Stratéegies lombriciennes. – In: Lohm, U. & T. Persson (eds): Soil organisms as components of ecosystems. – Ecological Bulletins NFR **25**: 122–132.

Csuzdi, C. & A. Zicsi (2003): Earthworms of Hungary (Annelida: Oligochaeta, Lumbricidae). – Pedozoologica Hungarica **1**: 1–272.

Dorow, W. H. O., G. Flechtner & J.-P. Kopelke (1992): Zoologische Untersuchungen — Konzept. Naturwaldreservate in Hessen 3. – Mitteilungen der Hessischen Landesforstverwaltung **26**: 1–159 [http://www.senckenberg.de/root/index.php?page_id=16851].

Dorow, W. H. O., G. Flechtner & J.-P. Kopelke (2001): Schönbuche. Zoologische Untersuchungen 1990-1992, Teil

1. Naturwaldreservate in Hessen 6/2.1. – FIV Ergebnis- und Forschungsbericht **28**/1: 1–306 [http://www.senckenberg.de/root/index.php?page_id=16859].

Dorow, W. H. O., G. Flechtner & J.-P. Kopelke (2004): Schönbuche. Zoologische Untersuchungen 1990-1992, Teil 2. Naturwaldreservate in Hessen 6/2.2. – FIV Ergebnis- und Forschungsbericht **28**/2: 1–352 [http://www.senckenberg.de/root/index.php?page_id=16859].

Dorow, W. H. O. & J.-P. Kopelke (2007): Hohestein. Zoologische Untersuchungen 1994-1996, Teil 2. Naturwaldreservate in Hessen 7/2.2. – Mitteilungen der Hessischen Landesforstverwaltung **42**: 1–341 [http://www.senckenberg.de/root/index.php?page_id=16859].

Dorow, W. H. O., T. Blick & J.-P. Kopelke (2009): Goldbachs- und Ziebachsrück. Zoologische Untersuchungen 1994-1996, Teil 1. Naturwaldreservate in Hessen 11/2.1. – Mitteilungen der Hessischen Landesforstverwaltung **45**: 1–326 [http://www.senckenberg.de/root/index.php?page_id=16859].

Dorow, W. H. O., T. Blick & J.-P. Kopelke (2010): Goldbachs- und Ziebachsrück – Zoologische Untersuchungen 1994-1996, Teil 2. Naturwaldreservate in Hessen 11/2.2. – Mitteilungen der Hessischen Landesforstverwaltung **46**: 1–271 [http://www.senckenberg.de/root/index.php?page_id=16859].

Edwards, C. A. (2004): Earthworm ecology. 2nd ed. – CRC Press, Boca Raton: 456 pp.

Edwards, C. A. & K. E. Fletcher (1988): Interactions between earthworms and microorganisms in organic-matter breakdown. – Agriculture, Ecosystems and Environment **24**: 235–247.

Edwards, C. A. & J. R. Lofty (1977): Biology of earthworms. 2nd ed. – Chapman & Hall, London: 333 pp.

Eggert, U. J. (1982): Vorkommen und Verbreitung der Regenwürmer (Lumbricidae) des Naturparks „Hoher Vogelsberg“. – Beiträge zur Naturkunde in Osthessen **18**: 61–103.

Fender, W. M. (1985): Earthworms of the western United States. Part I. Lumbricidae. – Megadrilogica **4**: 93–129.

Flechtner, G., W. H. O. Dorow & J.-P. Kopelke (1999): Niddahänge östlich Rudingshain. Zoologische Untersuchungen 1990-1992, Teil 1. Naturwaldreservate in Hessen 5/2.1. – Mitteilungen der Hessischen Landesforstverwaltung **32**/1: 1–746 [http://www.senckenberg.de/root/index.php?page_id=16859]

Flechtner, G., W. H. O. Dorow & J.-P. Kopelke (2000): Niddahänge östlich Rudingshain. Zoologische Untersuchungen 1990-1992, Teil 2. Naturwaldreservate in Hessen 5/2.2. – Mitteilungen der Hessischen Landesforstverwaltung **32**/2: 1–550 [http://www.senckenberg.de/root/index.php?page_id=16859].

Flechtner, G., W. H. O. Dorow & J.-P. Kopelke (2006): Hohestein. Zoologische Untersuchungen 1994-1996, Teil 1. Naturwaldreservate in Hessen 7/2.1. – Mitteilungen der Hessischen Landesforstverwaltung **41**: 1–247 [http://www.senckenberg.de/root/index.php?page_id=16859].

Fragoso, C. & P. Rojas-Fragoso (1996): Earthworms inhabiting bromeliads in Mexican tropical rainforests: ecological and historical determinants. – Journal of Tropical Ecology **12**: 729–734.

Gaume, L., M. Shenoy, M. Zacharias & R. M. Borges (2006): Co-existence of ants and an arboreal earthworm in a myrmecophyte of the Indian Western Ghats: anti-predation effect of the earthworm mucus. – Journal of Tropical Ecology **22**: 341–344.

Graefe, U. & A. Beylich (2003): Critical values of soil acidification for annelid species and the decomposer community. – Newsletter on Enchytraeidae **8**: 51–55.

Graff, O. (1953): Die Regenwürmer Deutschlands. – Schriftenreihe der Forschungsinstitut für Landwirtschaft **7**: 1–70.

Heungens, A. (1969): The physical decomposition of pine litter by earthworms. – Plant and Soil **31**: 22–30.

Holter, P. (1983): Effect of earthworms on the disappearance rate of cattle droppings. – In: Satchell, J. E. (ed.): Earthworm ecology — from Darwin to vermiculture. – Chapman & Hall, London: 49–57.

Höser, N. (2013): Zur Regenwurmfauna (Oligochaeta: Lumbricidae) in Wäldern Mecklenburgs. – Archiv der Freunde der Naturgeschichte Mecklenburgs **52**: 75–85.

IBV (Informations- und Koordinierungszentrum für Biologische Vielfalt) (2016): Datenbank Naturwaldreservate in Deutschland. – Bundesanstalt für Landwirtschaft und Ernährung [http://www.naturwaelder.de].

ISO (International Organization for Standardization) (2006): Soil quality – sampling of soil invertebrates. Part 1: Hand-sorting and formalin extraction of earthworms. – ISO (Genève) 23611-1: 1–17.

James, S. W. (2010): New genera and species of pheretimoid earthworms (Clitellata: Megascolecidae) from southern Luzon, Philippines). – Systematics and Biodiversity **2**: 271–279.

James, S. W. & G. G. Brown (2006): Earthworm ecology and diversity in Brazil. – In: Moreira, F. M. S., J. O. Siqueira & L. Brussaard (eds.): Soil biodiversity in Amazonian and other Brazilian ecosystems. – CABI Publications, Wallingford, UK: 56–116.

Kuusinen, J. (1962): Lierojen kiipeilystä seinillä [Über das Klettern von Regenwürmern an Wänden; On climbing of earthworms on walls]. – Lounaiis-Hämeen Luonto **13**: 22.

Lavelle, P. (1984): The soil system in the humid tropics. – Biology International **9**: 2–17.

Lee, K. E. (1959): The earthworm fauna of New Zealand. – New Zealand Department of Scientific & Industrial Research Bulletin **130**: 1–486.

Lee, K. E. (1983): Earthworms of tropical regions some aspects of their ecology and relationships with soils. – In: Satchell, J. (ed.): Earthworm ecology. – Chapman & Hall, London: 179–194.

Lee, K. E. (1985): Earthworms: their ecology and relationships with soils and land use. – Academic Press, Sydney: 411 pp.

Lehmitz, R., J. Römbke, U. Graefe, A. Beylich & S. Krück (2016): Rote Liste und Gesamtartenliste der Regenwürmer (Lumbricidae et Criodrillidae) Deutschlands. – Naturschutz und Biologische Vielfalt **70(4)**: 565–590.

Lehmitz, R., J. Römbke, S. Jänsch, S. Krück, A. Beylich & U. Graefe (2014): Checklist of earthworms (Oligochaeta: Lumbricidae) from Germany. – Zootaxa **3866**: 221–245.

Levinsen, G. M. R. (1884): Systematisk-geografisk oversigt over de nordiske Annulata, Gephyrea, Chaetognathi og Balanoglossi. – Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjöbenhavn **45**: 1–241.

Moeed, A. & M. J. Meads (1983): Invertebrate fauna of four tree species in Orongorongo Valley, New Zealand, as revealed by trunk traps. - New Zealand Journal of Ecology **6**: 39–53.

Mršić, N. (1990): Description of a new subgenus, three new species and taxonomic problems of the genus *Allolobophora* sensu Mršić and Sapkarev 1988 (Lumbricidae, Oligochaeta). – Biologija Vestnik **38**: 49–68.

Omodeo, P., E. Rota & M. Baha (2003): The megadrile fauna (Annelida: Oligochaeta) of Maghreb: a biogeographical and ecological characterization. – Pedobiologia **47**: 458–465.

Piearce, T. G. (1978): Gut content of some lumbricid earthworms. – Pedobiologia **18**: 153–157.

Reynolds, J. W. (1995): Status of exotic earthworm systematics and biogeography in North America. – In: Hendrix, P. F. (ed.): Earthworm ecology and biogeography in North America. – Lewis Publishers, Boca Raton: 1–28.

Richardson, B. A., S. Borges & M. J. Richardson (2006): Differences between epigeic earthworm populations in tank bromeliads from Puerto Rico and Dominica. – Carribean Journal of Science **42**: 380–385.

Römbke, J. (1985): Zur Biologie eines Buchenwaldbodens. 6. Die Regenwürmer. – Carolinea **43**: 93–104.

Römbke, J. (1999): Lumbricidae (Regenwürmer). – In: Niddahänge östlich Rudingshain. Zoologische Untersuchungen 1990-1992. Teil 1. Naturwaldreservate in Hessen 5/2.1. – Mitteilungen der Hessischen Landesforstverwaltung **32/1**: 57–83 [http://www.senckenberg.de/root/index.php?page_id=16859].

Römbke, J. (2001): Lumbricidae (Regenwürmer). – In: Schönbuche. Zoologische Untersuchungen 1990-1992. Teil 1. Naturwaldreservate in Hessen 6/2.1. – Hessen-Forst – FIV Ergebnis- und Forschungsbericht **28/1**: 27–52 [http://www.senckenberg.de/root/index.php?page_id=16859].

Römbke, J. (2006): Lumbricidae (Regenwürmer). – In: Hohestein. Zoologische Untersuchungen 1994-1996, Teil 1. Naturwaldreservate in Hessen 7/2.1. – Mitteilungen der Hessischen Landesforstverwaltung **41**: 29–59 [http://www.senckenberg.de/root/index.php?page_id=16859].

Römbke, J. (2009): Die Regenwürmer (Lumbricidae) des Naturwaldreservats Goldbachs- und Ziebachsrück (Hessen). Untersuchungszeitraum 1994–1996. – Mitteilungen der Hessischen Landesforstverwaltung **45**: 25–55 [http://www.senckenberg.de/root/index.php?page_id=16859].

Römbke, J., T. Blick & W. H. O. Dorow (2012): Die Regenwürmer (Lumbricidae) des Naturwaldreservats Kinzigaue (Hessen). Untersuchungszeitraum 1999–2001. – Naturwaldreservate in Hessen **12**: 23–51 [http://www.senckenberg.de/root/index.php?page_id=16859].

Römbke, J., W. H. O. Dorow, G. Flechtner & J.-P. Kopelke (2006): Sampling of earthworms with non-standard methods: Surprising results from German forest sites. – The 8th International Symposium on Earthworm Ecology 4th–9th September 2006, Abstracts, Kraków: 83 [http://www.senckenberg.de/root/index.php?page_id=16859].

Satchell, J. E. (1955): Some aspects of earthworm ecology. – In: McKevan, D. K. (ed.): Soil zoology. – Butterworths, London: 180–201.

Satchell, J. E. (1967): Lumbricidae. – In: Burgess, A & F. Raw (eds): Soil biology. – Academic Press, London, New York: 259–322.

Schmidt, O., J. Dyckmans & S. Schrader (2016): Photoautotrophic microorganisms as a carbon source for temperate soil invertebrates. – Biology Letters **12**: 20150646.

Shaw, P. (2015): How high do Collembola climb? Studies of vertical migration in arboreal Collembola. – Soil Organisms **87** (3): 229–235.

Sims, R. W. & B. M. Gerard (1999): Earthworms. – In: D. M. Kermack & R. S. K. Barnes (eds): Synopses of the British fauna. New series 31. – E. J. Brill/W. Backhuys, London: 169 pp.

Sutherland, W. J., R. P. Freckleton, H. C. J. Godfray, S. R. Beissinger, T. Benton, D. D. Cameron, Y. Carmel, D. A. Coomes, T. Coulson, M. C. Emmerson, R. S. Hails, G. C. Hays, D. J. Hodgson, M. J. Hutchings, D. Johnson, J. P. G. Jones, M. J. Keeling, H. Kokko, W. E. Kunin, X. Lambin, O. T. Lewis, Y. Malhi, N. Mieszkowska, J. M. Gulland, K. Norris, A. B. Phillimore, D. W. Purves, J. M. Reid, D. C. Reuman, K. Thompson, J. M. J. Travis, L. A. Turnbull, D. A. Wardle & T. Wiegand (2013): Identification of 100 fundamental ecological questions. – Journal of Ecology **101**: 58–67

Svendsen, J. A. (1957): The distribution of Lumbricidae in an area of Pennine moorland (Moor House Nature Reserve). – Journal of Animal Ecology **26**: 411–421.