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Habitat and seasonal activity patterns of the terrestrial isopods (Isopoda: Oniscidea) of Belgium

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Abstract

Field surveys carried out between 2011 and 2020 resulted in an extensive dataset of terrestrial isopod observations covering the complete territory of Belgium. Every grid cell of the UTM 10 × 10 km² grid was visited and in each grid cell a forest, a riverbank or streamside, and an anthropogenic habitat were surveyed. 35 out of the 36 species living in Belgium were recorded. Habitat information was added to the records ex situ to allow for further analysis of the dataset. For all species detailed and quantitative habitat information is presented accompanied by a distribution map that differentiates between the main habitat types, i.e., forest, open landscape, coastal habitat, and anthropogenic habitat. Additionally, we present for all species phenology graphs for each habitat type, represented by seasonal activity patterns per two-month period, after a correction for search intensity in each period and differentiating per main habitat type. We shortly discuss the observed patterns per species. Ordination plots allow us to identify characteristic species per habitat type and per season in Belgium. Different species have a strong preference for forest or anthropogenic habitat while hardly any species has a strong preference for open habitat. There is a temporal complementarity between the activity of small and drought sensitive species which are found mainly from autumn till spring and larger drought resistant species which are mainly found between spring and autumn. Habitat preference could be characterized in detail for most species but for seven rare species, the habitat preference is still somewhat illusive and we encourage to report all new observations of these rare species and their habitat in detail.

Keywords: anthropogenic, distribution, forest, open landscape, phenology, woodlice

Contents

Introduction

Landscapes worldwide are subject to large-scale transformation through land conversion, agricultural intensification, climate change, biological invasions and many more. These fast changes make quantification of the existing ecosystems crucial to evaluate the effects of environmental pressures on the biological community and subsequently ecosystem functioning. Soils are a vital component of almost all terrestrial ecosystems and vital for a wide array of functions and associated ecosystem services (JEFFERY *et al.*, 2010). The delivery of these ecosystem services is directly or indirectly linked to functions performed by soil organisms, which are poorly studied compared to above ground taxa.

Woodlice are important organisms in and on terrestrial soils since they are known as fragmenters (DAVID, 2014), performing the first step in the breakdown of soil organic matter and they are therefore key to nutrient cycling (JOLY *et al.*, 2020). Woodlice can be extremely abundant in terrestrial soils (PAOLETTI & HASSALL, 1999; JEFFERY *et al.*, 2010) and are efficient detritivores (VOS *et al.*, 2011; DE SMEDT *et al.*, 2018c). Research has shown that terrestrial isopod communities are shaped by environmental change like forest fragmentation (DE SMEDT *et al.*, 2018a), climate change (SFENTHOURAKIS & HORNUNG, 2018) and urbanisation (HORNUNG *et al.*, 2007; OOMS *et al.*, 2020). Therefore, woodlice have the potential to be good indicators of habitat quality, ecosystem functioning and subsequently the effect of environmental change on ecosystem functioning.

A good characterisation of the current habitat preferences of terrestrial isopods is crucial in understanding shifts in species distribution due to environmental change. In Belgium, the distribution of terrestrial isopods was thoroughly investigated during the past decade through inventories carried out in every 10 × 10 km² square and is presented in detailed distribution maps for every species in Belgium (DE SMEDT *et al.*, 2020a). However, habitat data was only provided in a qualitative way based on expert knowledge and therefore the aim of the present study is to provide detailed quantitative habitat data since this enables to identify characteristic species for different habitat types and estimate the further impact of environmental change on terrestrial isopod assemblages in future habitats. Preferred habitat types of species can differ across environmental gradients and geographical regions. Across both altitudes and latitudes, we can find changing habitat preferences of terrestrial isopods (DE SMEDT *et al.*, 2018a; SFENTHOURAKIS & HORNUNG, 2018). HARDING & SUTTON (1985) for example carefully documented this for several species of terrestrial isopods in the UK based on detailed habitat data.

Belgium is a small country (approx. 30.500 km²) but with a rich geology. Eleven distinct ecological regions (map 1) span from a small coastline in the west to hilly landscapes with old (Mesozoic and Palaeozoic) deposits in the south. This gradient holds a wide range of habitats, which makes Belgium and interesting case to document habitat preferences of terrestrial isopods. Some isopod species are distinctly eurytopic and widely distributed across the country, others have a limited geographical range and are only found within a very limited distribution range or in a particular habitat type. Our first aim is to make a detailed habitat preference description and habitat distribution maps for all 36 terrestrial isopods of Belgium.

Besides their distribution across different habitat types also their activity throughout the year is of major importance for ecosystem functioning. Terrestrial isopods are, for arthropods, relatively long-lived (two years and more) and can reproduce several times per year (WARBURG, 1987). However, the phenology of most species is poorly studied and only a limited number of papers report phenology diagrams for terrestrial isopods. ZIMMER (2004) discusses the population dynamics for four species which also occur in Belgium, i.e. *Oniscus asellus*, *Philoscia muscorum*, *Porcellio scaber* and *Hyloniscus riparius*. The phenology of *Armadillidium opacum*, *Ligidium hypnorum* and *Trachelipus rathkii* are reported by ZIMMER & BRAUCKMANN (1997). Researchers in the United Kingdom have studied population dynamics of *Philoscia muscorum* and *Trichoniscus pusillus* (SUTTON, 1968) and *Armadillidium vulgare* (DANGERFIELD & HASSALL, 1992). These previous studies mostly report patterns for larger species while there can be a strong difference in intra-annual activity patterns between large and small species due to their ability to cope with environmental conditions (BERG *et al.*, 2008; DE SMEDT *et al.*, 2021; GREGORY, 2009; SUTTON, 1968). For most species of terrestrial isopods, these intra-annual activity patterns and how they depend on habitat type are largely unknown. Our second aim is therefore to investigate intra-annual activity patterns of Belgian terrestrial isopods.

Material and methods

FIELD SURVEY

The field surveys carried out by the authors consisted of monthly field excursions in search for terrestrial isopods in different habitats through hand collection by sieving litter and top soil as well as by turning stones, wood etc... The primary goal of the field excursions was to acquire distribution data for all species. The UTM 10 × 10 km² grid was chosen as survey unit balancing between efficient time investment and necessary resolution to create representative distribution maps. A total of 380 squares are (partly) covered by Belgian territory, located in both the 31U and 32U UTM zone. The 14 squares directly east and west of the meridian 6° east are 1.5 to 4.5 km in width. Consequently, two adjacent squares around the meridian 6° have been threated as one square. This gives a total count of 373 squares.

In every square at least three different habitats were visited, namely, if present, (1) a forest and if possible an ancient deciduous forest, (2) a streamside, riverbank or (wet) grassland and (3) an anthropogenic habitat (Fig. 1). Old quarries (Fig. 1 B) and coastal habitat were also visited if present in the square. Graveyards (Fig. 1 D) were the preferred anthropogenic habitat due to their public status and omnipresence but also a number of public parks, (old) farms and allotment gardens were visited. These biotope types cover the habitat niches of most terrestrial isopod species in Belgium.

Three other sources were used to expand the dataset, which were (1) records gathered by the authors outside the field survey project; (2) pitfall trap samples from other surveys and identified by the authors and (3) observations made by other volunteers with acquired knowledge on the Belgian terrestrial isopod fauna. This was checked through photographical identification or identification of reference individuals collected by the volunteer and identified by one of the authors. It was also important that the volunteer recorded year-round and registered accurate coordinates. We only included records from the period 2011 until 2020 in the dataset.

A large share of the field surveys was conducted by volunteers, therefore we checked for bias inherent to citizen science data, like sampling effort and sampling period (DICKINSON *et al.*, 2010). We corrected for this bias in both the habitat and phenology dataset (see further). All participants were skilled observers so observer errors are not expected.

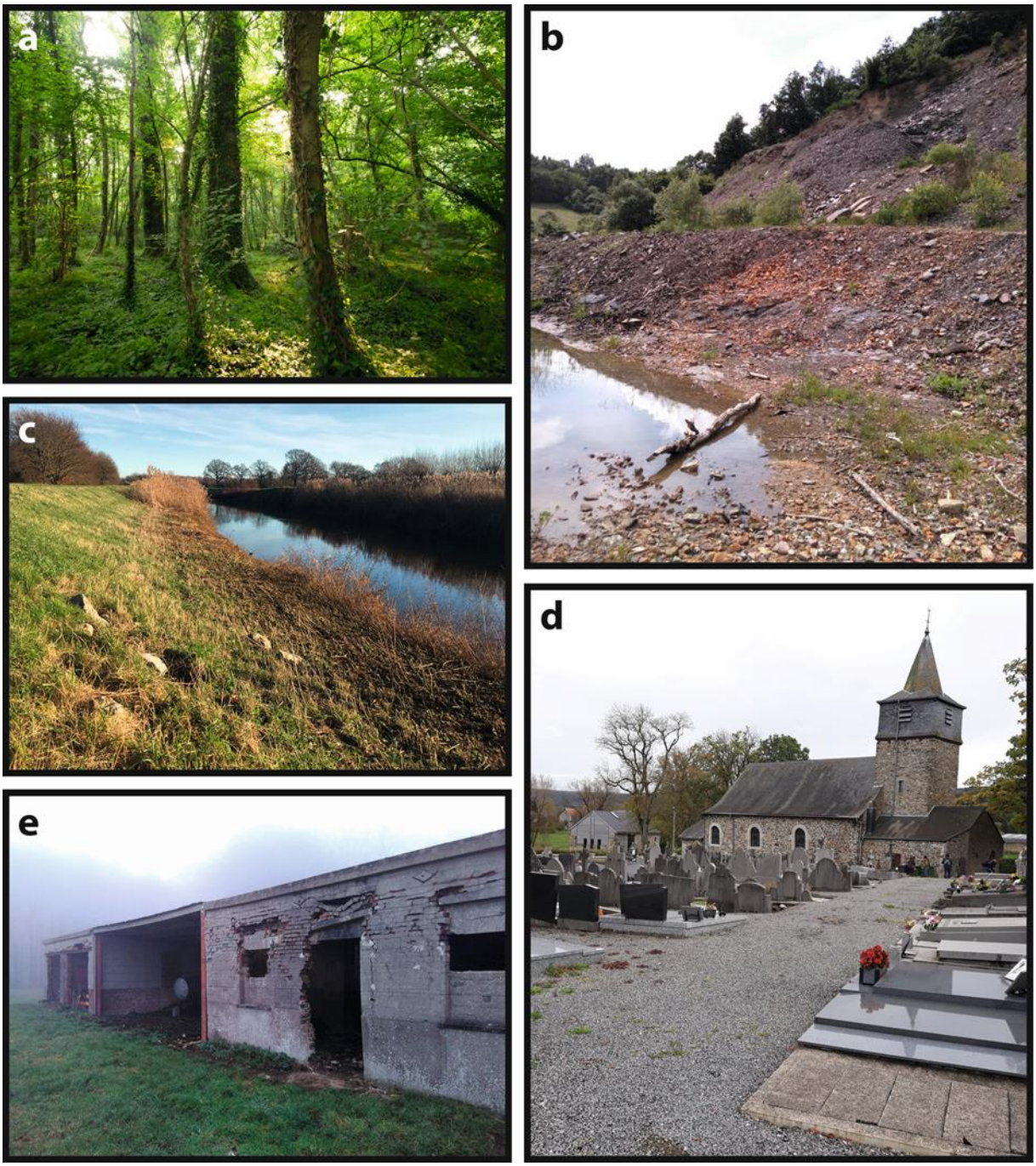


Fig. 1. Different habitats in Belgium well suited for terrestrial isopods. a, old forest in Parike, Belgium; b, disused quarry in Reuland, Belgium; c, stream side (dyke) of the Dyle river in Rijmenam, Belgium; d, old cemetery in Rahier, Belgium; e, old stable in a meadow near Saint-Saveur, Belgium.

HABITAT DATASET

During the field surveys, habitat data was not systematically recorded. However, all records in the dataset contained accurate coordinates and by tracing the position of the observation on satellite images and topographic maps, habitat information was registered for every location ex situ. A location was defined as a group of one or more observations within close range and within the same habitat. The maximum distance between observations in one location was on average 210 m and maximal 2847 m. A total of 2397 locations were defined with detailed habitat information.

Table 1. General and synthesis habitats for the surveyed locations.

General habitat	Synthesis habitats
Anthropogenic	farm; gardens and parks; near water in urban area; near roads and buildings in urban area; graveyard
Forest	coniferous forest; deciduous forest; near water in deciduous forest; near roads and buildings in forest
Open landscape	cropland and orchards; grassland; disused quarry, near roads and buildings in open landscape; near water in open landscape; river or canal dykes
Coast	coast

Table 2. Characteristics of the habitat dataset and the phenology dataset.

	Habitat dataset	Phenology dataset
Total number of records	6222	7628
Total number of locations	1982	2238
Number of squares with records	373	373
Average # records per square	16.7 (σ=8.5)	20.5 (σ=17.6)
Average # species per square	10.3 (σ=3.2)	10.3 (σ=3.2)
Average # locations per square	5.4 (σ=3.5)	6.0 (σ=5.2)

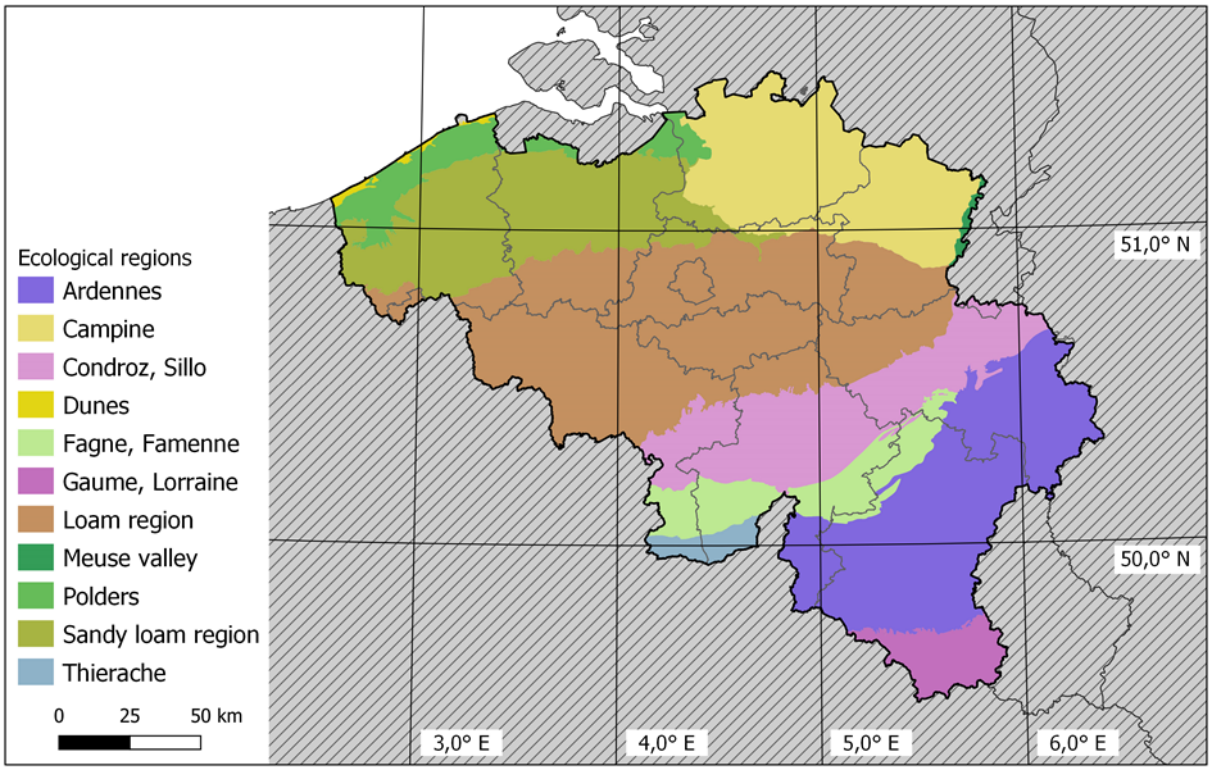
We composed a list of 39 detailed habitats (see appendix A Table A.1), combined into 16 synthesis habitats that could be allocated to four general habitats (Table 1). For every location, the detailed habitat was identified and subsequently the corresponding general and synthesis habitat were linked (see appendix A Table A.1). We maintained one record per species per synthesis habitat per 10 × 10 km² square to build up the habitat dataset. In this way we corrected for geographical observer bias. This resulted in 6222 records evenly distributed across the country (Table 2, Map B.1 in appendix B). The records for each species are presented in tabular form (Tables 4 to 38) and on a species-specific distribution map (Maps 2 to 36) with different markers per general habitat type. The map of the ecological regions in Belgium (Map 1) serves as background.

PHENOLOGY DATASET

All records retrieved from pitfall trap surveys were removed from the phenology dataset if they were not sampled year-round. All analysis of the phenology dataset was based on a two-month interval to allow for a maximum number of records per interval but still have multiple periods to compare. The climatic conditions in Belgium are rather similar for the two months of each period. We maintained one record per species per synthesis habitat per 10 × 10 km² square per two-month period and per year to build up the phenology dataset. This resulted in 7628 records evenly distributed across the country (Table 2, Map B.2 in appendix B).

The phenology diagrams of the species are based on the number of records per two-month period, which is in the present study considered as an accurate proxy to analyse seasonal activity patterns. This was done for three out of four general habitat types separately, being “forest”, “anthropogenic” and “open landscape”. The general habitat “coast” is included in “open landscape” for sake of readability.

Since there was no regular interval for the field surveys, it is necessary to correct for the variation in search effort throughout the year when analyzing the phenology data. We calculated



Map 1. The ecological regions in Belgium.

a correction factor ($f_{p,h}$) per main habitat type ($_h$) and per two-months ($_p$) by dividing the average number of visited locations in a particular habitat per two-month period ($\overline{L}_h$) by the number of visited locations in the same habitat during the two-month period ($L_{p,h}$) (Formula 1). An $f_{p,h}$ lower than one indicates that this habitat type was over-recorded during a particular two-month period and an $f_{p,h}$ higher than one indicates that the particular habitat was under-recorded (Table 3). For each species a corrected number of records (cN) is calculated for the three different main habitat types separately and per two-month period by multiplying the number of records in the phenology dataset for a certain species in a certain habitat during a two-month period ($N_{p,h}$, see Appendix C Table C.1) by its correction factor ($f_{p,h}$) (Formula 2). This corrected number is used in the phenology diagrams.

Formula 1: $f_{p,h} = \overline{L}_h / L_{p,h}$

Formula 2: $cN = N_{p,h} \times f_{p,h}$

Table 3. Number of visited locations ($L_{p,h}$) and correction factors ($f_{p,h}$) for the three main habitat types and per two-months.

	anthropogenic		**forest**		**open landscape**	
	$L_{p,h}$	**$f_{p,h}$**	**$L_{p,h}$**	**$f_{p,h}$**	**$L_{p,h}$**	**$f_{p,h}$**
January, February	151	1.12	123	1.29	82	1.08
March, April	160	1.06	180	0.88	109	0.81
May, June	156	1.08	159	1.00	102	0.87
July, August	126	1.34	149	1.07	61	1.45
September, October	162	1.04	168	0.95	77	1.14
November, December	259	0.65	176	0.90	100	0.89
Total	**917**		**847**		**474**	
Average ($\overline{L}_h$)	**169.0**		**159.2**		**88.5**	

ORDINATION ANALYSIS

In order to summarize the datasets in one visual representation, we ran two principal component analyses (PCA); one based on the habitat dataset and one based on the phenology dataset. The input of the habitat PCA was the percentage of records for each general habitat type for every individual species. Since relatively few observations were made at the coastal region, we added these observations to open landscape habitat. We only included species with at least 10 records (28 species) in the PCA with habitat data as input. We stepwise excluded the species with the lowest number of records until a readable PCA was obtained. In this way, outliers are excluded which prevent a good readability of the graph. The input of the phenology PCA was the percentage of the corrected number of records (cN) for each species for each two-month period. We only included species with at least 70 corrected number of records (21 species). PCA analyses were performed using the *FactoMineR*- package (HUSSON *et al.*, 2020) and visualized using the *factoextra*-package (KASSAMBARA & MUNDT, 2020) in R (R CORE TEAM, 2020).

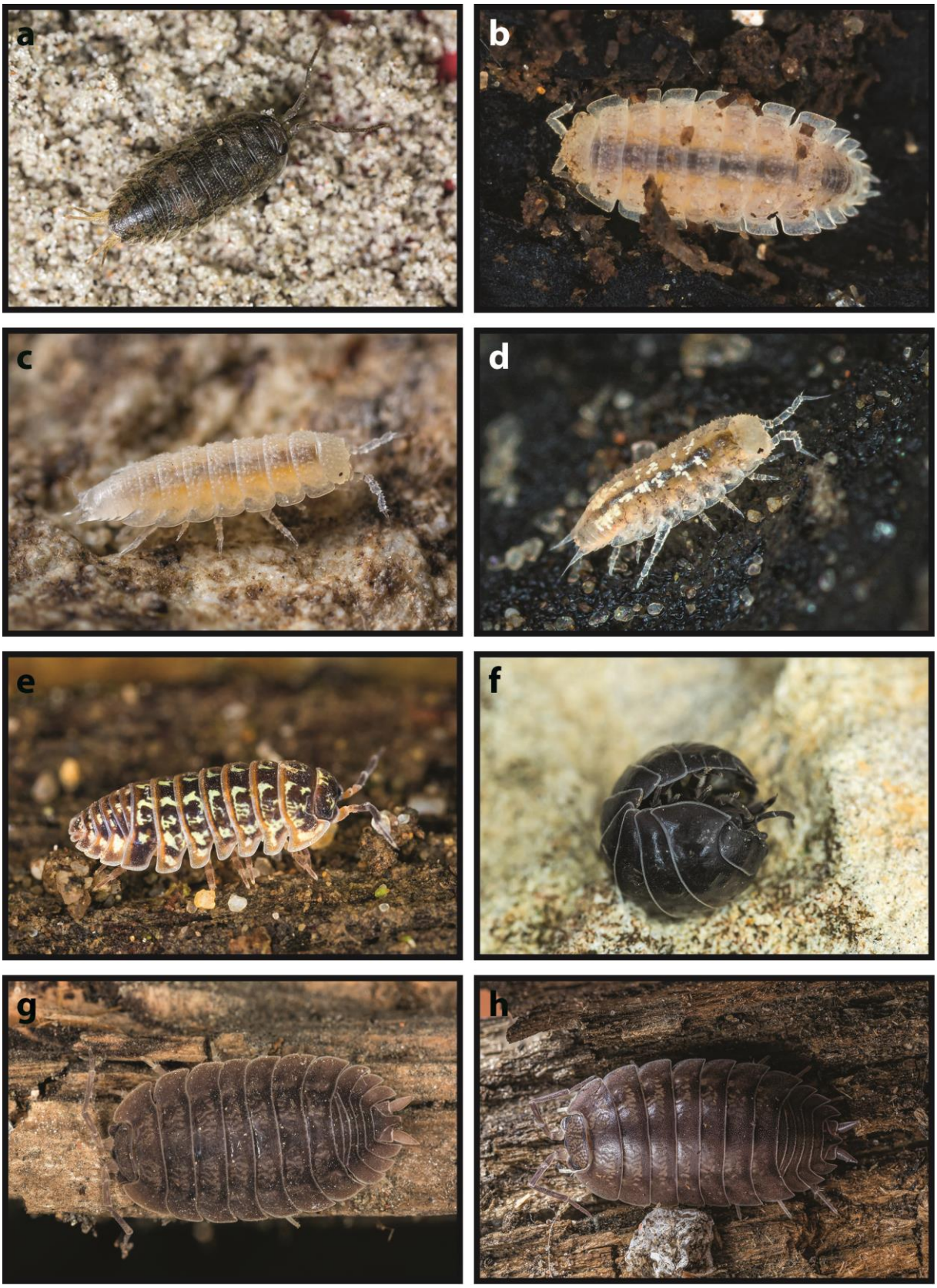
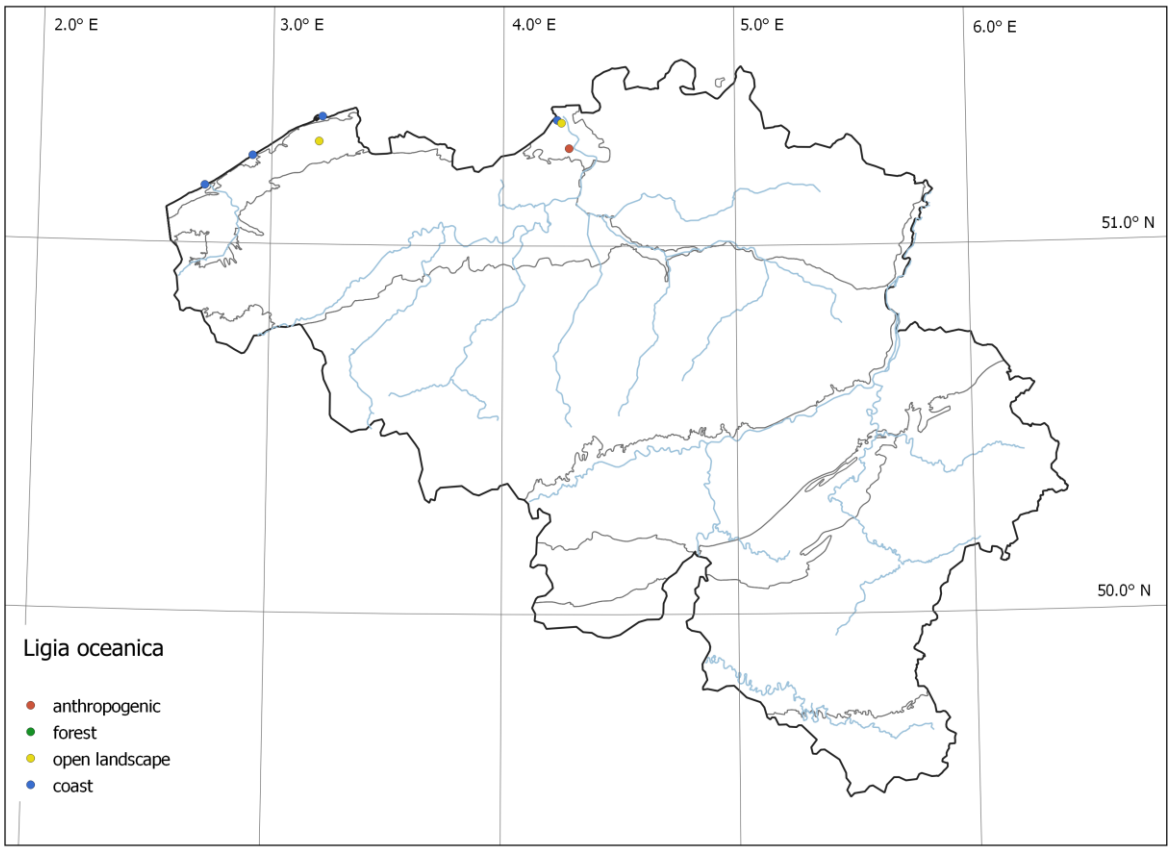


Fig. 2. a, *Ligia oceanica*; b, *Haplophthalmus danicus*; c, *Miktoniscus patience*; d, *Trichoniscus pygmaeus*; e, *Armadillidium pictum*; f, *Armadillidium vulgare*; g, *Porcellio dilatatus*; h, *Porcellio laevis*.

Results and discussion

1. *Ligia oceanica* (Linnaeus, 1767)
(Fig. 2 a, Fig. 3, Map 2, Table 4)



Map 2. Distribution map for *Ligia oceanica*.

A species bound to coastal habitat with human-made structures with plenty of small crevices, like breakwaters, sea dykes and harbour walls. In these habitats, *Ligia oceanica* can be very common and easily found. Occasionally found further inland but then always near brackish water, e.g. dykes of canals in direct connection to a harbour or tidal rivers close to the sea. The number of observations is low, mainly due to the limited amount of coastal habitat in Belgium. However, an extensive survey in the 1980's has proved that the species is very common along the coast in the above-described habitat (TAVERNIER & WOUTERS, 1986). There is no reason to expect that this species is less common nowadays. *L. oceanica* is nocturnal (HARDING & SUTTON, 1985) and it can be very hard to find the species when it is hidden, in particular when there are no objects to turn in search for the species like e.g. on wave breakers. Therefore, nocturnal surveys could result in new observations.

The low number of observations (Fig. 3) indicates that the species' phenology should be interpreted with care. Although, it seems like the species is less commonly found during summer, possibly because of its low desiccation resistance (DIAS *et al.*, 2013). Therefore, we recommend additional year-round surveys to get a better understanding about the species' phenology.

Table 4. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Ligia oceanica*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**1**	**14.3%**
farm	0	0.0%		
gardens and parks	0	0.0%		
near water in urban area	1	100.0%		
near roads and buildings in urban area	0	0.0%		
graveyard	0	0.0%		
forest			**0**	**0.0%**
coniferous forest	0	0.0%		
deciduous forest	0	0.0%		
near water in deciduous forest	0	0.0%		
near roads and buildings in forest	0	0.0%		
open landscape			**2**	**28.6%**
cropland and orchards	0	0.0%		
grassland	0	0.0%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	0	0.0%		
near water in open landscape	0	0.0%		
river or canal dykes	2	100.0%		
coast			**4**	**57.1%**
total			**7**	

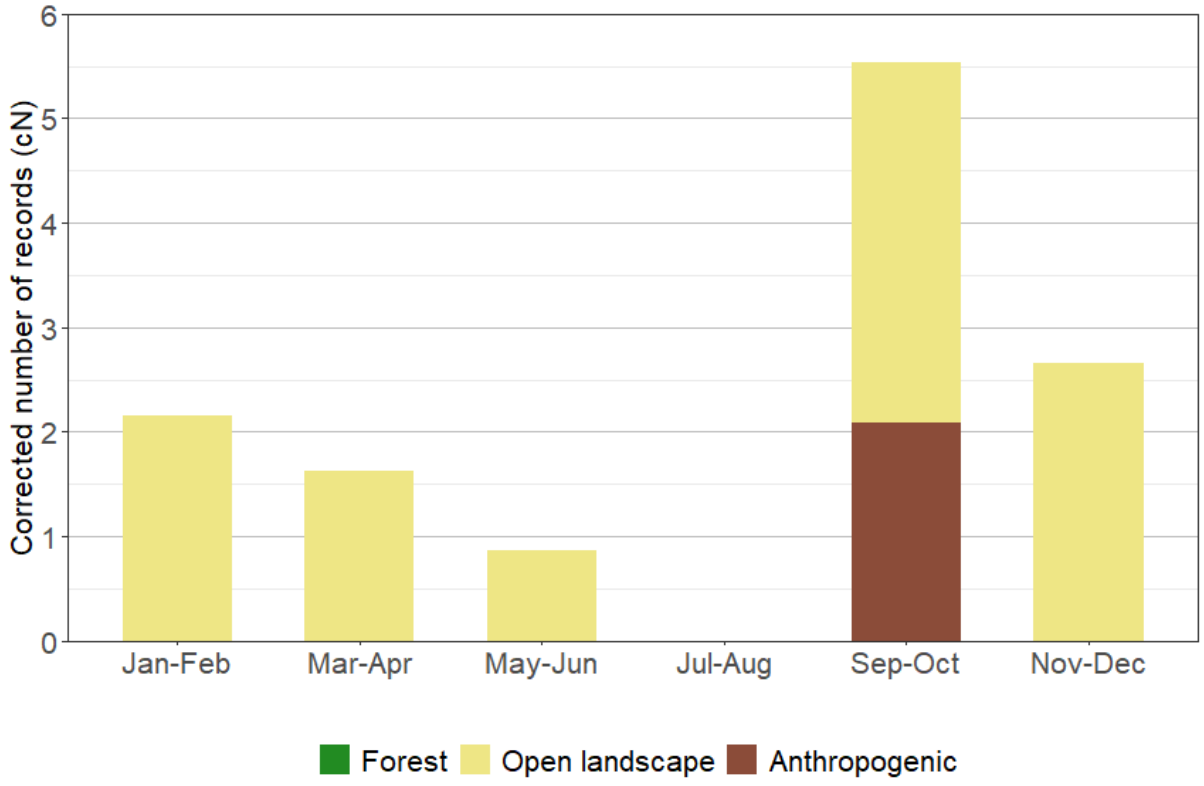
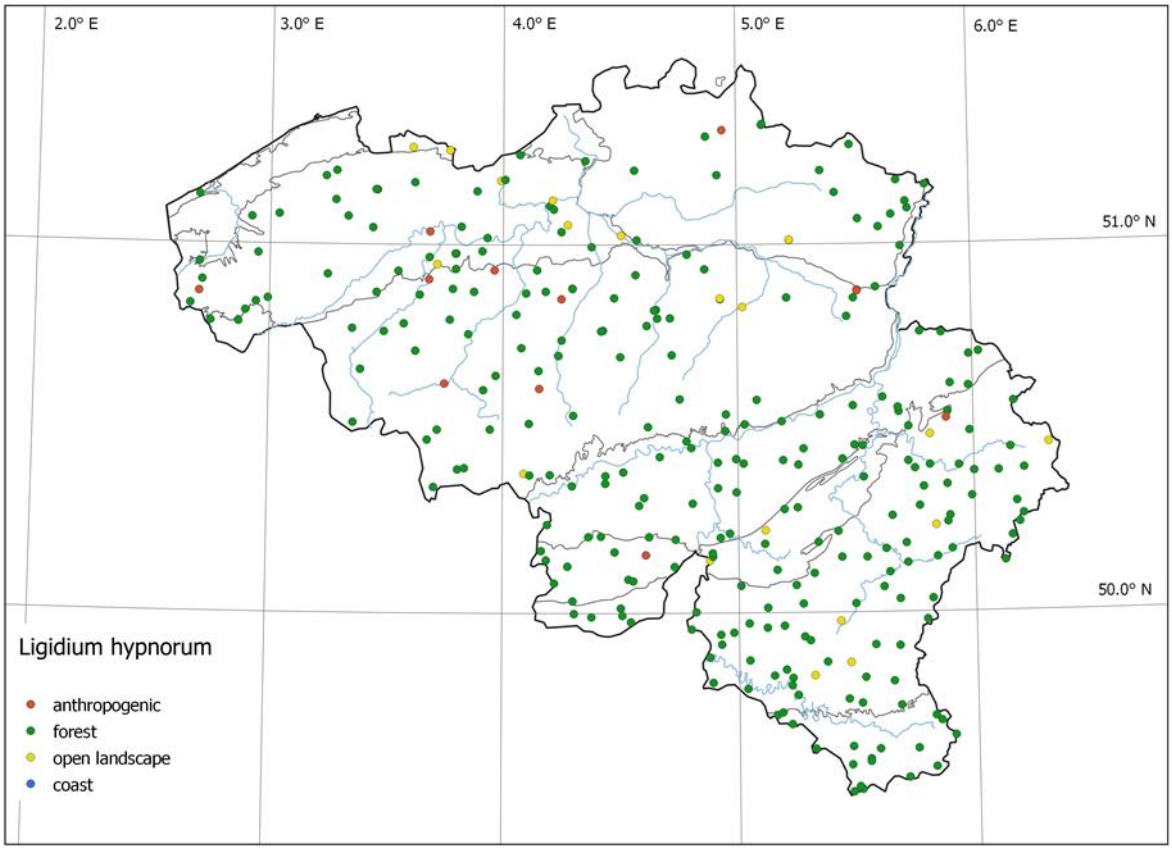


Fig. 3. Corrected number of observations per two-month period for *Ligia oceanica* (N = 13).

2. *Ligidium hypnorum* (Cuvier, 1792)
(Fig. 4, Fig. 11 a, Map 3, Table 5)



Map 3. Distribution map for *Ligidium hypnorum*.

Deciduous forest is the most important habitat for *Ligidium hypnorum* and in this habitat the species is very common and can occur in high numbers. As a drought-sensitive species, *L hypnorum* prefers wet conditions in forests and an important share of the observations were made along ditches, streams and riverbanks in forests (Table 5). In Belgium (and across Western Europe), the species seems to strongly favour forest interiors because they have a higher humidity compared to forest edges (DE SMEDT *et al.*, 2018d). Although *L. hypnorum* is a characteristic species of closed forest habitat (DE SMEDT *et al.*, 2020b), the species can also be recorded in gardens, parks, grasslands and at stream- and riverbanks in open landscapes (Table 5). Since hand collection is more challenging in grasslands and other open habitats, the species could be under recorded in open landscape habitats in the present study. The distribution map shows that the species is less common or absent in certain regions, mostly regions with low deciduous forest cover (like the northern part of the country).

The species was more commonly found in the months March–April, July–August and November–December (Fig. 4). This is probably a random pattern and we assume that *L. hypnorum* activity pattern is quite constant during the year. Its dominant breeding period is summer (June–July) (ZIMMER & BRAUCKMANN, 1997), a pattern that is absent in the phenological diagram.

Table 5. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Ligidium hypnorum*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**13**	**4.4%**
farm	0	0.0%		
gardens and parks	12	92.3%		
near water in urban area	1	7.7%		
near roads and buildings in urban area	0	0.0%		
graveyard	0	0.0%		
forest			**263**	**89.2%**
coniferous forest	0	0.0%		
deciduous forest	144	54.8%		
near water in deciduous forest	109	41.4%		
near roads and buildings in forest	10	3.8%		
open landscape			**19**	**6.4%**
cropland and orchards	1	5.3%		
grassland	5	26.3%		
disused quarry	1	5.3%		
near roads and buildings in open landscape	1	5.3%		
near water in open landscape	7	36.8%		
river or canal dykes	4	21.1%		
coast			**0**	**0.0%**
total			**295**	

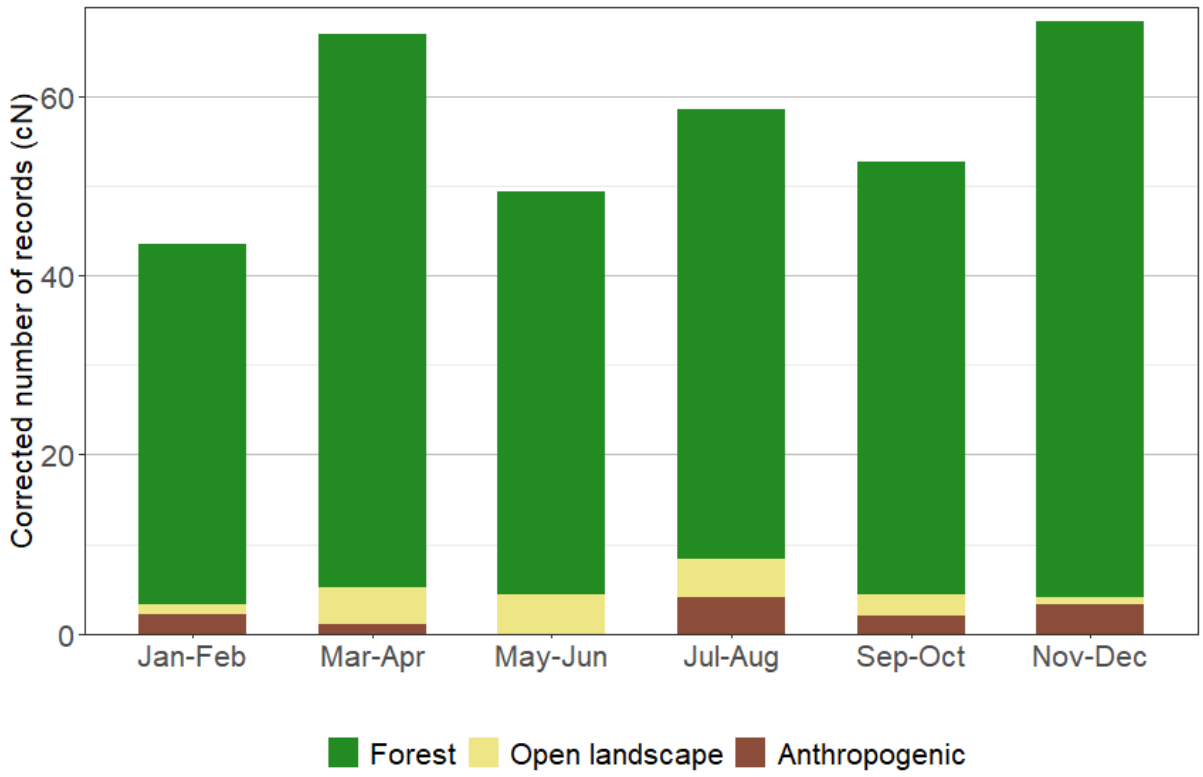
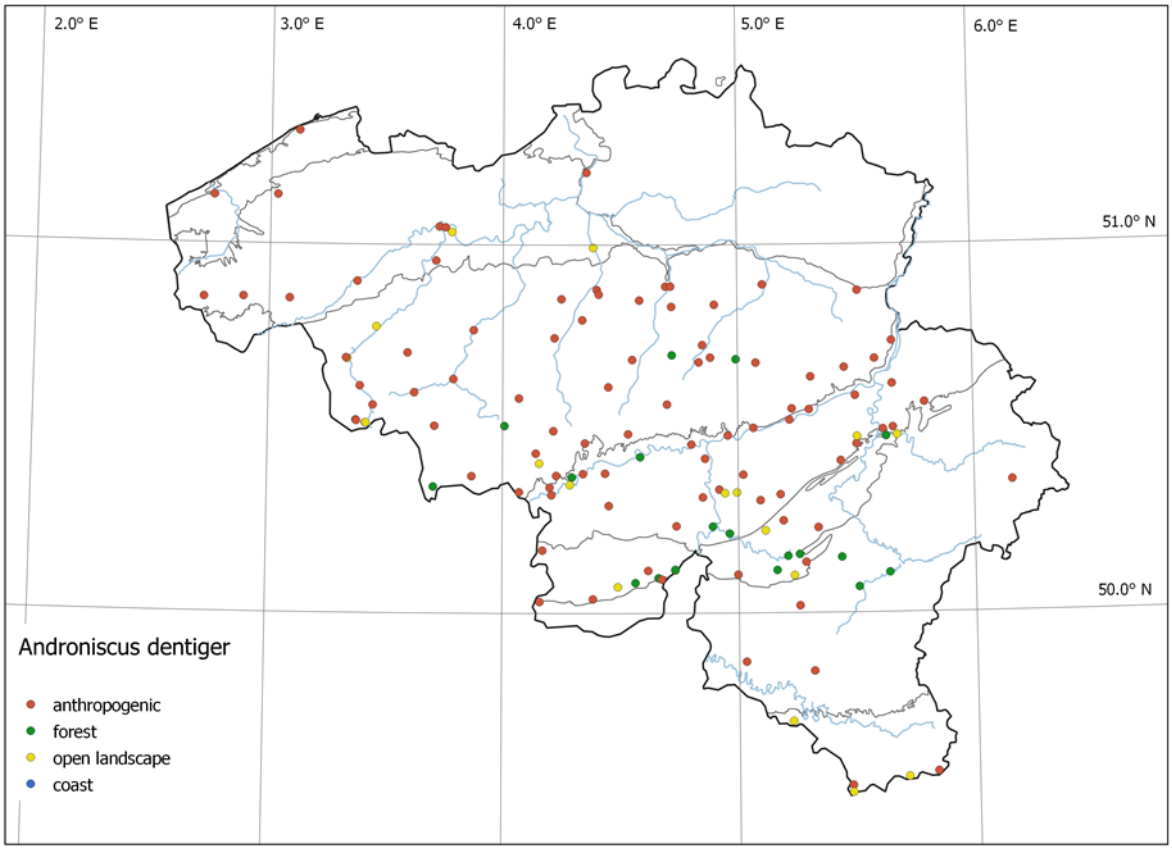


Fig. 4. Corrected number of observations per two-month period for *Ligidium hypnorum* (N = 345).

3. ***Androniscus dentiger*** Verhoeff, 1908
(Fig. 5, Fig. 11 b, Map 4, Table 6)



Map 4. Distribution map for *Androniscus dentiger*.

A species commonly found in anthropogenic habitats but there are also a number of records from forests and open landscapes (Table 6). In the northern part of the country *Androniscus dentiger* is mostly found in anthropogenic habitats in urban areas, with other records situated in habitats with at least some degree of human influence, like gardens, river dykes and near buildings in open landscape. In southern Belgium the species also occurs in forests, with some locations having a clear human influence (roads or buildings) but others not. In the last case, it concerns observations of the species at stream- or riverbanks and mostly in areas with calcareous soil. Based on the numerous records in habitats with human influence, e.g. graveyards, gardens, parks and old quarries, it can be presumed that dispersion by human activity is an important vector for its dispersion. *A. dentiger* is known to be troglophile (VANDEL, 1960; GREGORY, 2009) but no caves were searched for isopods during the 2014–2020 field surveys. The species has been found in caves in Belgium in the 1930's and 1980's, see DE SMEDT *et al*. (2018b) for all literature references.

Androniscus dentiger seems to be more active in open landscape during winter months (Fig. 5), possibly because these habitats are too dry in summer months. In anthropogenic habitats the lowest corrected number of records is in January–February, followed by the highest number in March–April. From May until August *A. dentiger* appears to be slightly less active than in the months September until December. Since this species has a Mediterranean origin (VANDEL, 1960) and seems to prefer wet microhabitats, the pattern in phenology might be explained by a combination of low temperatures in January-February and dryer conditions in the summer months.

Table 6. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Androniscus dentiger*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**92**	**71.3%**
farm	2	2.2%		
gardens and parks	10	10.9%		
near water in urban area	4	4.3%		
near roads and buildings in urban area	13	14.1%		
graveyard	63	68.5%		
forest			**18**	**14.0%**
coniferous forest	0	0.0%		
deciduous forest	3	16.7%		
near water in deciduous forest	8	44.4%		
near roads and buildings in forest	7	38.9%		
open landscape			**19**	**14.7%**
cropland and orchards	0	0.0%		
grassland	1	5.3%		
disused quarry	9	47.4%		
near roads and buildings in open landscape	2	10.5%		
near water in open landscape	3	15.8%		
river or canal dykes	4	21.1%		
coast			**0**	**0.0%**
total			**129**	

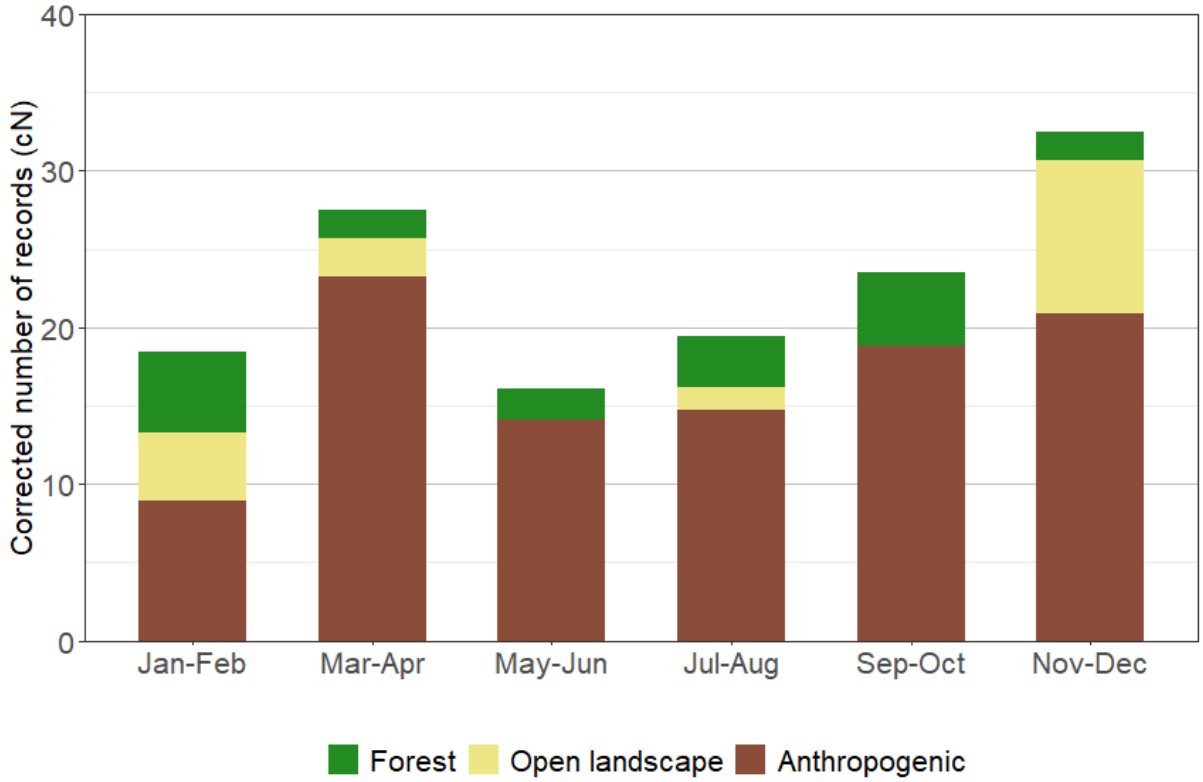
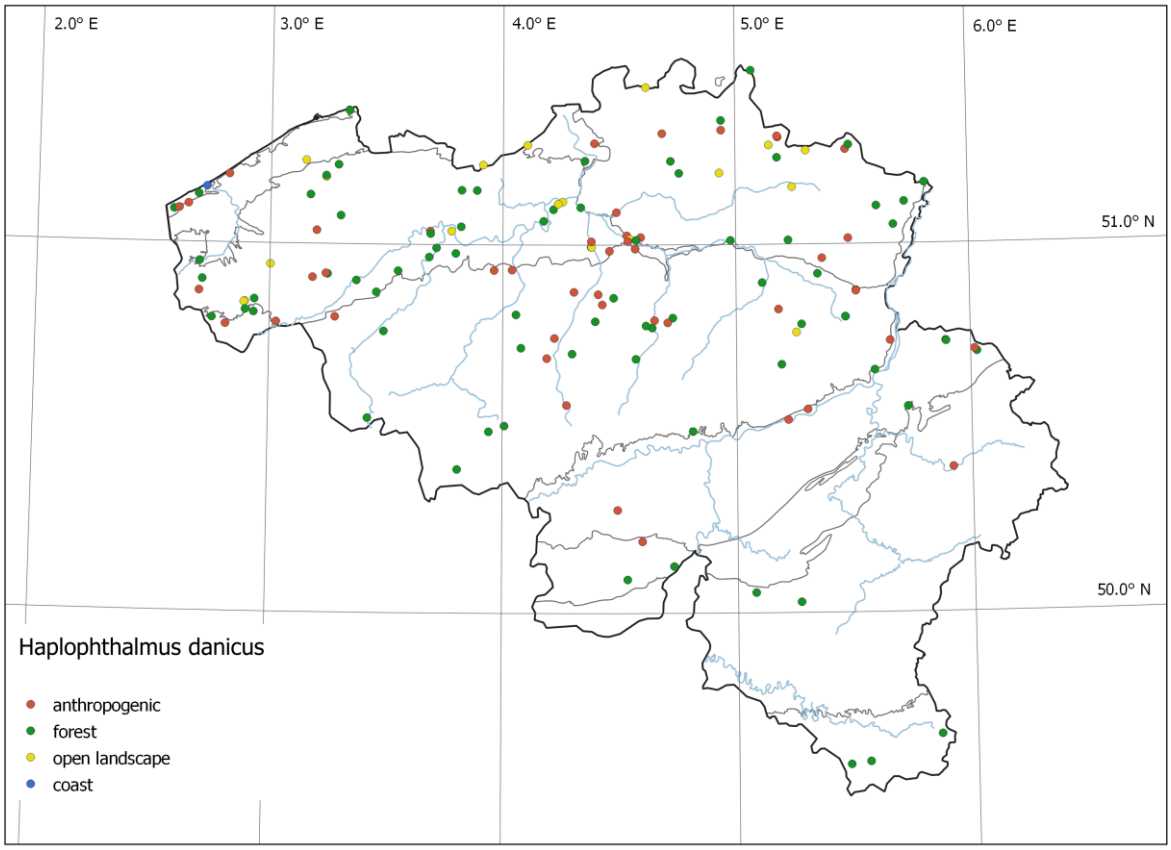


Fig. 5. Corrected number of observations per two-month period for *Androniscus dentiger* (N = 141).

4. ***Haplophthalmus danicus*** Budde-Lund, 1880
(Fig. 2 b, Fig. 6, Map 5, Table 7)



Map 5. Distribution map for *Haplophthalmus danicus*.

A small species occurring in a wide range of habitats (Table 7) and more common in the northern part of the country (Map 5). The species is common as well on the sandy soils in the Campine region in contrast to most other species. In the south, the species is absent from open landscape habitat. The species is mostly found in the humus layer or in decaying wood or other organic material and this results in more than 50% of the records located in forest habitats (Table 7). In anthropogenic habitat, *H. danicus* occurs commonly in gardens and parks, where compost heaps are favoured.

In both anthropogenic and forest habitats, *H. danicus* is more commonly found during winter months (Fig. 6) (see also DE SMEDT *et al.*, 2021). This pattern is less clear in open landscapes, possibly due to the limited number of records in this habitat. Despite being more commonly found in colder months, the species is less common in southern Belgium, where average temperatures are lower throughout the year. This could indicate a low tolerance for low temperatures. *H. danicus* is a drought-sensitive species (DIAS *et al.*, 2013) and we can assume that the lower humidity during summer months causes a decrease in observations because the species retreats deeper into the soil.

Table 7. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Haplophthalmus danicus*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**47**	**33.1%**
farm	1	2.1%		
gardens and parks	25	53.2%		
near water in urban area	6	12.8%		
near roads and buildings in urban area	0	0.0%		
graveyard	15	31.9%		
forest			**75**	**52.8%**
coniferous forest	0	0.0%		
deciduous forest	47	62.7%		
near water in deciduous forest	24	32.0%		
near roads and buildings in forest	4	5.3%		
open landscape			**18**	**12.7%**
cropland and orchards	0	0.0%		
grassland	5	27.8%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	7	38.9%		
near water in open landscape	2	11.1%		
river or canal dykes	4	22.2%		
coast			**2**	**1.4%**
total			**142**	

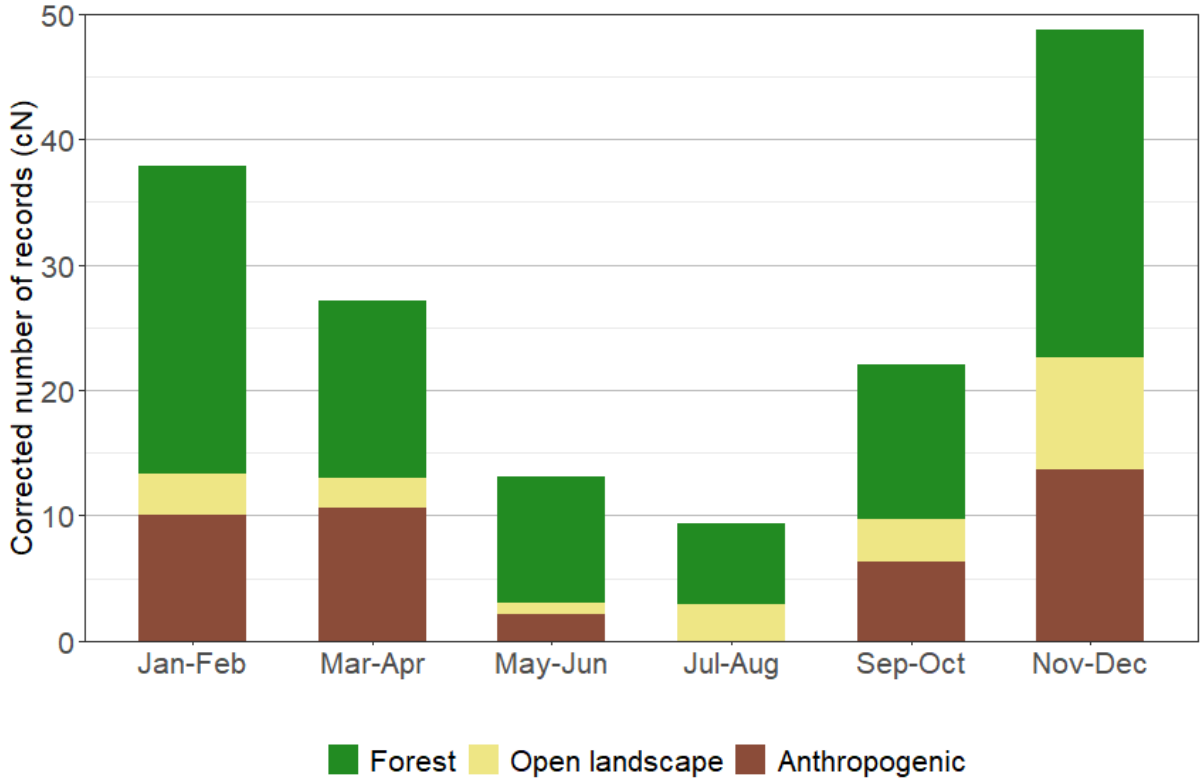
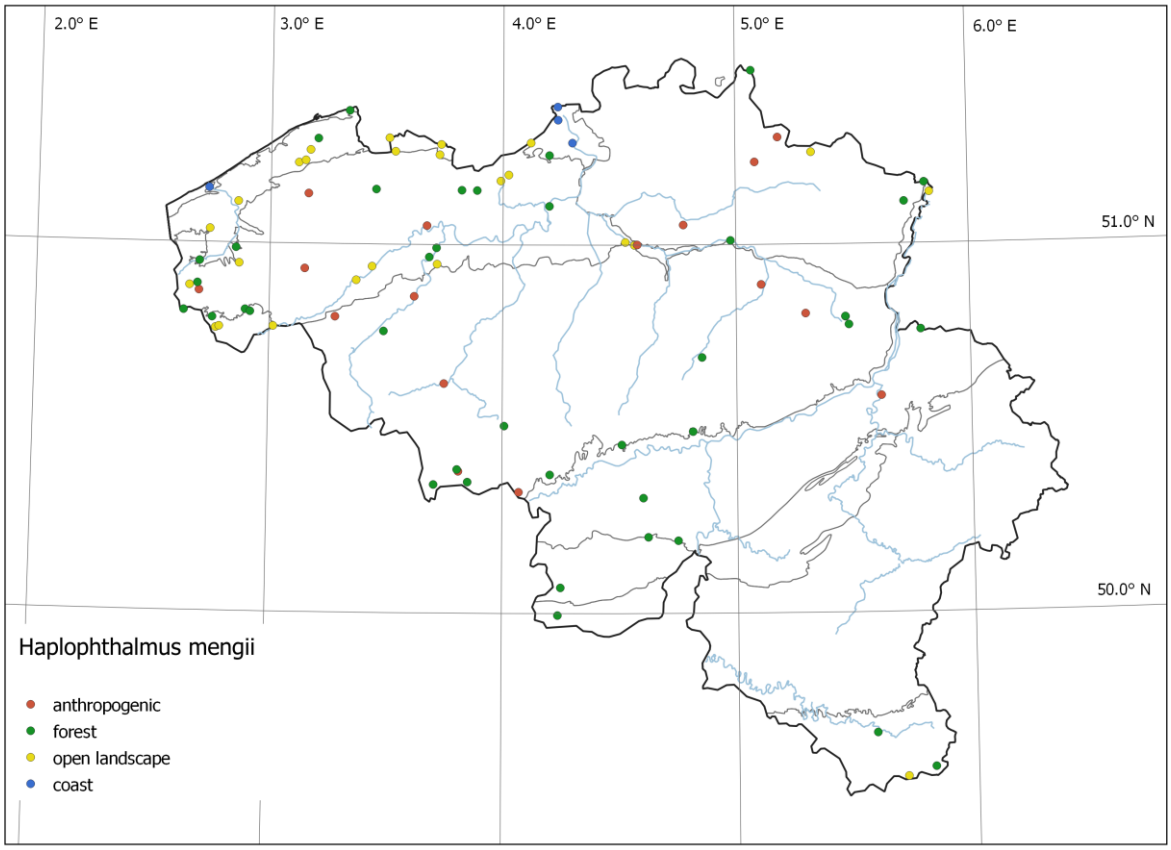


Fig. 6. Corrected number of observations per two-month period for *Haplophthalmus danicus* (N = 163).

5. ***Haplophthalmus mengii*** (Zaddach, 1844)
(Fig. 7, Fig. 11 c, Map 6, Table 8)



Map 6. Distribution map for *Haplophthalmus mengii*.

Similar to the other *Haplophthalmus*-species *H. mengii* is found in a wide variety of landscapes and habitats. Compared to *H. danicus* and *H. montivagus*, the species was less frequently observed in graveyards, parks and gardens. Since the species is only occasionally found in anthropogenic habitats and the records are not clustered in a certain geographic region, we cannot consider the species a synanthropic species, as in the Netherlands (BERG *et al.*, 2008). Depending on the habitat type the species is more or less bound to water. In anthropogenic habitats only 12.5% of the observations were near streams, rivers and canals (Table 8). In forest habitat, this rate rises to 42.5% and in open landscapes even to 76%. Records in open landscape are mostly limited to the polder and sand-loam ecological region (Map 6). In Southern Belgium, the species is mostly found in forests and categorized as a species with strong forest affinity (DE SMEDT *et al.*, 2020b).

The number of observations of *H. mengii* in forest habitat throughout the year is more or less constant (Fig. 7), possibly due to the more stable moisture conditions in forest habitat. The number of observations is however strongly reduced during summer months in open landscapes. In open habitat types the species is mostly found near water and so during summer months they probably crawl deeper into the soil because of lower soil humidity.

Table 8. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Haplophthalmus mengii*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**16**	**18.8%**
farm	0	0.0%		
gardens and parks	7	43.8%		
near water in urban area	2	12.5%		
near roads and buildings in urban area	1	6.3%		
graveyard	6	37.5%		
forest			**40**	**47.1%**
coniferous forest	0	0.0%		
deciduous forest	20	50.0%		
near water in deciduous forest	17	42.5%		
near roads and buildings in forest	3	7.5%		
open landscape			**25**	**29.4%**
cropland and orchards	0	0.0%		
grassland	0	0.0%		
disused quarry	1	4.0%		
near roads and buildings in open landscape	5	20.0%		
near water in open landscape	12	48.0%		
river or canal dykes	7	28.0%		
coast			**4**	**4.7%**
total			**85**	

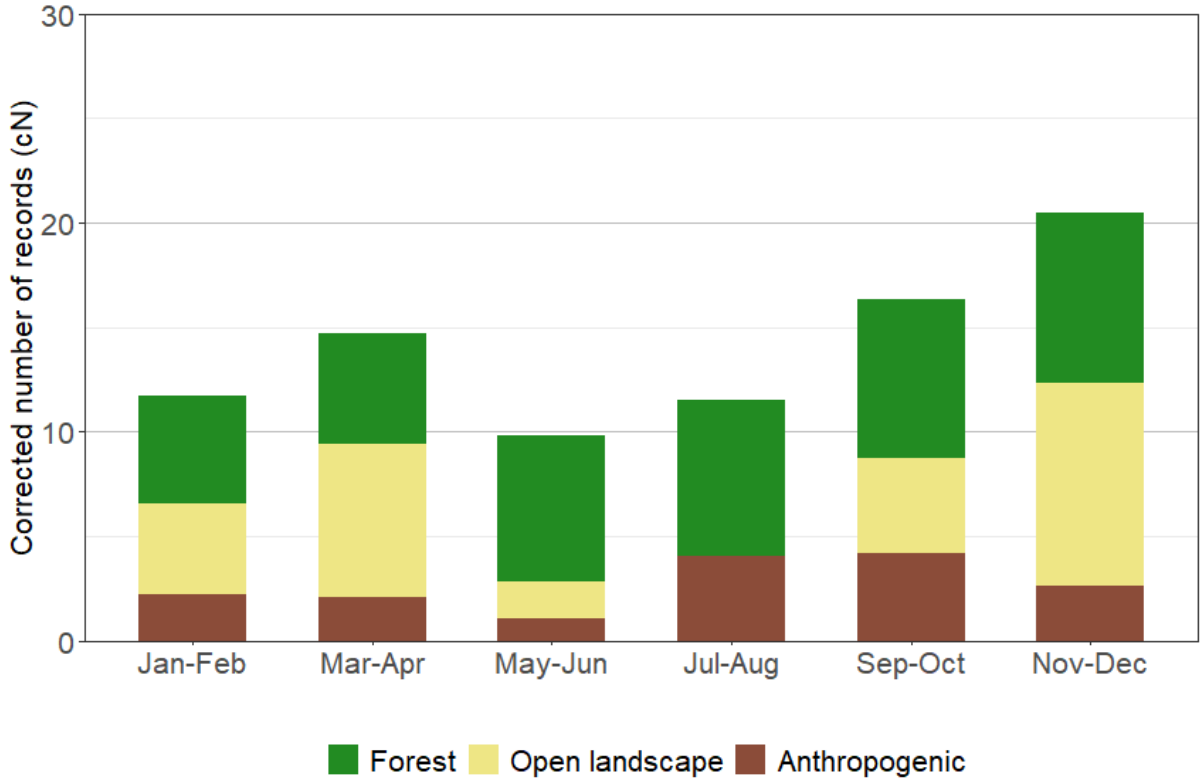
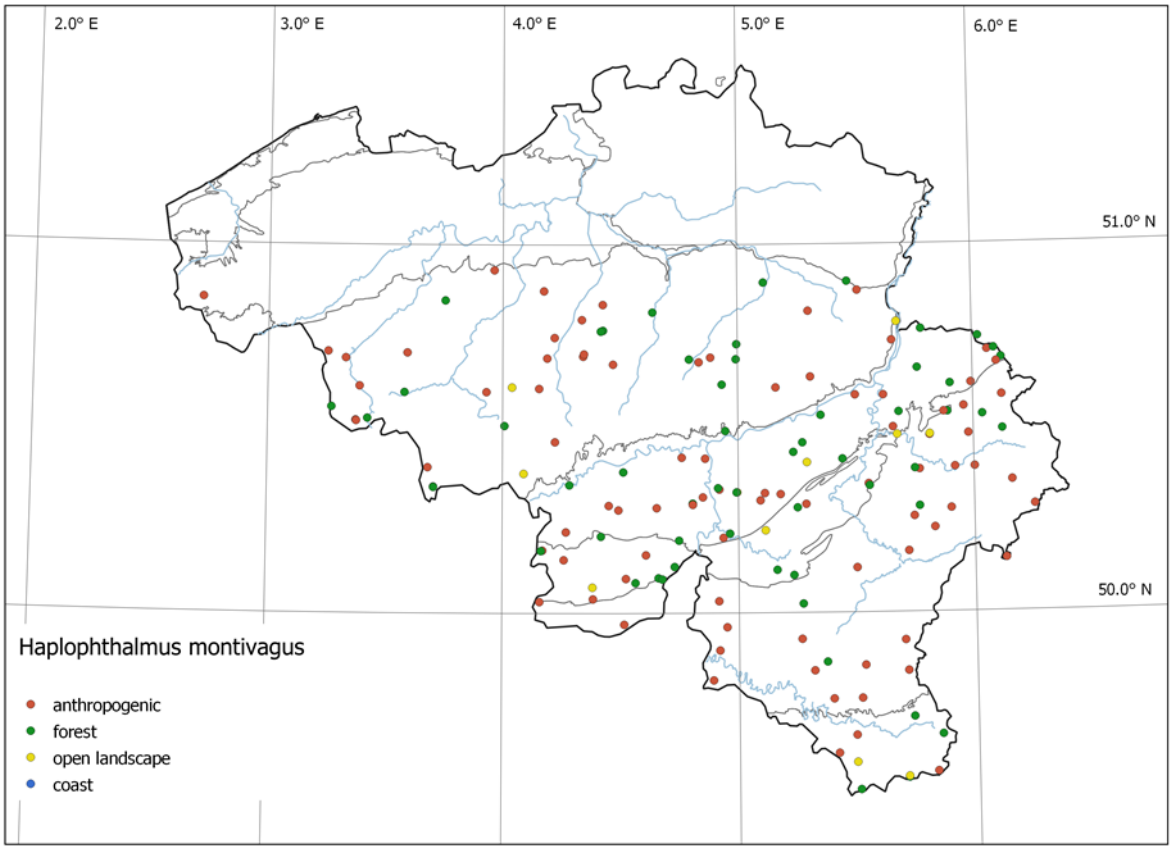


Figure 7. Corrected number of observations per two-month period for *Haplophthalmus mengii* (N = 87).

6. ***Haplophthalmus montivagus*** Verhoeff, 1941
(Fig. 8, Map 7, Table 9)



Map 7. Distribution map for *Haplophthalmus montivagus*.

Haplophthalmus montivagus closely resembles *H. mengii* (Fig. 11 c) and was only discovered for the first time in Belgium in 2006 (LOCK, 2007). Despite the close resemblance to *H. mengii,* it has a very different habitat use. It has a more southern distribution than *H. mengii* and is more frequently found in anthropogenic habitat. It is less confined to forests and open landscapes compared to *H. mengii*. In anthropogenic habitat, only 10.6% of locations were close to water but in forests *H. montivagus* is clearly bound to water, with 67.9% of records made at ditches and stream and river banks (Table 9). This is higher than for *H. mengii* (42.5%).

For the anthropogenic habitat, the lowest number of records was in January–February, followed by the highest number in March–April (Fig. 8). In May–June *H. montivagus* was slightly less observed than in the months July until December. This is a similar pattern compared with *Androniscus dentiger*, a species with a very similar number of observations in anthropogenic habitats and graveyards in particular (92 records and 68.5% in graveyards). In forests, the lowest corrected number of records is for the months January–February, which can probably be attributed to low temperatures and higher amount of frosty days in those months in southern Belgium. For September–October, it is less clear why the corrected number of records is rather low in forests.

Table 9. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Haplophthalmus montivagus*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**85**	**55.9%**
farm	0	0.0%		
gardens and parks	10	11.8%		
near water in urban area	9	10.6%		
near roads and buildings in urban area	6	7.1%		
graveyard	60	70.6%		
forest			**56**	**36.8%**
coniferous forest	0	0.0%		
deciduous forest	13	23.2%		
near water in deciduous forest	38	67.9%		
near roads and buildings in forest	5	8.9%		
open landscape			**11**	**7.2%**
cropland and orchards	0	0.0%		
grassland	1	9.1%		
disused quarry	6	54.5%		
near roads and buildings in open landscape	0	0.0%		
near water in open landscape	4	36.4%		
river or canal dykes	0	0.0%		
coast			**0**	**0.0%**
total			**152**	

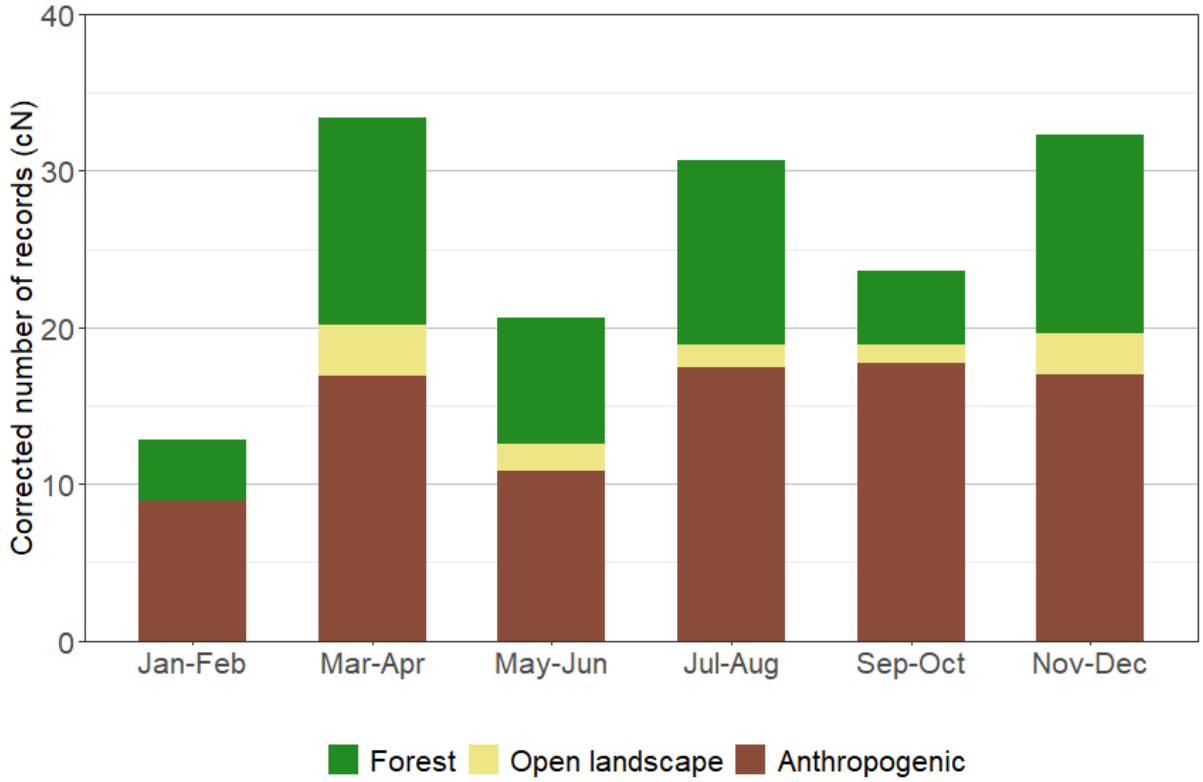
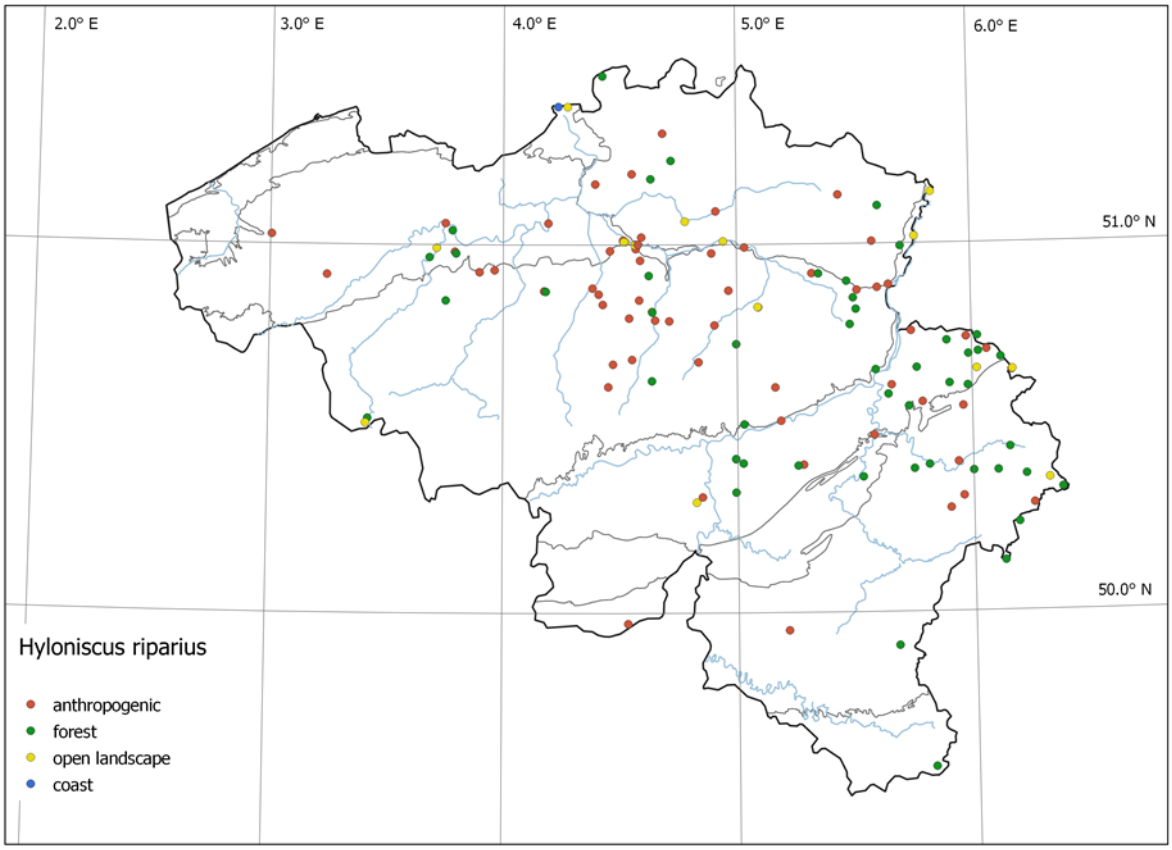


Fig. 8. Corrected number of observations per two-month period for *Haplophthalmus montivagus* (N = 157).

7. ***Hyloniscus riparius*** (C. Koch, 1838)
(Fig. 9, Fig. 11 d, Map 8, Table 10)



Map 8. Distribution map for *Hyloniscus riparius.*

In Belgium, *Hyloniscus riparius* reaches its western border of its distribution in Europe. DE SMEDT *et al.* (2020a) conclude that the species has relatively recently appeared in Belgium, mostly based on its absence in museum collections (DE SMEDT *et al.*, 2018b). Therefore, the species may still be expanding its distribution in Belgium to the west. The species is also expanding its range on a European scale from its original distribution in Central and Eastern Europe (SCHMALFUSS, 2003) to further west in France (SÉCHET *et al.*, 2012). In the east, *H. riparius* has reached Russia (GONGALSKY *et al.*, 2013).

The species is mostly found in forests and in anthropogenic habitats (Table 10) but some observations were also made in open landscape. In the western part of Belgium, *H. riparius* is still rare, with an important number of observations in anthropogenic habitat, in contrast to the eastern part of Belgium where most records are from forests (Map 8). *H. riparius* has a very high inundation resistance (OOMS *et al.*, 2020) and is frequently found close to water, however there is a large difference in its affinity to water based on habitat type. In forests, 65.3% of records were near water whereas in anthropogenic habitats this rate stands at only 24.1% (Table 10).

H. riparius is in anthropogenic habitats mostly observed from September until December, with considerably lower numbers of records from January until August (Fig. 9). In forests, the corrected number of records is highest in May–June followed by November–December but it is unclear why detection is so much higher compared to other months.

Table 10. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Hyloniscus riparius.*

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**58**	**46.4%**
farm	1	1.7%		
gardens and parks	7	12.1%		
near water in urban area	14	24.1%		
near roads and buildings in urban area	15	25.9%		
graveyard	21	36.2%		
forest			**49**	**39.2%**
coniferous forest	0	0.0%		
deciduous forest	13	26.5%		
near water in deciduous forest	32	65.3%		
near roads and buildings in forest	4	8.2%		
open landscape			**17**	**13.6%**
cropland and orchards	0	0.0%		
grassland	3	17.6%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	4	23.5%		
near water in open landscape	5	29.4%		
river or canal dykes	5	29.4%		
coast			**1**	**0.8%**
total			**125**	

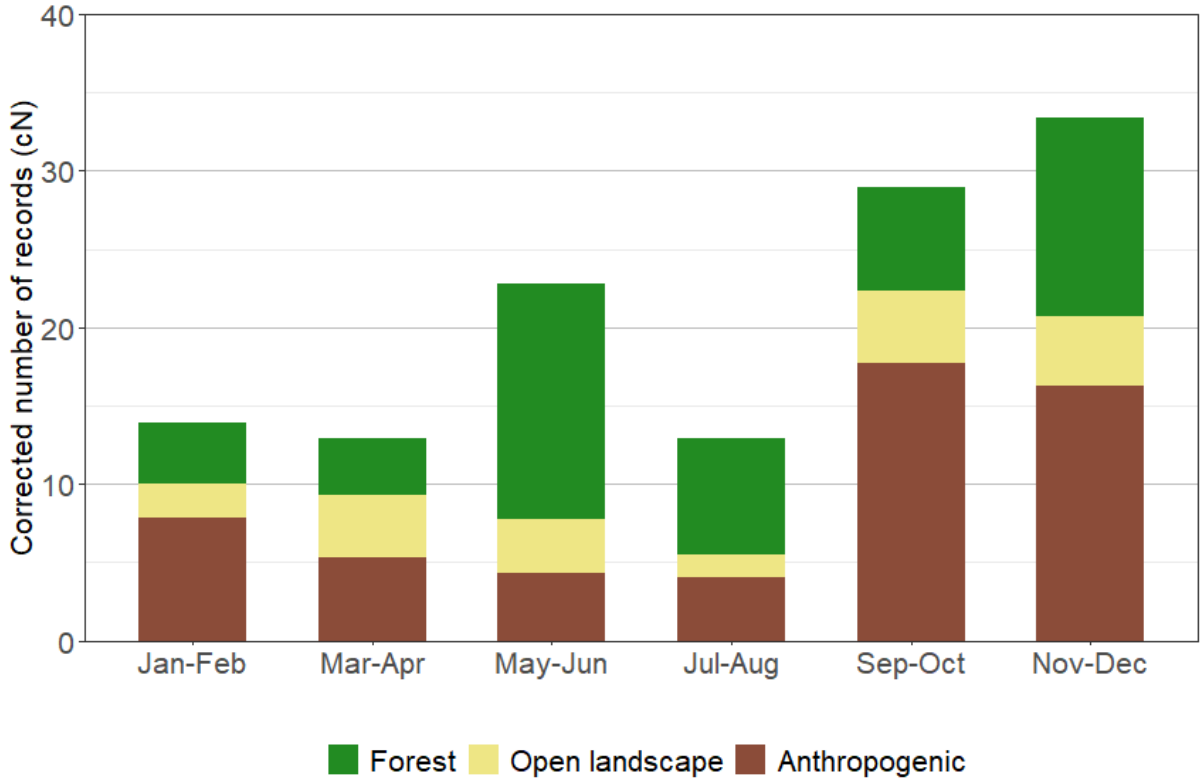
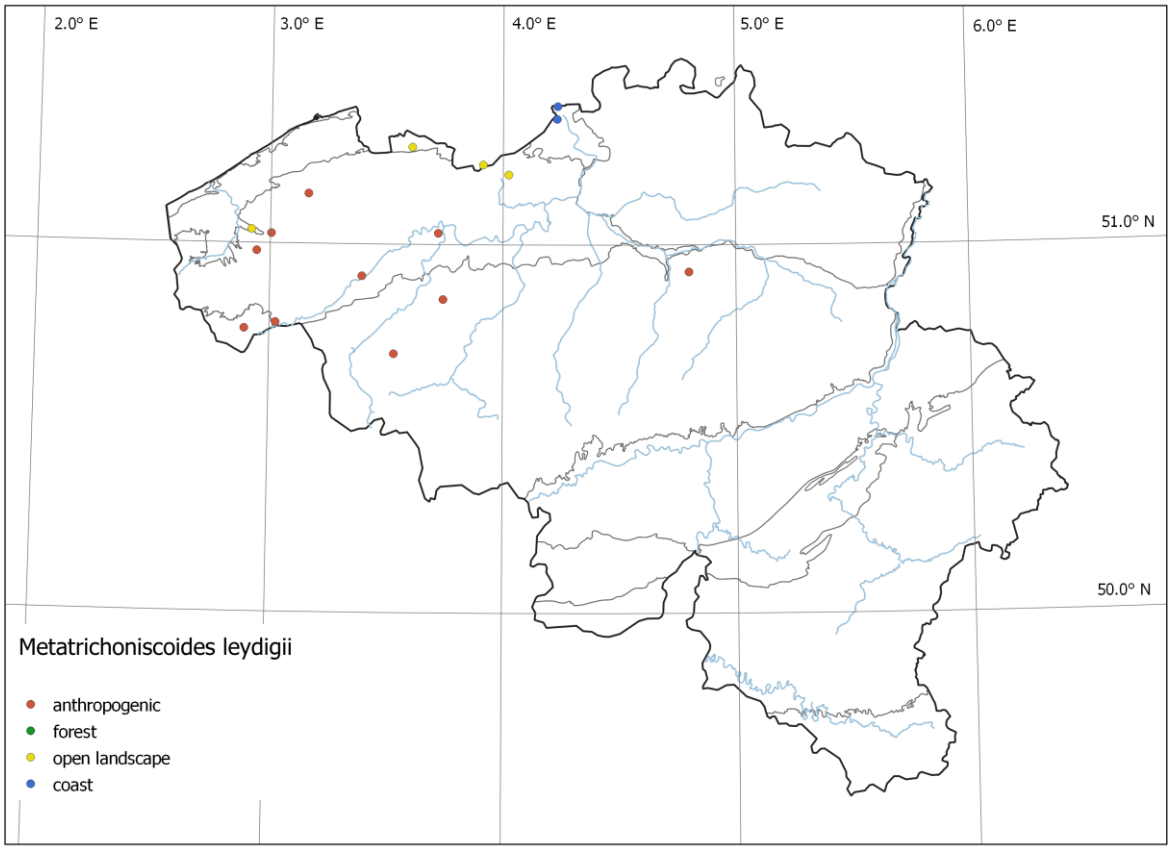


Fig. 9. Corrected number of observations per two-month period for *Hyloniscus riparius* (N = 132).

8. ***Metatrichoniscoides leydigii*** (Weber, 1880)
(Fig. 10, Fig. 11 e, Map 9, Table 11)



Map 9. Distribution map for *Metatrichoniscoides leydigii*.

This small and enigmatic species is only rarely found in Belgium since it lives somewhat deeper into the soil. Most observations of the species concern only a few individuals and this means that, together with its soil dwelling habits, it is a hard to find. We therefore assume that the species is still under-recorded in Belgium. *M. leydigii* is found in coastal habitat and in the ecological region of the polders in open landscape (Map 9), then mostly near water (Table 11). Further inland, the species is limited to anthropogenic habitats, such as graveyards, gardens and near roads and buildings in urban areas.

Due to limited data on this species, little can be concluded about its phenology (Fig. 10). However, most observations were done during the months September until December which can be assumed to be the period when the species migrates from deeper soil layers to the surface of the soil. *M. leydigii* is one of our most drought-sensitive species (DIAS *et al.*, 2013) and therefore extremely vulnerable to low moisture conditions at the soil surface during warmer months.

Table 11. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Metatrichoniscoides leydigii*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**10**	**62.5%**
farm	0	0.0%		
gardens and parks	1	10.0%		
near water in urban area	0	0.0%		
near roads and buildings in urban area	3	30.0%		
graveyard	6	60.0%		
forest			**0**	**0.0%**
coniferous forest	0	0.0%		
deciduous forest	0	0.0%		
near water in deciduous forest	0	0.0%		
near roads and buildings in forest	0	0.0%		
open landscape			**4**	**25.0%**
cropland and orchards	0	0.0%		
grassland	0	0.0%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	1	25.0%		
near water in open landscape	1	25.0%		
river or canal dykes	2	50.0%		
coast			**2**	**12.5%**
total			**16**	

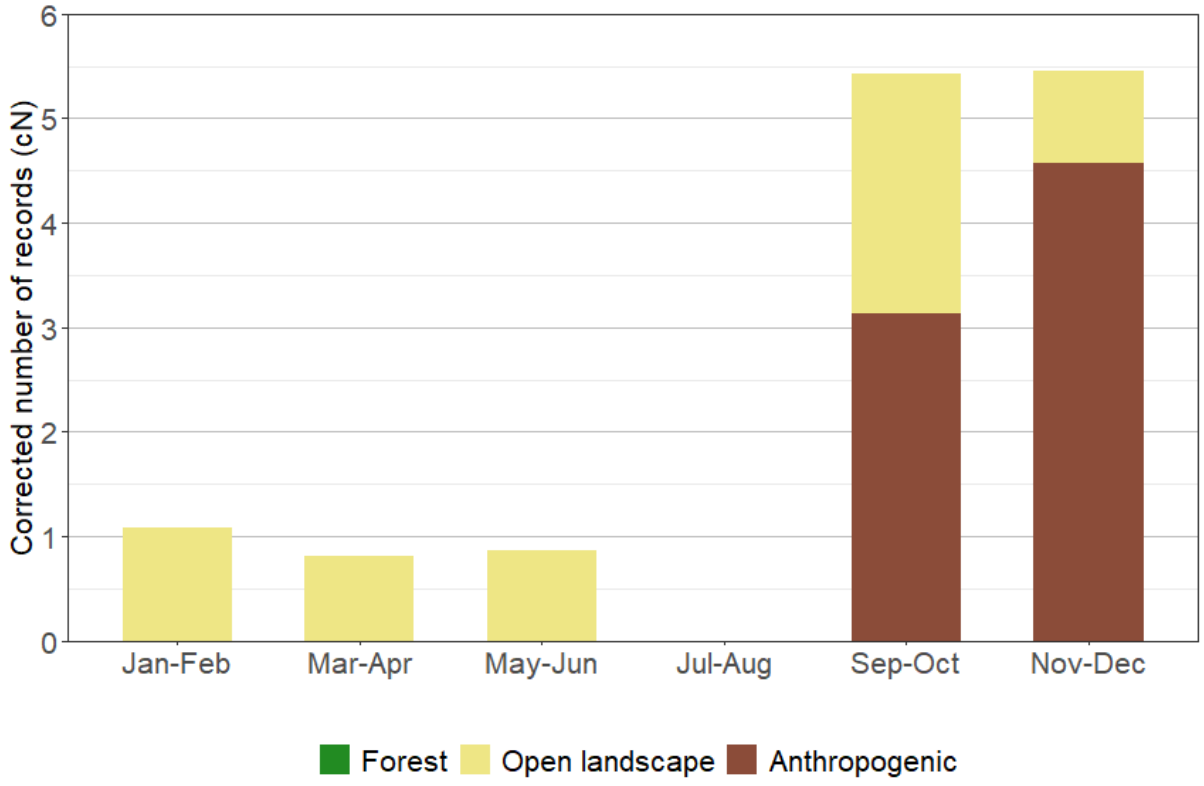


Fig. 10. Corrected number of observations per two-month period for *Metatrichoniscoides leydigii* (N = 16).

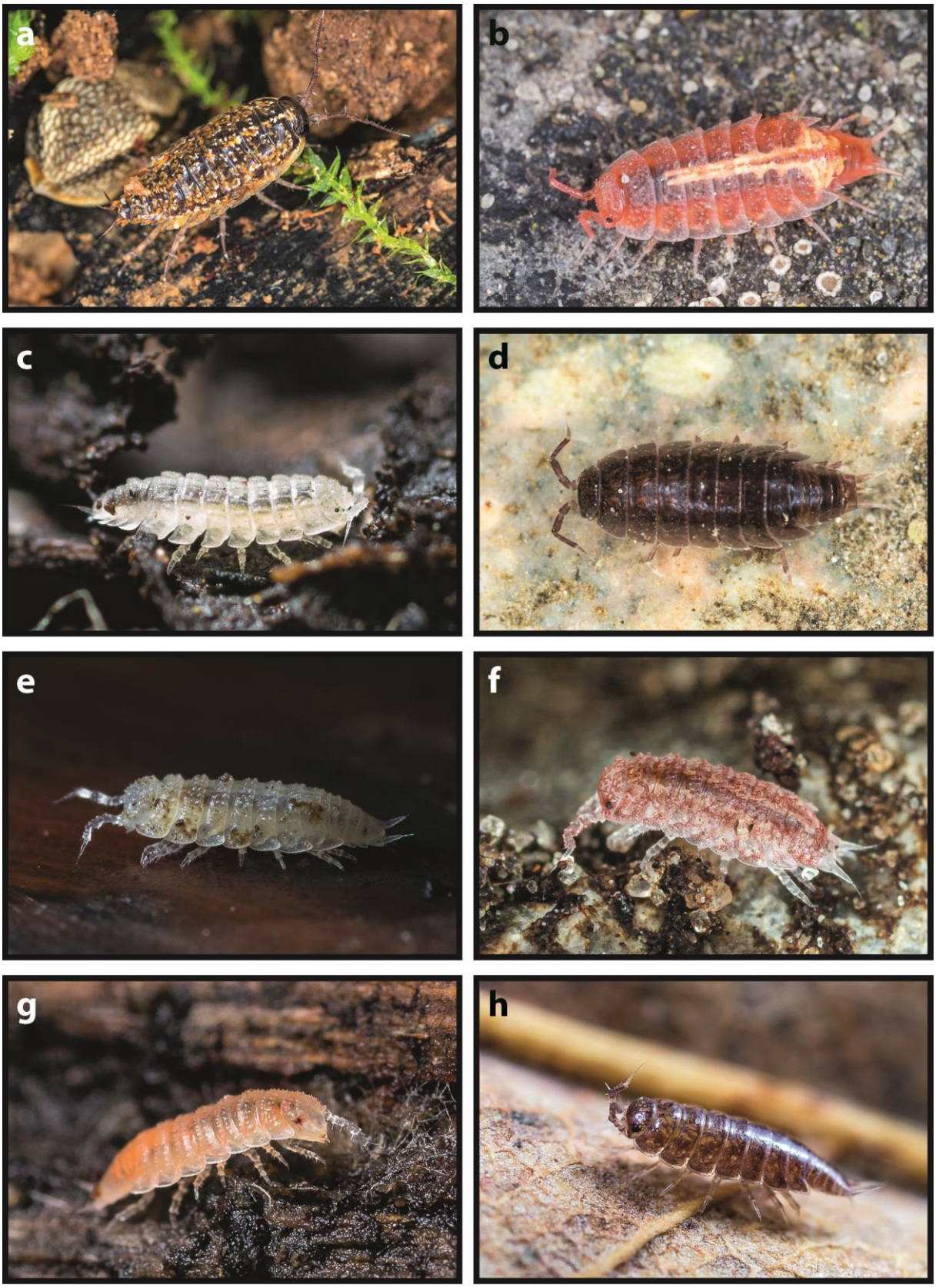


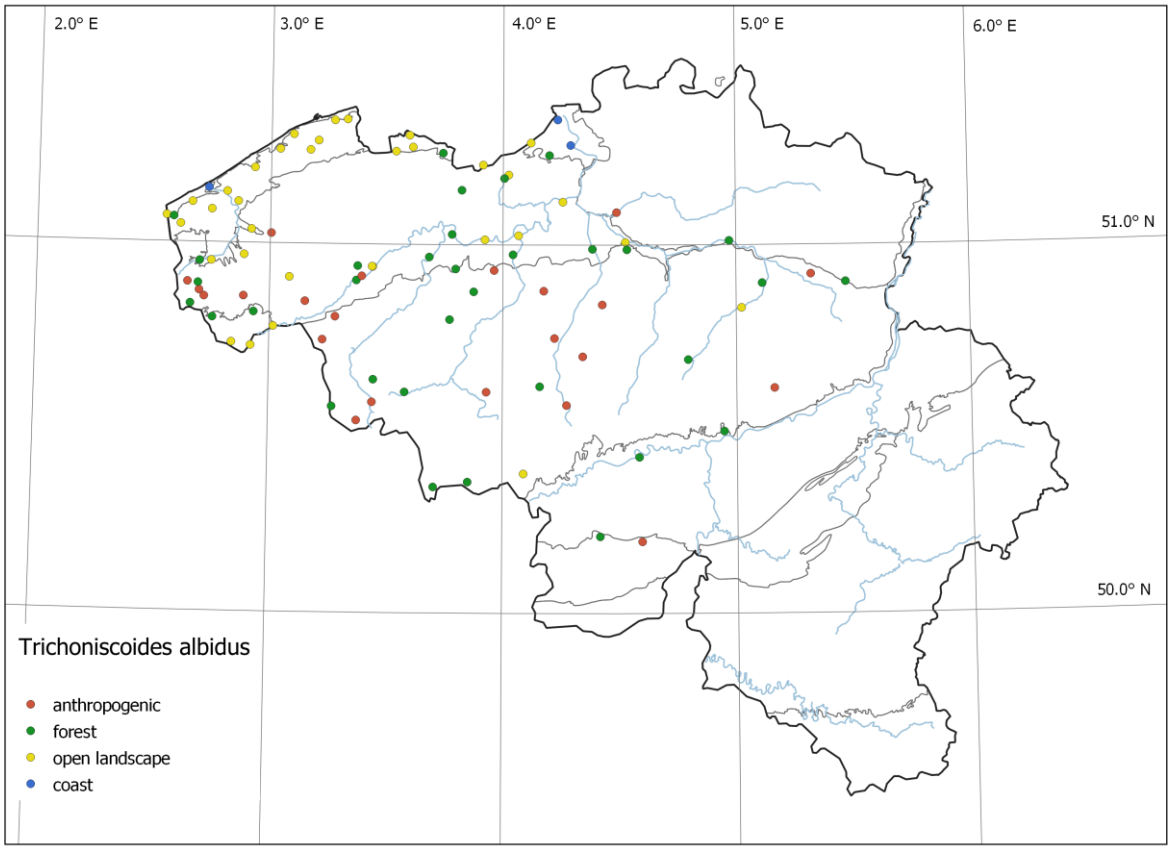
Fig. 11. a, *Ligidium hypnorum*; b, *Androniscus dentiger*; c, *Haplophthalmus mengii*; d, *Hyloniscus riparius*; e, *Metatrichoniscoides leydigii*; f, *Trichoniscoides albidus*; g, *Trichoniscoides helveticus*; h, *Trichoniscus provisorius*.

9. *Miktoniscus patiencei* Vandel, 1946
(Fig. 2 c)

Miktoniscus patiencei is probably the rarest woodlouse species in Belgium and presumably extinct (DE SMEDT *et al.*, 2018b). It has not been found in the recent surveys. We refer to LOCK & DURWAEL (2000), LOCK (2001) and DE SMEDT *et al.* (2020a) for information on the habitat in Belgium, however based on only two observations. *M. patiencei* is a coastal species found just above the high-water mark. There it can be found by turning drift wood and other waste. The only two records of the species are from the end of the 20th century and the beginning of the 21st century in March and July respectively, see LOCK & DURWAEL (2000) and LOCK (2001).

The habitat in the Netherlands is discussed by BERG *et al.* (2008) and for the United Kingdom by GREGORY (2009).

10. *Trichoniscoides albidus* (Budde-Lund, 1880)
(Fig. 11 f, Fig. 12, Map 10, Table 12)



Map 10. Distribution map for *Trichoniscoides albidus*.

A small species found in a wide variety of habitats. In the ecological region of the polders *Trichoniscoides albidus* is almost exclusively found in open landscape, further inland the species is also recorded in forests and anthropogenic habitats (Map 10). *T. albidus* is an atlantic species in Belgium and very rare in the continental part of the country. In the northern part of the country the species is completely absent in the Campine ecological region, where the soil is mostly sandy and acidic. The species is in forests, compared to open landscape habitat, less bound to water. In forest habitat, 42.4% of the records are close to ditches, stream- and riverbanks and dykes of canals and rivers, while this is 76.5% of the records in open habitat (Table 12). Since *T. albidus* has a low desiccation resistance (DIAS *et al.*, 2013), this can be attributed to the higher and more stable moisture conditions in forests.

In both open landscapes and anthropogenic habitats, *T. albidus* is more commonly found during winter months (Fig. 12), which can be explained by the dryer conditions in these habitats during warmer months. The corrected number of records in forests is rather constant throughout the year, with the exception of March–April. The reason for the increased number of observations during March–April could be high ground water levels, which peak in this period in Belgium, forcing the species to higher soil layers.

Table 12. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Trichoniscoides albidus*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**22**	**23.9%**
farm	0	0.0%		
gardens and parks	5	22.7%		
near water in urban area	5	22.7%		
near roads and buildings in urban area	7	31.8%		
graveyard	5	22.7%		
forest			**33**	**35.9%**
coniferous forest	0	0.0%		
deciduous forest	16	48.5%		
near water in deciduous forest	14	42.4%		
near roads and buildings in forest	3	9.1%		
open landscape			**34**	**37.0%**
cropland and orchards	0	0.0%		
grassland	2	5.9%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	6	17.6%		
near water in open landscape	16	47.1%		
river or canal dykes	10	29.4%		
coast			**3**	**3.3%**
total			**92**	

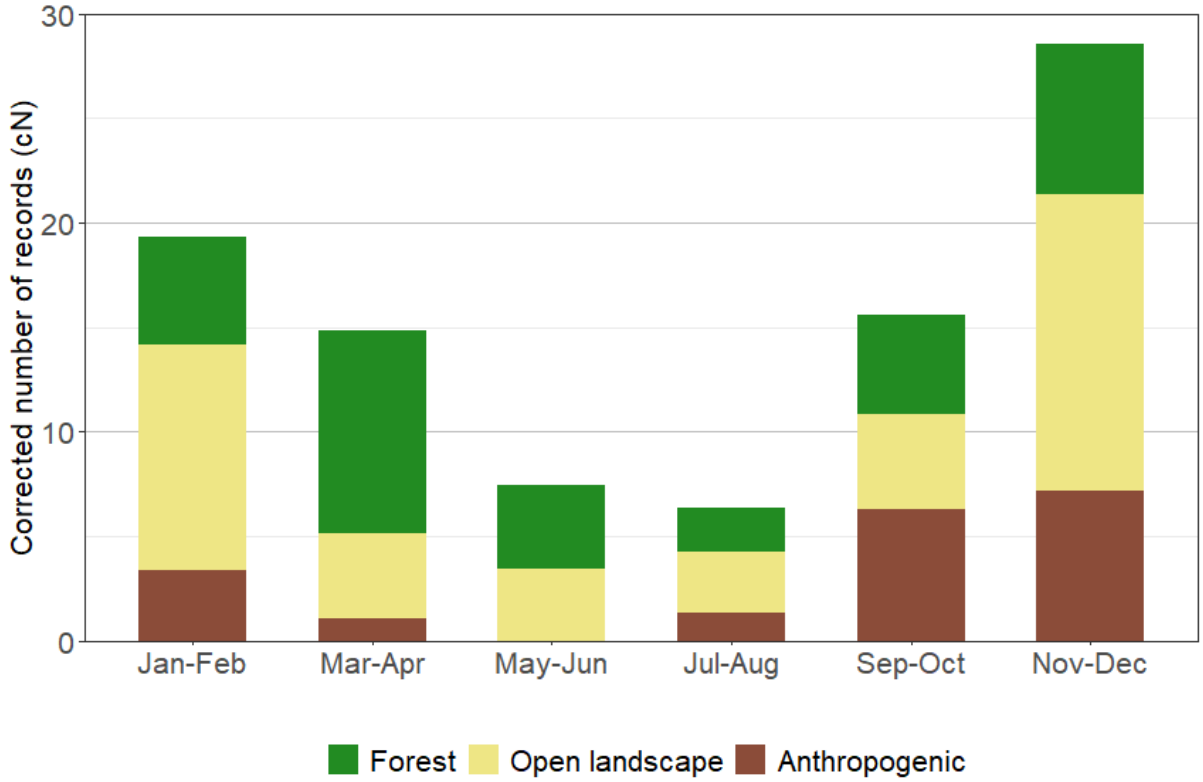
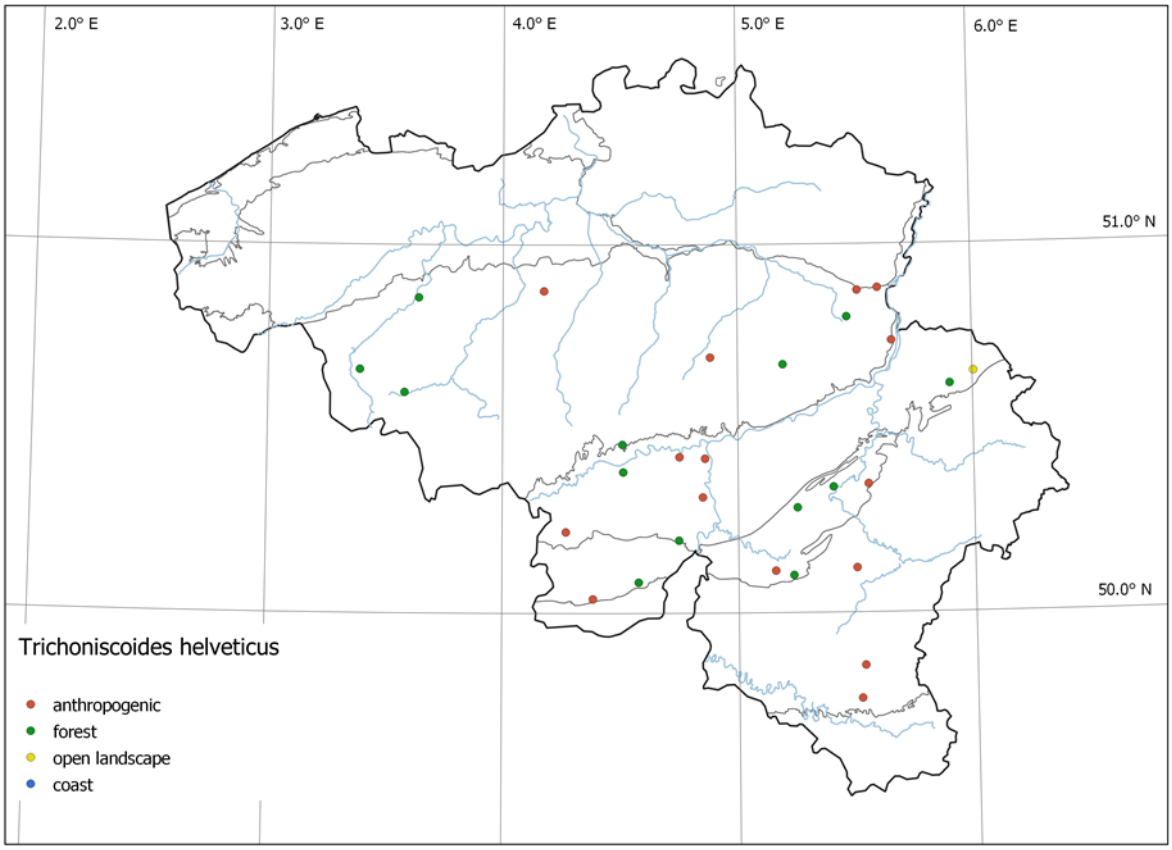


Fig. 12. Corrected number of observations per two-month period for *Trichoniscoides albidus* (N = 97).

11. ***Trichoniscoides helveticus*** (Carl, 1908)
(Fig. 11 g, Fig. 13, Map 11, Table 13)



Map 11. Distribution map for *Trichoniscoides helveticus*.

A small, soil-dwelling species with only a scarce number of records in Belgium. The species is nearly absent in open landscape. Forests are an important habitat for *T. helveticus* and most (76.9%) records in forests are made near ditches and along streams (Table 13). Not surprising since this species has, together with the next species, one of the lowest desiccation resistance values of all native species (DIAS *et al*., 2013). The anthropogenic habitat is of equal importance to forests with 51.7% of the records (44.8% for forest). In anthropogenic habitat, the species is less dependent on the proximity of water, with only 13.3% of the records near water in anthropogenic habitat.

Trichoniscoides helveticus is, similar to most soil-dwelling and drought-sensitive species, more observed during winter months (Fig. 13). In forest habitat, the most important months are from November until April but in anthropogenic habitat most records are from September through February. Due to the limited number of records, it is uncertain whether this represents a true shift.

Table 13. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Trichoniscoides helveticus*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**15**	**51.7%**
farm	0	0.0%		
gardens and parks	3	20.0%		
near water in urban area	2	13.3%		
near roads and buildings in urban area	4	26.7%		
graveyard	6	40.0%		
forest			**13**	**44.8%**
coniferous forest	0	0.0%		
deciduous forest	3	23.1%		
near water in deciduous forest	10	76.9%		
near roads and buildings in forest	0	0.0%		
open landscape			**1**	**3.4%**
cropland and orchards	0	0.0%		
grassland	0	0.0%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	1	100.0%		
near water in open landscape	0	0.0%		
river or canal dykes	0	0.0%		
coast			**0**	**0.0%**
total			**29**	

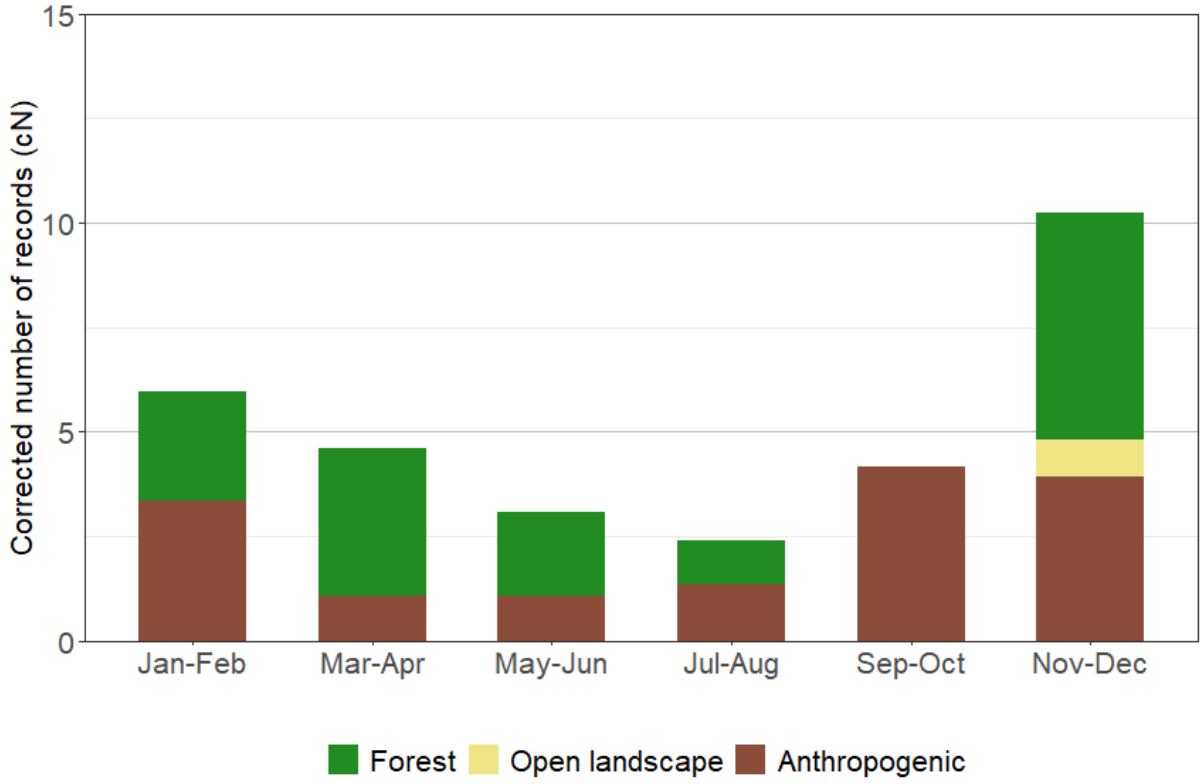
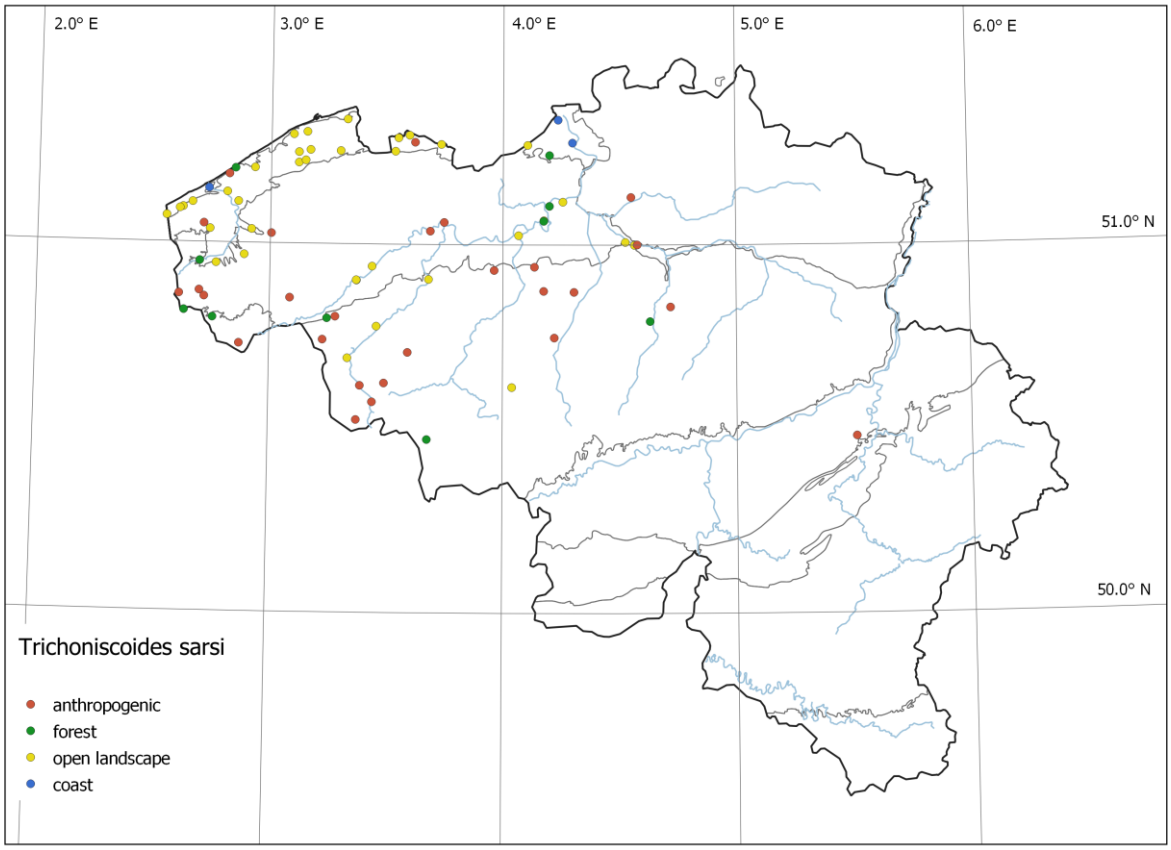


Fig. 13. Corrected number of observations per two-month period for *Trichoniscoides helveticus* (N = 32).

12. ***Trichoniscoides sarsi*** Patience, 1908
(Fig. 14, Map 12, Table 14)



Map 12. Distribution map for *Trichoniscoides sarsi*.

Trichoniscoides sarsi is closely related and morphologically very similar to *T. helveticus* (Fig. 11 g) but its habitat and activity patterns resemble more *T. albidus.* It is common in coastal habitat and open landscape, with an important share of these records situated in the polders ecological region (Map 12). As *T. albidus,* further inland the species is more frequently found in forests and anthropogenic habitats and it seems to avoid sandy soil types. However, in contrast *to T.* albidus, anthropogenic habitat and open landscape are more important for *T. sarsi* (Table 14) while forests are more important for *T. albidus*. Compared to *T. helveticus*, *T. sarsi* is less bound to water in forest habitat (36.4% compared to 76.9% for *T. helveticus*), but again comparable to *T. albidus* (42.4% of forest locations are near water). In anthropogenic habitat, the species is most frequently found in graveyards. There is very few overlap in the distribution of *T. sarsi* and *T. helveticus* in Belgium, which is observed in other countries as well (BERG, 2008). There is only one known location where both species co-occurred i.e. a graveyard in the centre of the country.

Trichoniscoides sarsi is mostly recorded from November until February in all habitat types (Fig. 14). Like most small and drought-sensitive species it retreats deeper into the soil when soil moisture levels are lower in warmer months.

Table 14. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Trichoniscoides sarsi*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**27**	**35.5%**
farm	0	0.0%		
gardens and parks	7	25.9%		
near water in urban area	1	3.7%		
near roads and buildings in urban area	3	11.1%		
graveyard	16	59.3%		
forest			**11**	**14.5%**
coniferous forest	0	0.0%		
deciduous forest	6	54.5%		
near water in deciduous forest	4	36.4%		
near roads and buildings in forest	1	9.1%		
open landscape			**35**	**46.1%**
cropland and orchards	0	0.0%		
grassland	2	5.7%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	7	20.0%		
near water in open landscape	19	54.3%		
river or canal dykes	7	20.0%		
coast			**3**	**3.9%**
total			**76**	

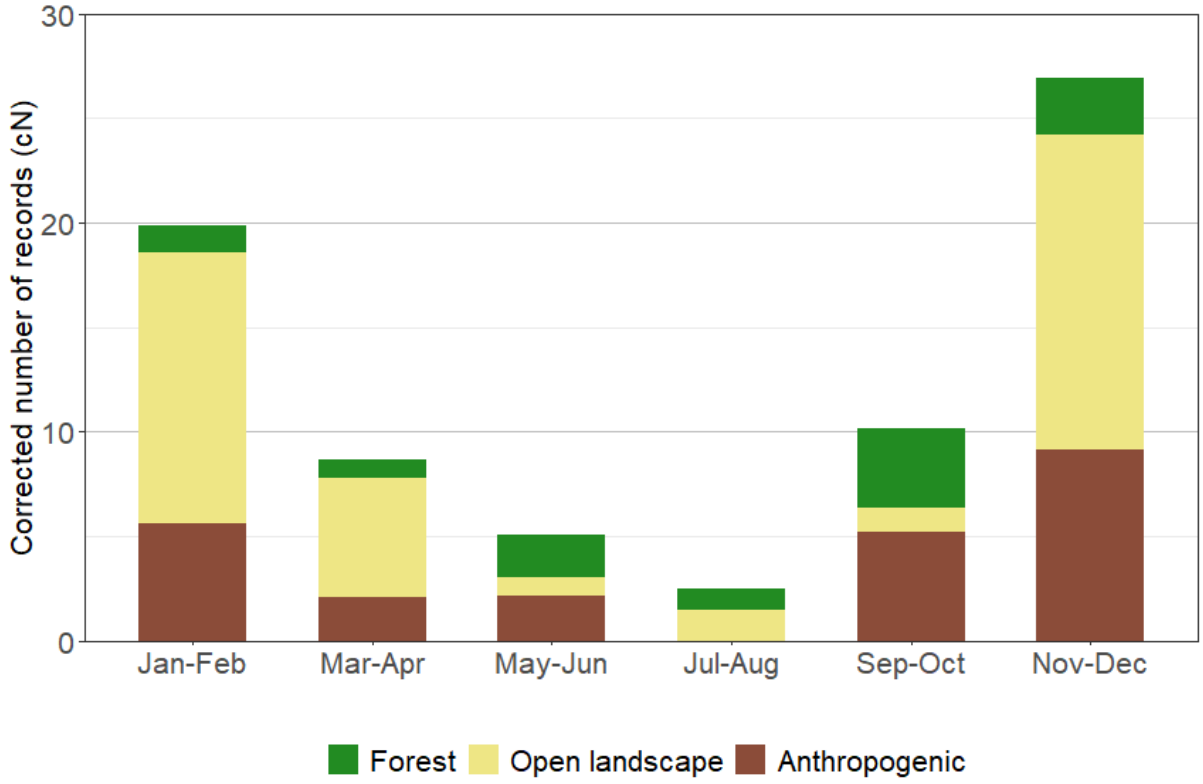
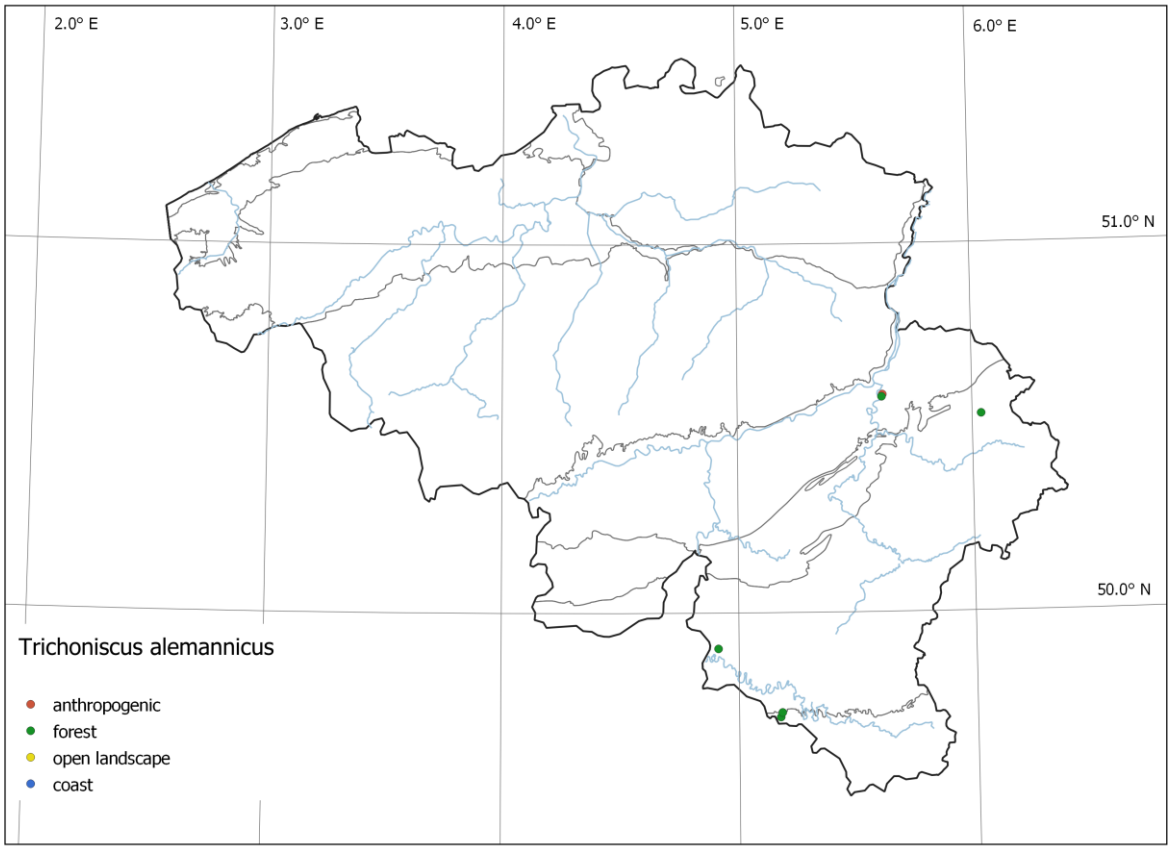


Fig 14. Corrected number of observations per two-month period for *Trichoniscoides sarsi* (N = 79).

13. ***Trichoniscus alemannicus*** Verhoeff, 1917
(Fig. 15, Map 13, Table 15)



Map 13. Distribution map for *Trichoniscus alemannicus*.

Trichoniscus alemannicus is a very rare and only recently discovered species in Belgium (DE SMEDT *et al.*, 2016a). The species is morphologically almost similar to *T. provisorius* (Fig. 11 h) and *T. pusillus*. Based on only six observations, the main habitat of this species is deciduous forest and mostly close to water (Table 15). There is only one observation in anthropogenic habitat, on a graveyard, but this location was surrounded by deciduous forest.

The few observations do not allow to evaluate the species seasonal activity patterns (Fig. 15).

Table 15. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Trichoniscus alemannicus*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**1**	**16.7%**
farm	0	0.0%		
gardens and parks	0	0.0%		
near water in urban area	0	0.0%		
near roads and buildings in urban area	0	0.0%		
graveyard	1	100.0%		
forest			**5**	**83.3%**
coniferous forest	0	0.0%		
deciduous forest	0	0.0%		
near water in deciduous forest	4	80.0%		
near roads and buildings in forest	1	20.0%		
open landscape			**0**	**0.0%**
cropland and orchards	0	0.0%		
grassland	0	0.0%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	0	0.0%		
near water in open landscape	0	0.0%		
river or canal dykes	0	0.0%		
coast			**0**	**0.0%**
total			**6**	

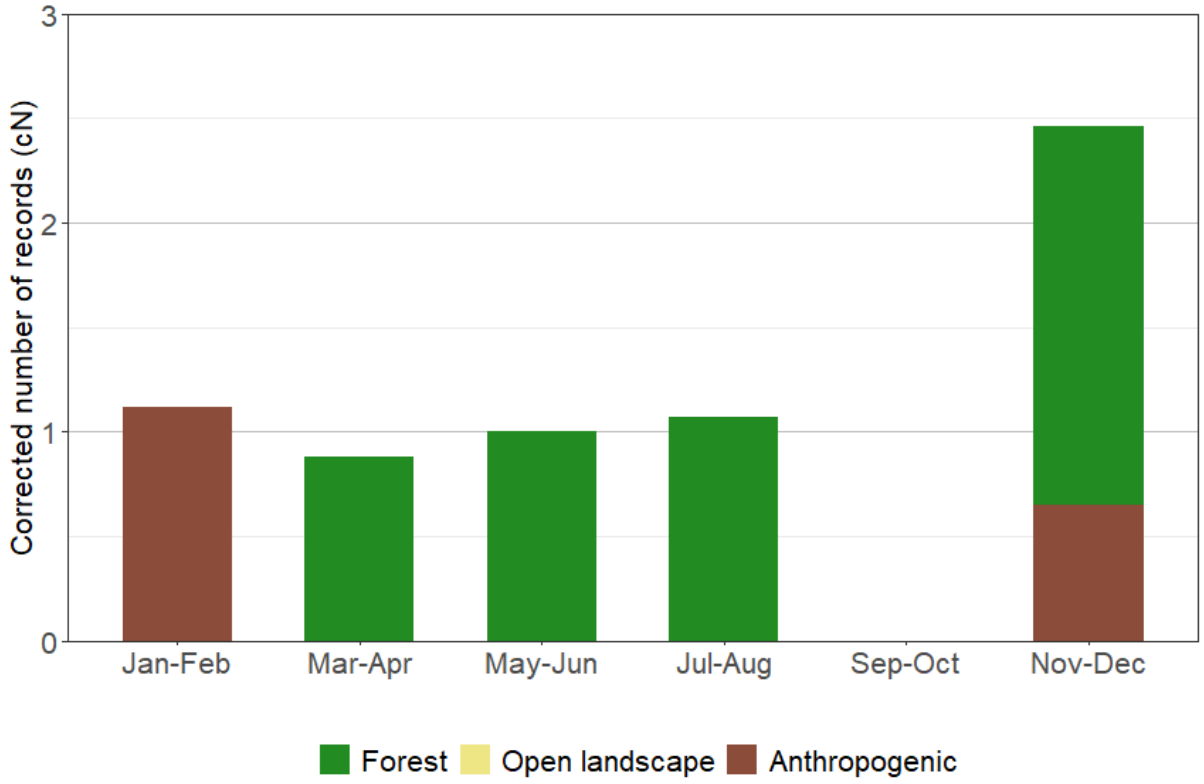
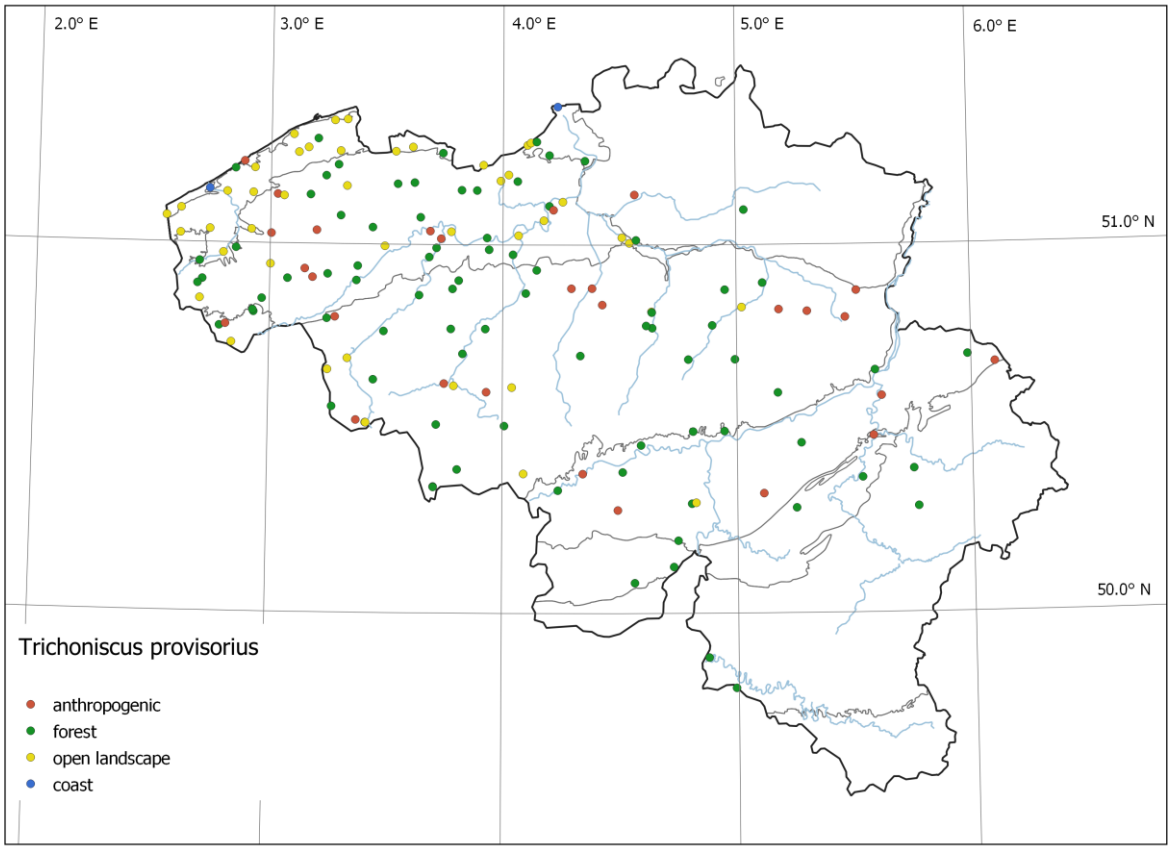


Fig. 15. Corrected number of observations per two-month period for *Trichoniscus alemannicus* (N = 7).

14. ***Trichoniscus provisorius*** Racovitza, 1908
(Fig. 11 h, Fig. 16, Map 14, Table 16)



Map 14. Distribution map for *Trichoniscus provisorius*.

More than 50% of the records are done in forest habitat (Table 16). However, it is important to note that due to the close resemblance of *T. provisorius* and *T. pusillus* there was a need to collect larger numbers to assess the sex ratio of the population to get a confident identification (*T. pusillus*-populations have less than 1% males while this is more equal for *T. provisorius*-populations) (see also DE SMEDT *et al.*, 2020a). Abundances of these two species are generally higher in forest habitat and therefore this habitat was preferred to collect a sufficient number of individuals. Therefore, other habitats might be under-recorded, for instance gardens, parks, grasslands and river banks in open landscape. The species is (very) common in forest habitat, open landscape and anthropogenic habitat in the north-western part of the country (Map 14). An absence in the Campine region, marked by quickly heating and acidic sandy soils, could possibly be due to a lower drought resistance of this species compared to *T. pusillus* since *T. provisorius* is on average smaller and has possibly the lowest desiccation resistance of all native woodlice species (see DIAS *et al.* (2013) based on the data *from T. pusillus*). A lower resistance against acidic soil conditions may explain why the species is absent in the Ardenne and Lorraine region.

In all habitat types *T. provisorius* is more observed during winter months (Fig. 16), however the period with highest number of records shifts slightly between different habitat types. Furthermore, it appears that the drop in corrected numbers of records during summer months is lower in forests compared to open landscape habitats. We assume this can be related to soil moisture conditions, which are more buffered in forests.

Table 16. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Trichoniscus provisorius*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**28**	**17.9%**
farm	0	0.0%		
gardens and parks	13	46.4%		
near water in urban area	4	14.3%		
near roads and buildings in urban area	4	14.3%		
graveyard	7	25.0%		
forest			**82**	**52.6%**
coniferous forest	0	0.0%		
deciduous forest	46	56.1%		
near water in deciduous forest	33	40.2%		
near roads and buildings in forest	3	3.7%		
open landscape			**44**	**28.2%**
cropland and orchards	0	0.0%		
grassland	6	13.6%		
disused quarry	1	2.3%		
near roads and buildings in open landscape	7	15.9%		
near water in open landscape	20	45.5%		
river or canal dykes	10	22.7%		
coast			**2**	**1.3%**
total			**156**	

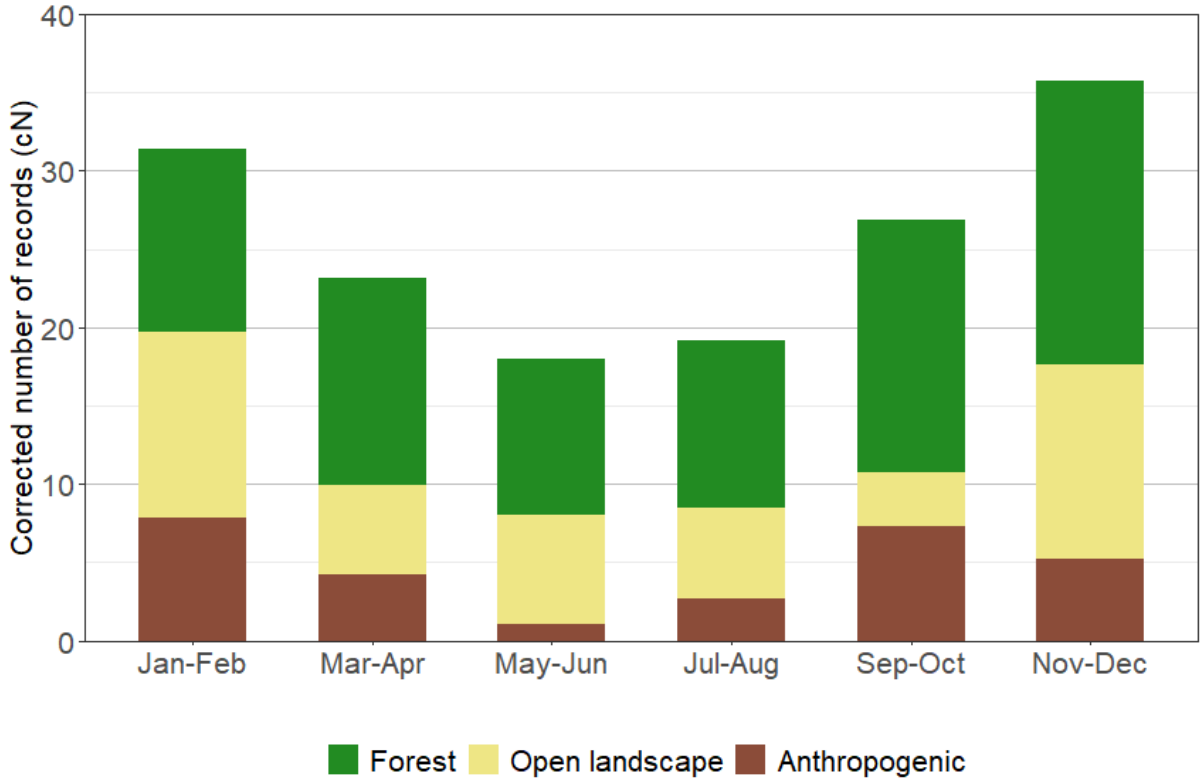
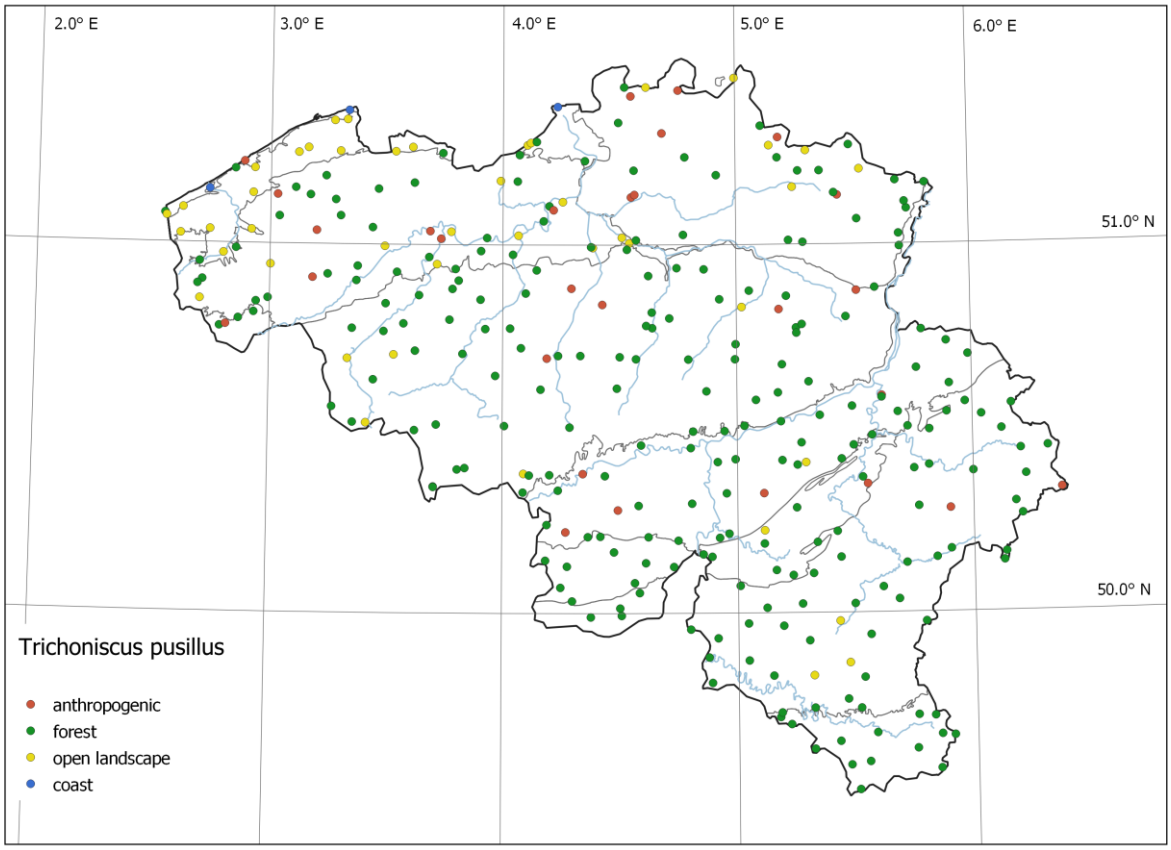


Fig. 16. Corrected number of observations per two-month period for *Trichoniscus provisorius* (N = 157).

15. ***Trichoniscus pusillus*** Brandt, 1833
(Fig. 17, Map 15, Table 17)



Map 15. Distribution map for *Trichoniscus pusillus.*

Similar to *T. provisorius* (Fig. 11 h), the habitat preferences of *Trichoniscus pusillus* are probably biased towards forest habitat (see the notes for *Trichoniscus provisorius*). However, there is no doubt that forest habitat is one of the major habitats for *T. pusillus*, where it reaches high numbers. This small species is drought sensitive and reaches its highest numbers in forest interiors rather than forest edges (DE SMEDT *et al.*, 2018d). *T. pusillus* is a very common species and much more widespread compared to *T. provisorius*.

The number of observations shows a small decline for anthropogenic and open landscape habitats during summer months (Fig. 17) (supported by DE SMEDT *et al.*, 2021). This is however not the case for forest habitat. The smaller decline in number of observations during the summer months compared to *T. provisorius*, can possibly be attributed to its slightly larger size and therefore higher drought resistance.

Table 17. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Trichoniscus pusillus*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**28**	**9.0%**
farm	0	0.0%		
gardens and parks	13	46.4%		
near water in urban area	6	21.4%		
near roads and buildings in urban area	1	3.6%		
graveyard	8	28.6%		
forest			**235**	**75.8%**
coniferous forest	0	0.0%		
deciduous forest	138	58.7%		
near water in deciduous forest	93	39.6%		
near roads and buildings in forest	4	1.7%		
open landscape			**44**	**14.2%**
cropland and orchards	0	0.0%		
grassland	5	11.4%		
disused quarry	2	4.5%		
near roads and buildings in open landscape	8	18.2%		
near water in open landscape	18	40.9%		
river or canal dykes	11	25.0%		
coast			**3**	**1.0%**
total			**310**	

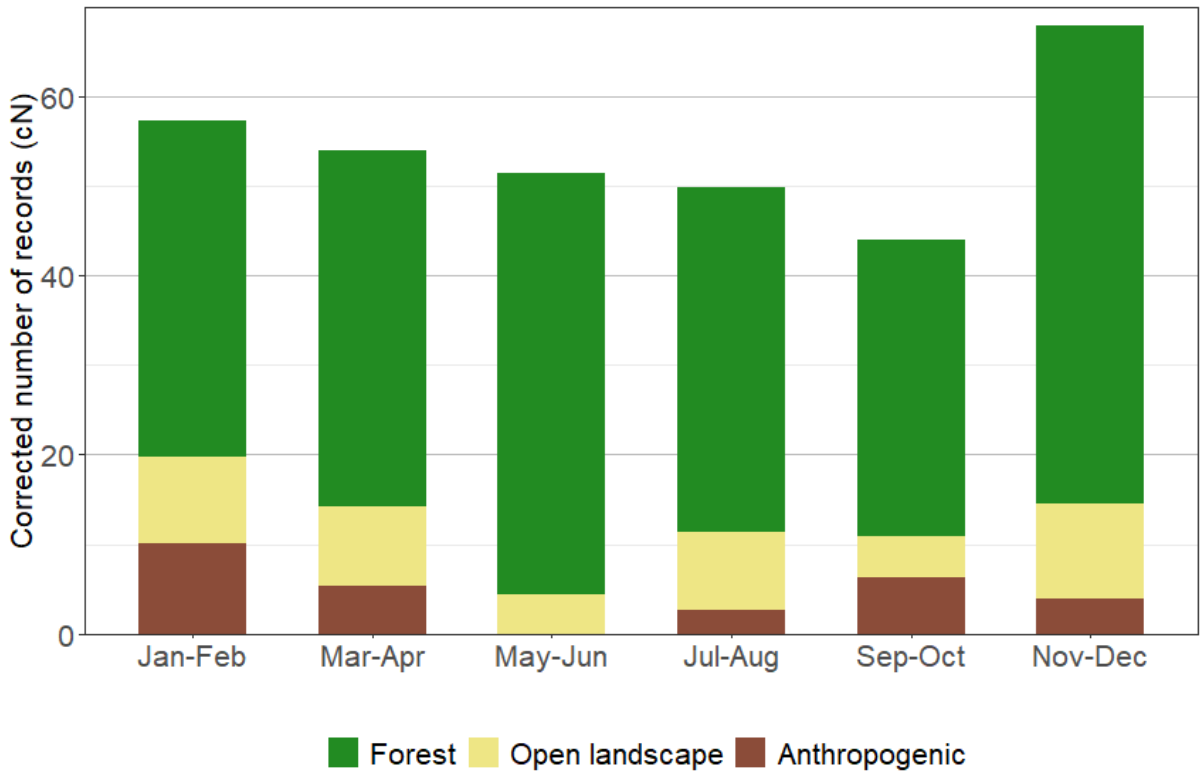
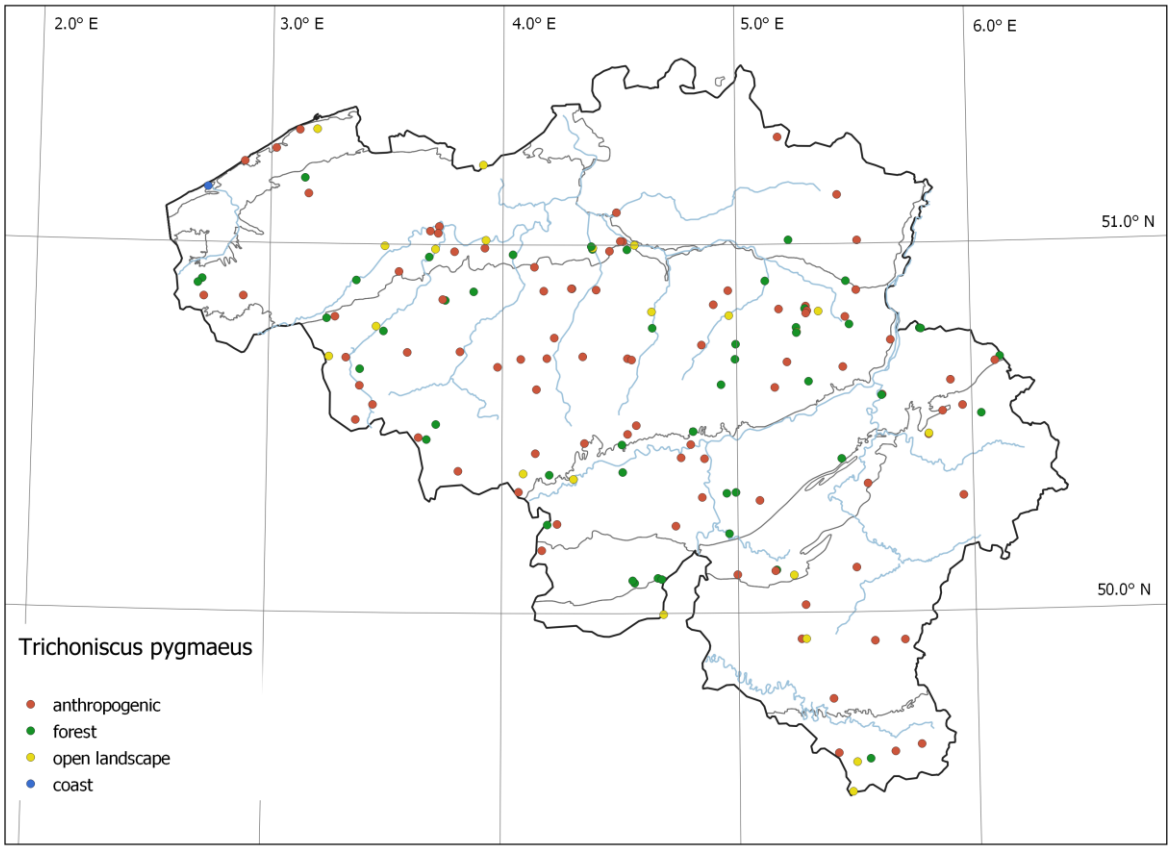


Fig. 17. Corrected number of observations per two-month period for *Trichoniscus pusillus* (N = 326).

16. ***Trichoniscus pygmaeus*** Sars, 1898
(Fig. 2 d, Fig. 18, Map 16, Table 18**)**



Map 16. Distribution map for *Trichoniscus pygmaeus*.

Trichoniscus pygmaeus is found in a wide range of habitats (Table 18). In the northern part of the country, the species is less common and rare (Map 16). In Southern Belgium, *T. pygmaeus* is almost exclusively found in anthropogenic habitats. In the other parts, the species is more common and forests are an important habitat for the species. Forests consist of almost 50% of the records and half of it are near water in forests (Table 18). In anthropogenic habitats only a limited number of records (6.9%) is near water, most records (65.5%) are from graveyards. The largest share of observations of *T. pygmaeus* in open landscape (66.7%) is located near water. Moist conditions in open landscape are probably only relatively stable close to stream- and riverbanks ensuring suitable habitat year-round for this soil-dwelling species.

In line with other small, soil-dwelling species, *T. pygmaeus* is less commonly found during summer months (Fig. 18). This pattern is particularly obvious in anthropogenic and forest habitat, but less pronounced in open landscape habitat, although this habitat type has the lowest number of records. The patterns of *T. pygmaeus* in open landscape are comparable to the patterns in open landscape for *T. pusillus*.

Table 18. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Trichoniscus pygmaeus*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**87**	**55.4%**
farm	2	2.3%		
gardens and parks	12	13.8%		
near water in urban area	6	6.9%		
near roads and buildings in urban area	10	11.5%		
graveyard	57	65.5%		
forest			**48**	**30.6%**
coniferous forest	0	0.0%		
deciduous forest	19	39.6%		
near water in deciduous forest	24	50.0%		
near roads and buildings in forest	5	10.4%		
open landscape			**21**	**13.4%**
cropland and orchards	0	0.0%		
grassland	1	4.8%		
disused quarry	3	14.3%		
near roads and buildings in open landscape	3	14.3%		
near water in open landscape	10	47.6%		
river or canal dykes	4	19.0%		
coast			**1**	**0.6%**
total			**157**	

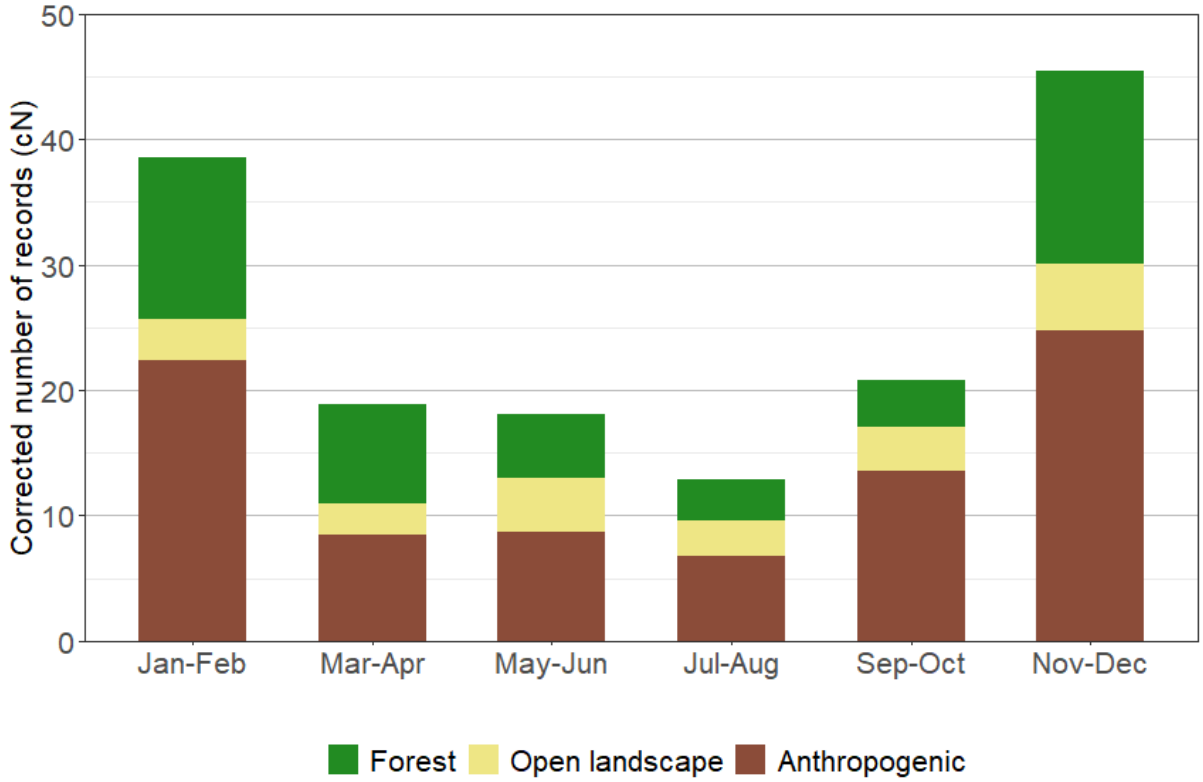


Fig. 18. Corrected number of observations per two-month period for *Trichoniscus pygmaeus* (N = 162).

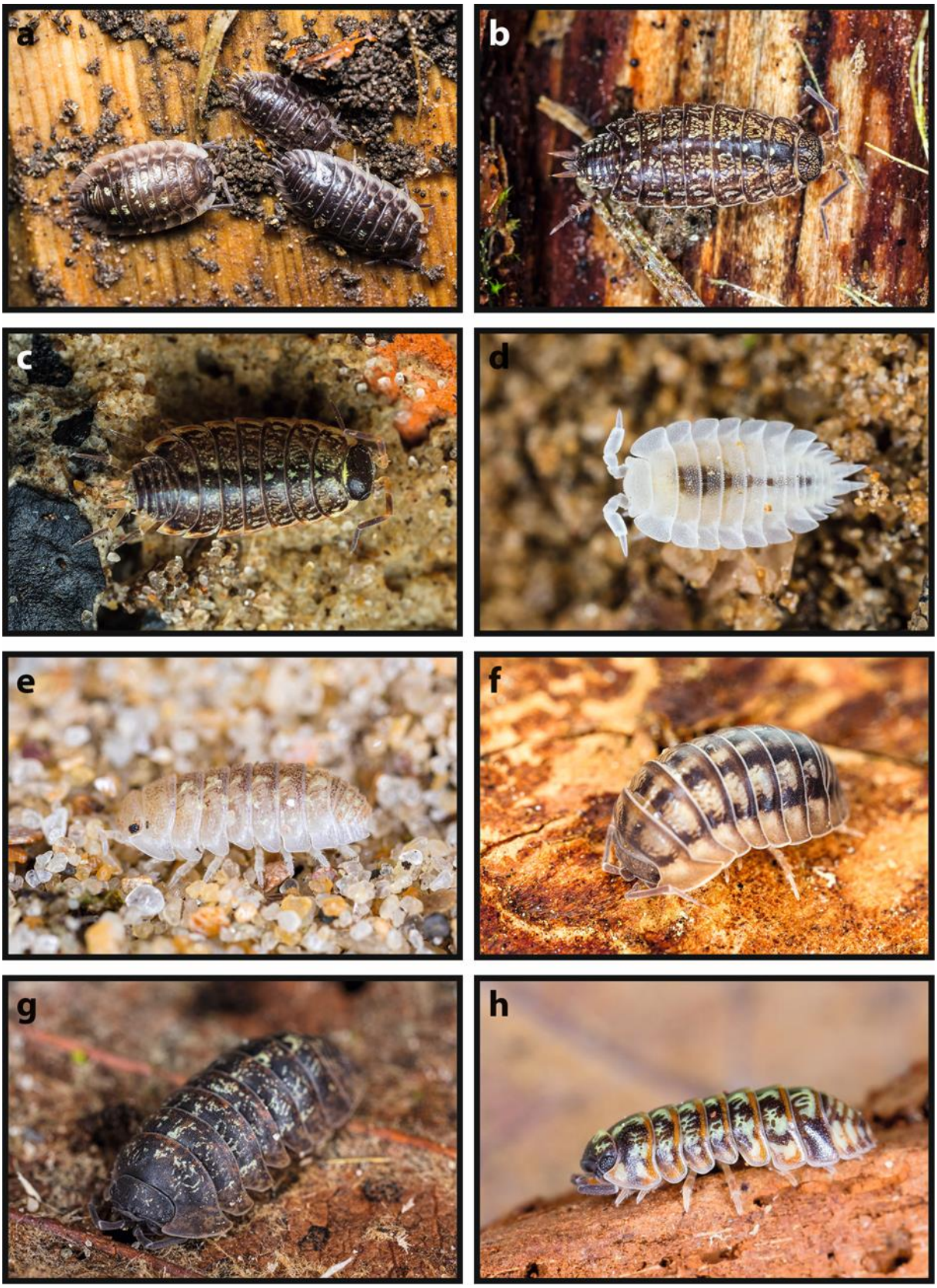
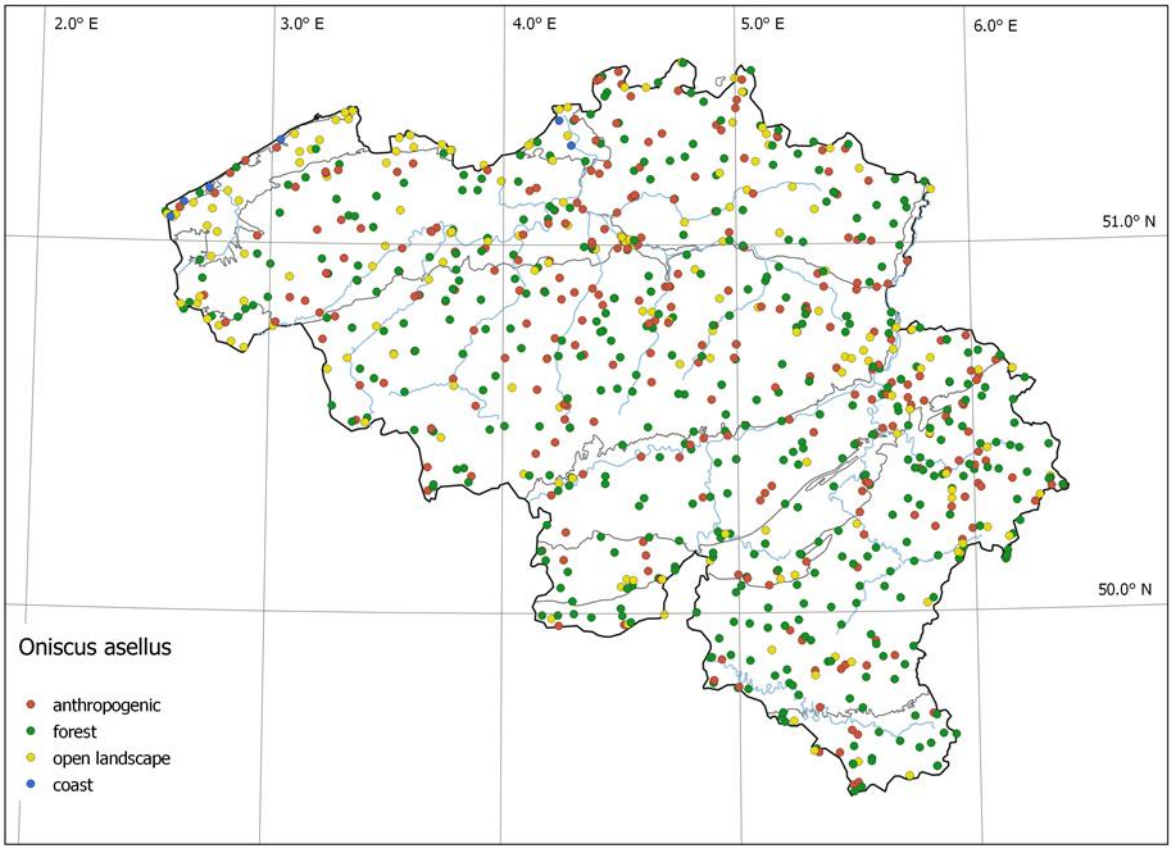


Fig. 19. a, *Oniscus asellus*; b, *Philoscia affinis*; c, *Philoscia muscorum*; d, *Platyarthrus hoffmannseggii*; e, *Armadillidium album*; f, *Armadillidium nasatum*; g, *Armadillidium opacum*; h, *Armadillidium pulchellum*.

Fig. 20. a, *Eluma caelata*; b, *Cylisticus convexus*; c, *Porcellio monticola*; d, *Porcellio scaber*; e, *Porcellio spinicornis*; f, *Porcellionides pruinosus*; g, *Porcellium conspersum*; h, *Trachelipus rathkii*.

17. ***Oniscus asellus*** Linnaeus, 1758
(Fig. 19 a, Fig. 21, Map 17, Table 19)



Map 17. Distribution map for *Oniscus asellus*.

Oniscus asellus is a eurytopic and very common species across the country (Map 17). The species is very common in every habitat type and in every ecological region in Belgium. Forests are probably its most important natural habitat but the species has adapted to all kinds of anthropogenic conditions (Table 19). Observed numbers of *O. asellus* in forest habitat are generally higher compared to other larger very common species like *Porcellio scaber* and *Philoscia muscorum.* In forest interiors, *O. asellus* is probably the most common species of woodlice (DE SMEDT *et al.*, 2018a). It is one of the few species common in coniferous forest. The species is almost always present in open landscapes when cover of sufficient size is available (like stones, logs etc.), otherwise more rarely detected.

The species is slightly less observed from March until August, with the largest decrease in corrected number of records in May–June (Fig. 21).

Table 19. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Oniscus asellus*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**279**	**31.5%**
farm	13	4.7%		
gardens and parks	84	30.1%		
near water in urban area	22	7.9%		
near roads and buildings in urban area	57	20.4%		
graveyard	103	36.9%		
forest			**434**	**49.0%**
coniferous forest	8	1.8%		
deciduous forest	250	57.6%		
near water in deciduous forest	132	30.4%		
near roads and buildings in forest	44	10.1%		
open landscape			**166**	**18.7%**
cropland and orchards	1	0.6%		
grassland	37	22.3%		
disused quarry	16	9.6%		
near roads and buildings in open landscape	51	30.7%		
near water in open landscape	39	23.5%		
river or canal dykes	22	13.3%		
coast			**7**	**0.8%**
total			**886**	

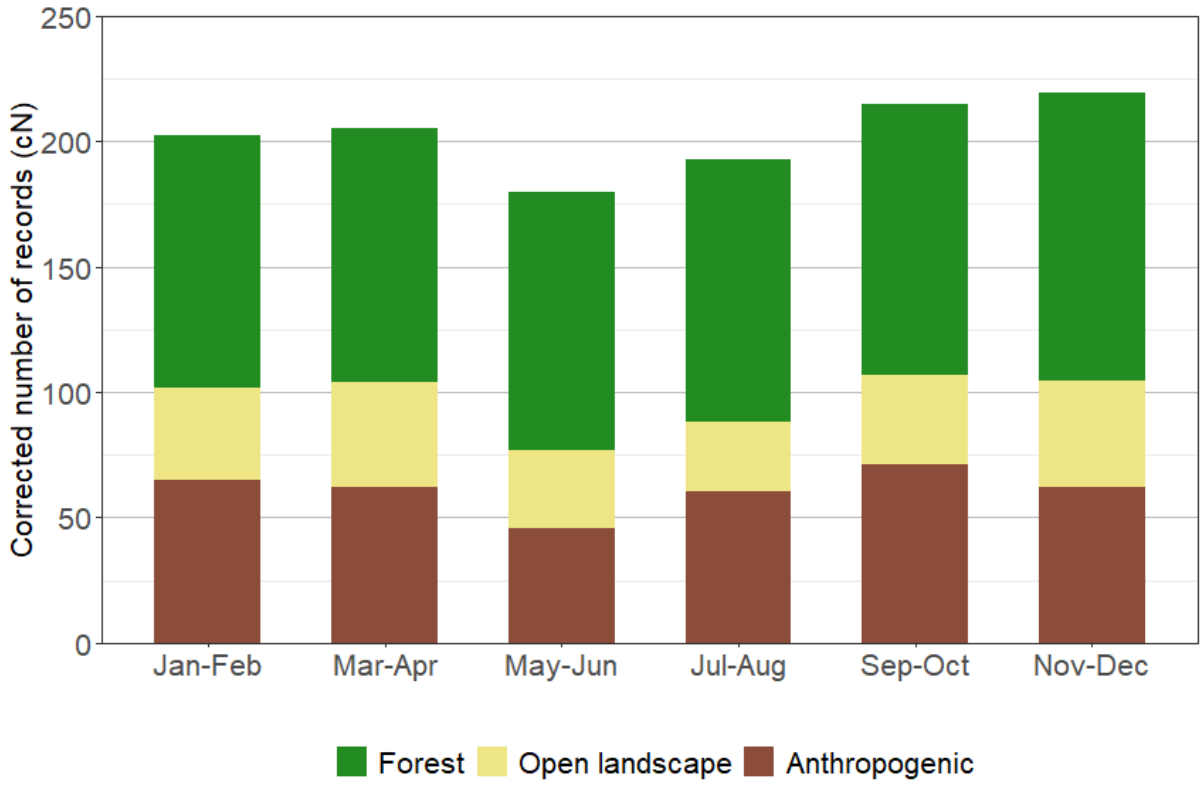
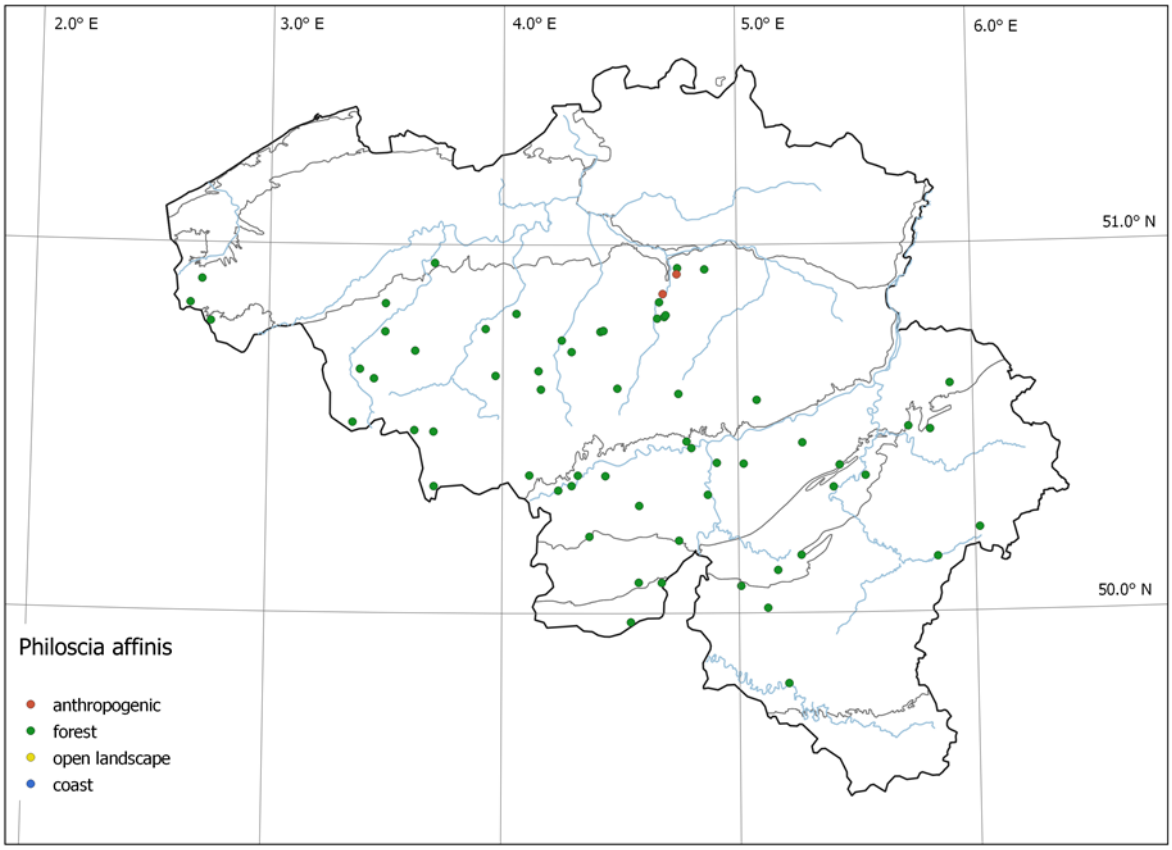


Fig. 21. Corrected number of observations per two-month period for *Oniscus asellus* (N = 1221).

18. *Philoscia affinis* Verhoeff, 1908
(Fig. 19 b, Fig. 22, Map 18, Table 20)



Map 18. Distribution map for *Philoscia affinis*.

Discovered for the first time in Belgium in 2014 (BOERAEVE *et al.*, 2017), since then *Philoscia affinis* has been recorded in most parts of the country (Map 18). Almost exclusively found in deciduous forests (Table 20). In the northern part of the country, the species is a good indicator of ancient forests (DE SMEDT & VANDEKERKHOVE, 2020) and it was categorized as a species with a strong affinity to closed forest habitat (DE SMEDT *et al.*, 2020b). Most of the records are from forests dominated by Oak trees (*Quercus petraea/robur*), sometimes mixed with beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*) (BOERAEVE *et al.*, 2017). It is only found twice in Black Alder (*Alnus glutinosa*) dominated forest (BOERAEVE *et al.*, 2017). Besides the records in forest habitat, the species has been recorded twice from gardens. However, both gardens were bordering forest habitat.

Despite being considered of Mediterranean origin (VANDEL 1962), *P. affinis* is more often recorded during winter months (Fig. 22). It is a rather drought-sensitive species (unpublished data) and this could possibly explain the observed pattern since the species retreat deeper in the litter layer (or soil) when temperatures are high.

Table 20. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Philoscia affinis*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**2**	**3.1%**
farm	0	0.0%		
gardens and parks	2	100.0%		
near water in urban area	0	0.0%		
near roads and buildings in urban area	0	0.0%		
graveyard	0	0.0%		
forest			**62**	**96.9%**
coniferous forest	0	0.0%		
deciduous forest	48	77.4%		
near water in deciduous forest	13	21.0%		
near roads and buildings in forest	1	1.6%		
open landscape			**0**	**0.0%**
cropland and orchards	0	0.0%		
grassland	0	0.0%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	0	0.0%		
near water in open landscape	0	0.0%		
river or canal dykes	0	0.0%		
coast			**0**	**0.0%**
total			**64**	

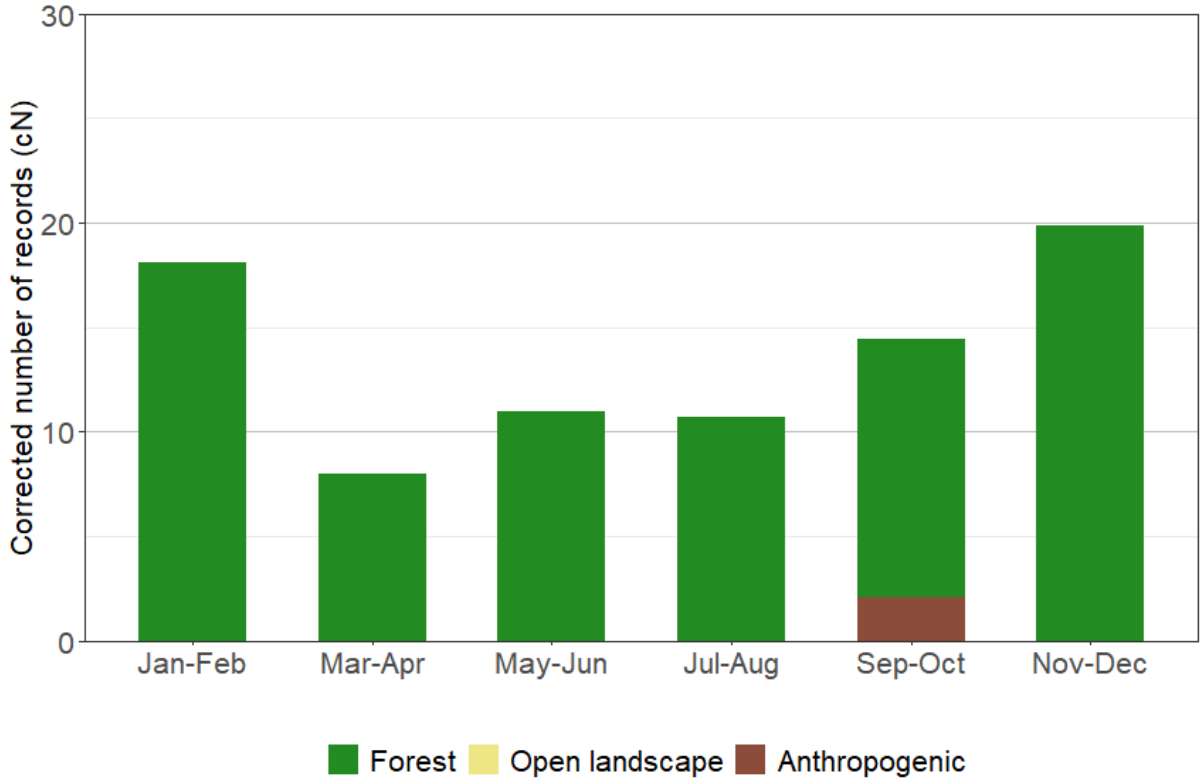
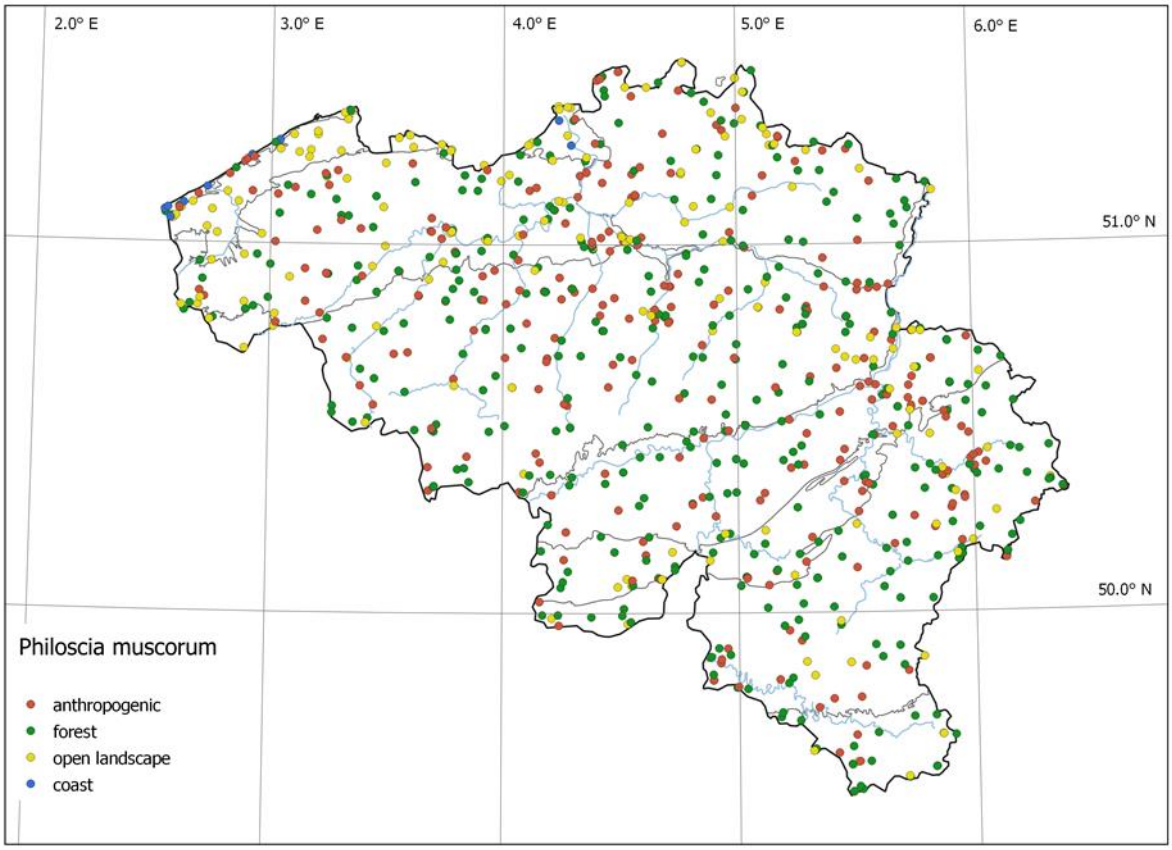


Fig. 22. Corrected number of observations per two-month period for *Philoscia affinis* (N = 81).

19. *Philoscia muscorum* (Scopoli, 1763)
(Fig. 19 c, Fig. 23, Map 19, Table 21)



Map 19. Distribution map for *Philoscia muscorum*.

Philoscia muscorum is very common in all kind of habitats across the country and maybe the most eurytopic species in Belgium. Its habitat preferences (Table 21) closely resemble the pattern observed for *Oniscus asellus*. Although, this species is very common in forest habitat, it is always less abundant compared to *O. asellus* (e.g. DE SMEDT *et al.*, 2016b, 2018b). In open landscape on the contrary, *P. muscorum* is very often the more abundant species compared to *O. asellus* (unpublished data from pitfall research).

The corrected number of records are highest from November until April in both open landscape and anthropogenic habitats (Fig. 23). In forest habitat the corrected number of records is only somewhat lower in September–October and somewhat higher in November–December. Despite having a higher drought resistance than *O. asellus* (DIAS *et al.*, 2013), the drop in records during summer months is considerably bigger for *P. muscorum* than for *O. asellus*. This may be explained by the different strategies the species have to avoid desiccation. *O. asellus* tends to shelter in a locally more humid spot (for instance under bark of dead wood) whereas *P. muscorum* will run further to search for more humid shelter places. This could mean that during summer months *P. muscorum* is harder to detect compared with *O. asellus*, when searching by hand. Using pitfall traps, DE SMEDT *et al.* (2021) found however an activity peak in spring compared to other seasons.

Table 21. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Philoscia muscorum*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**256**	**31.9%**
farm	11	4.3%		
gardens and parks	77	30.1%		
near water in urban area	27	10.5%		
near roads and buildings in urban area	49	19.1%		
graveyard	92	35.9%		
forest			**369**	**46.0%**
coniferous forest	4	1.1%		
deciduous forest	212	57.5%		
near water in deciduous forest	120	32.5%		
near roads and buildings in forest	33	8.9%		
open landscape			**168**	**20.9%**
cropland and orchards	2	1.2%		
grassland	39	23.2%		
disused quarry	12	7.1%		
near roads and buildings in open landscape	48	28.6%		
near water in open landscape	40	23.8%		
river or canal dykes	27	16.1%		
coast			**10**	**1.2%**
total			**803**	

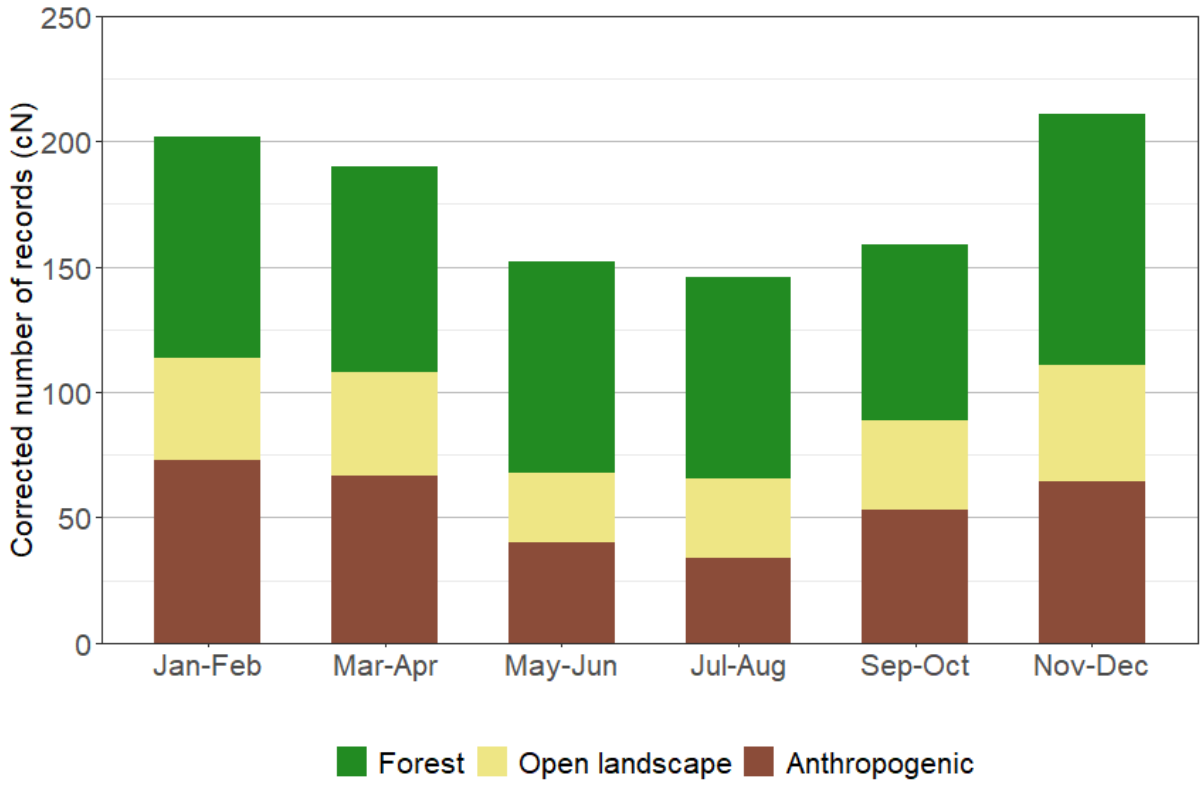
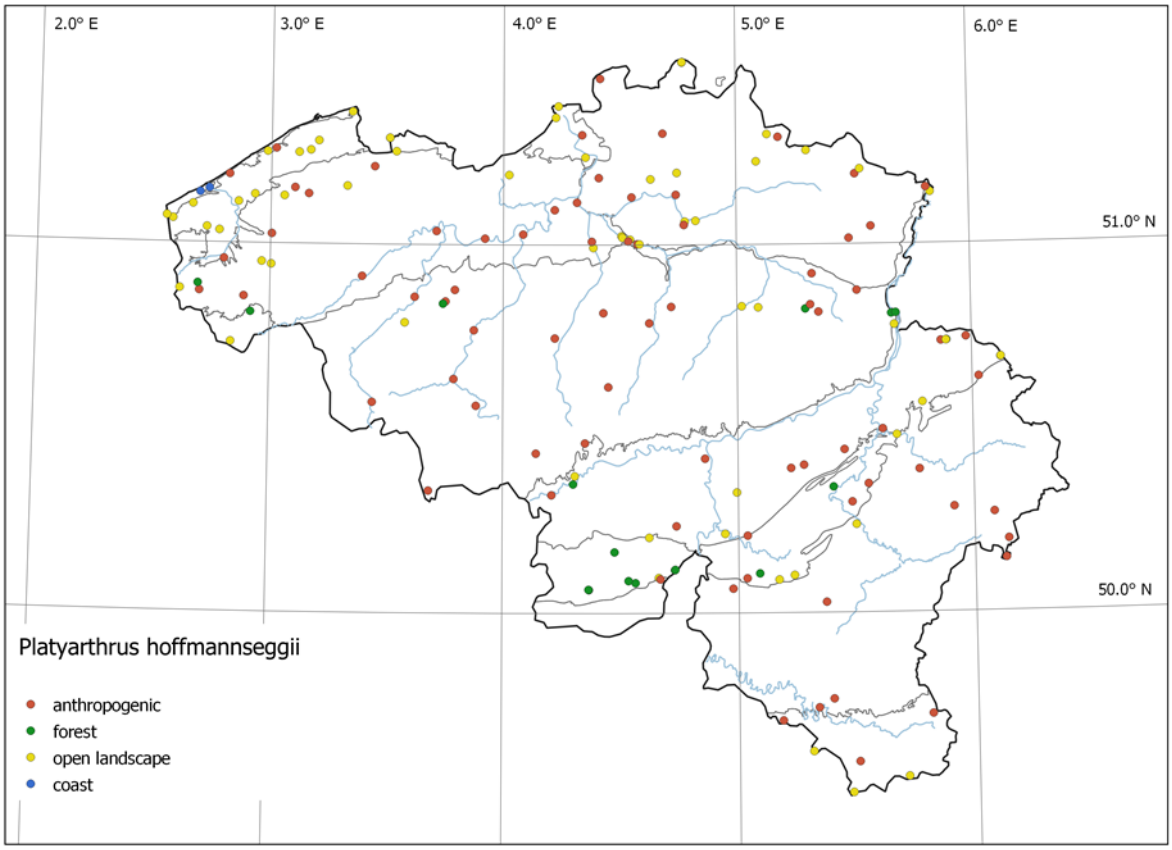


Fig. 23. Corrected number of observations per two-month period for *Philoscia muscorum* (N = 1071).

20. *Platyarthrus hoffmannseggii* Brandt, 1833
(Fig. 19 d, Fig. 24, Map 20, Table 22)



Map 20. Distribution map for *Platyarthrus hoffmannseggii*.

Platyarthrus hoffmannseggii is the only strict myrmecophilous species in Belgium. It lives in ant nests of a wide variety of species (BERG, 1995), where it scavenges on ant brood and ant prey but probably also feeds on other organic material in the nest (PARMENTIER *et al.*, 2017). It is commonly found across the country (Map 20). The species has been recorded in a wide range of habitats in open landscapes and anthropogenic habitat (Table 22). It is most commonly found on graveyards, grasslands, near roads and buildings in open landscape and in gardens and parks. The species is rare in forest habitat and in this habitat probably confined to forest edges and very open forest types.

The months with most records of *P. hoffmannseggii* are strongly linked to the phenology of ants. From May until October the corrected number of records is highest with a small decrease in November–December (Fig. 24). In anthropogenic habitat, the number of records peaks already in May–June. In open landscape, the increase happens more gradually and only starts to peak in July. The relative high number of records stays constant until November–December. The phenology shows a two-month shift in open landscapes compared to anthropogenic habitats, which can probably be attributed to the resulting consequences of the urban heat island effect on ant phenology (CHICK *et al.*, 2019). Although, *P. hoffmannseggii* is a drought-sensitive species (DIAS *et al.*, 2013), its phenology seems to be shaped by its host activity rather than by environmental variables. In forests, we do not see a clear phenological pattern, possibly due to the low number of records in this habitat.

Table 22. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Platyarthrus hoffmannseggii*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**76**	**48.7%**
farm	3	3.9%		
gardens and parks	20	26.3%		
near water in urban area	4	5.3%		
near roads and buildings in urban area	13	17.1%		
graveyard	36	47.4%		
forest			**18**	**11.5%**
coniferous forest	0	0.0%		
deciduous forest	10	55.6%		
near water in deciduous forest	3	16.7%		
near roads and buildings in forest	5	27.8%		
open landscape			**60**	**38.5%**
cropland and orchards	0	0.0%		
grassland	16	26.7%		
disused quarry	5	8.3%		
near roads and buildings in open landscape	20	33.3%		
near water in open landscape	9	15.0%		
river or canal dykes	10	16.7%		
coast			**2**	**1.3%**
total			**156**	

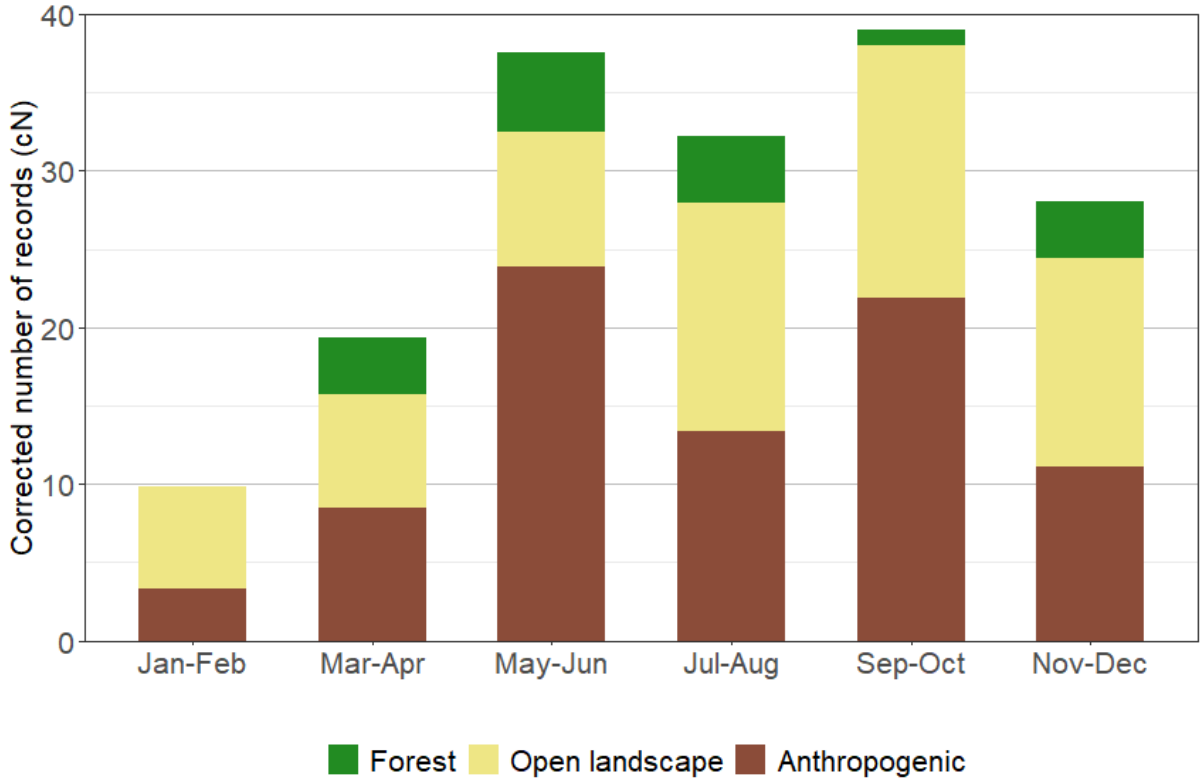
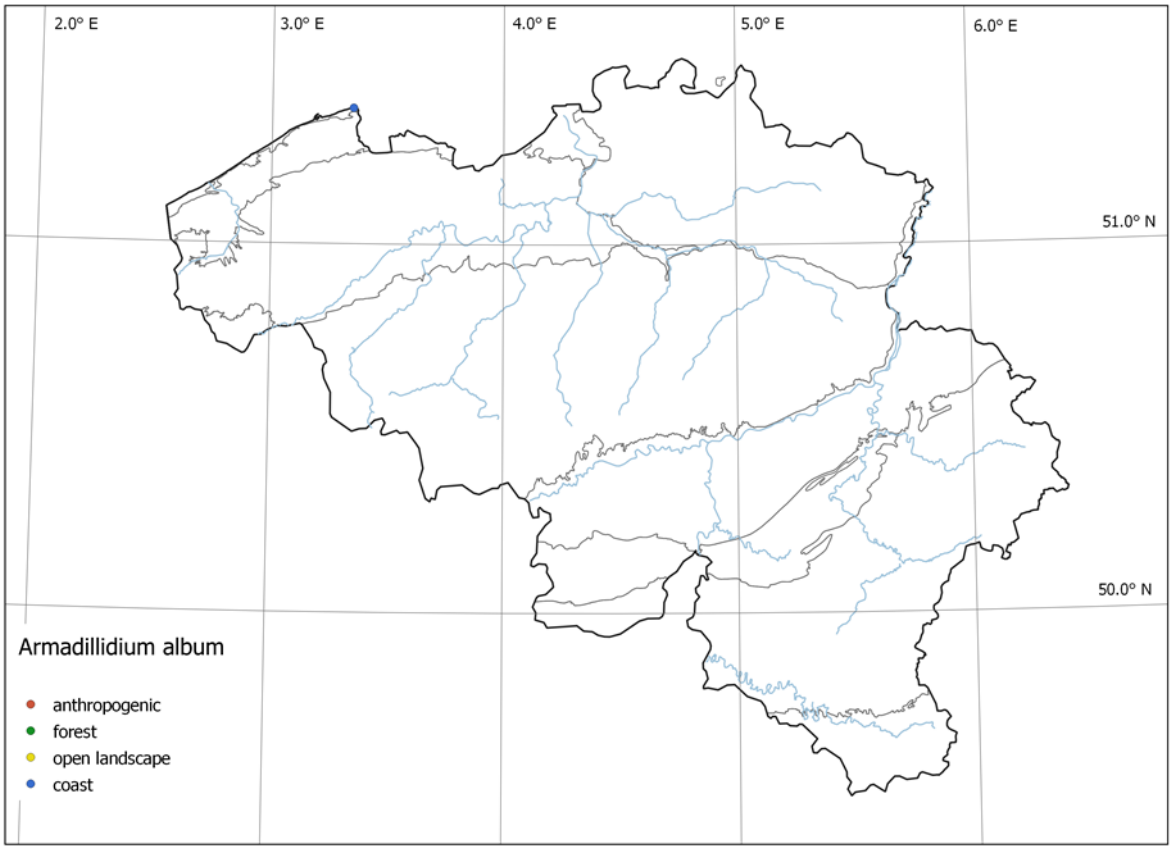


Fig. 24. Corrected number of observations per two-month period for *Platyarthrus hoffmannseggii* (N = 163).

21. *Armadillidium album* Dollfus, 1887
(Fig. 19 e, Fig. 25, Map 21, Table 23)



Map 21. Distribution map for *Armadillidium album*.

Armadillidium album is a very rare species in Belgium, found on sand beaches among sea drift material at the high-water line and up to the high-water mark of spring tides. It is unclear if the species has viable populations in Belgium, or if the species only accidentally arrives from neighbouring countries via sea drift. There are only three confirmed records and the two recent records were composed of only one individual. All records were from the most eastern part of the Belgian coast (Map 21).

Recent records are from July 2009 (not included in the dataset for the present study) and January 2016. An old confirmed record dates from May 1978 (KERSMAEKERS, 1988). These few observations do not allow us to make statements about the species phenology.

Table 23. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Armadillidium album*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**0**	**0.0%**
farm	0	0.0%		
gardens and parks	0	0.0%		
near water in urban area	0	0.0%		
near roads and buildings in urban area	0	0.0%		
graveyard	0	0.0%		
forest			**0**	**0.0%**
coniferous forest	0	0.0%		
deciduous forest	0	0.0%		
near water in deciduous forest	0	0.0%		
near roads and buildings in forest	0	0.0%		
open landscape			**0**	**0.0%**
cropland and orchards	0	0.0%		
grassland	0	0.0%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	0	0.0%		
near water in open landscape	0	0.0%		
river or canal dykes	0	0.0%		
coast			**1**	**100.0%**
total			**1**	

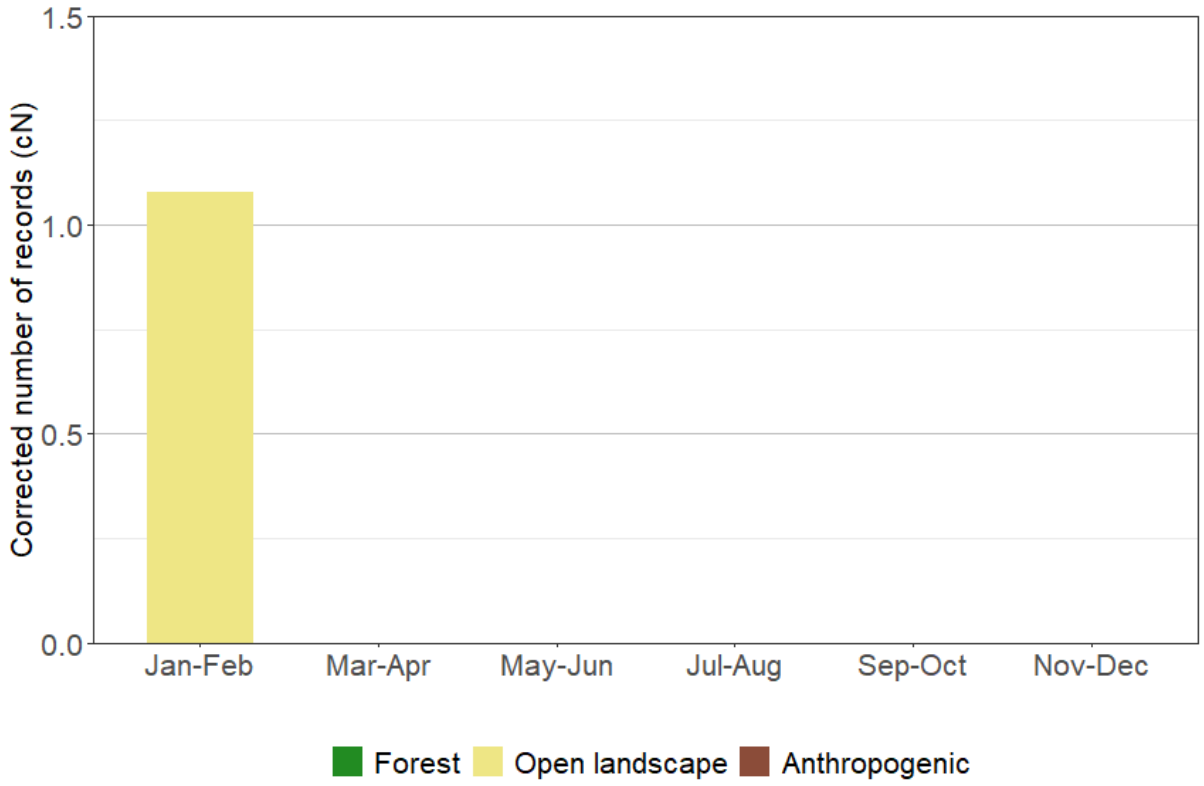
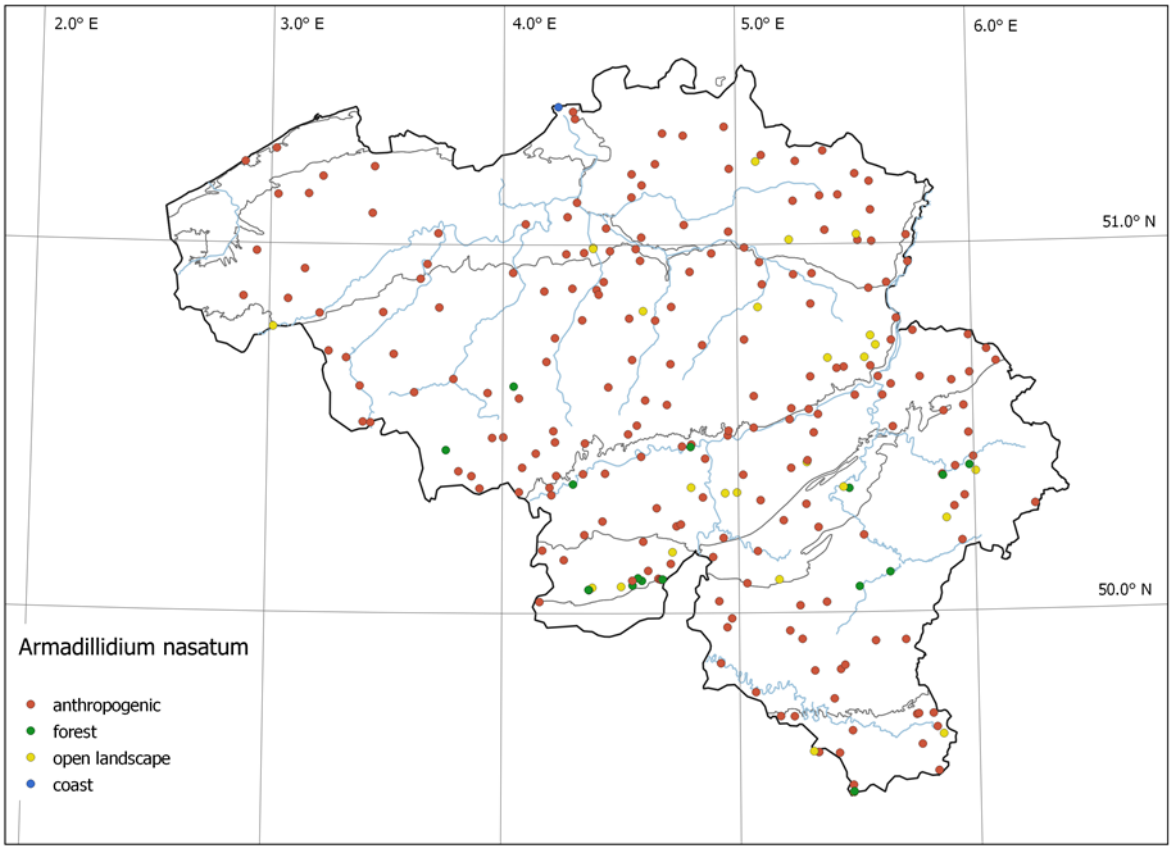


Fig. 25. Corrected number of observations per two-month period for *Armadillidium album* (N=1).

22. ***Armadillidium nasatum*** Budde-Lund, 1885
(Fig. 19 f, Fig. 26, Map 22, Table 24)



Map 22. Distribution map for *Armadillidium nasatum*.

Armadillidium nasatum is widespread across the country in anthropogenic habitats (Map 22). Only in the polders and sand-loam ecological region, *A. nasatum* is less common. In anthropogenic habitat, the species is very common on graveyards and can be seen as a characteristic species for graveyard fauna. *A. nasatum* is also very common in old quarries. The species is rarely found in grasslands unless heaps of stones are close by. We can assume that the species is easily transported via human activity through the transportation and dumping of stones. The species has been observed in forests but then mostly in habitats with clear human influence, i.e. near roads and buildings in forests. The four records in deciduous forest without clear human influence are situated in the south of the Fagne and Famenne ecological region. These observations are from very open forests with calcareous soil outcrops.

From its original centre of distribution in Northern Italy the species spread out to large parts of Europe (VANDEL, 1962). *A. nasatum* prefers habitat types with higher temperatures and is most commonly found in warmer months in all habitat types (Fig. 26). During winter, the species is harder to find and sometimes populations of thousands of individuals are almost undetectable when they hide deep in crevices to escape cold temperatures.

Table 24. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Armadillidium nasatum*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**207**	**82.5%**
farm	2	1.0%		
gardens and parks	6	2.9%		
near water in urban area	6	2.9%		
near roads and buildings in urban area	25	12.1%		
graveyard	168	81.2%		
forest			**16**	**6.4%**
coniferous forest	0	0.0%		
deciduous forest	5	31.3%		
near water in deciduous forest	0	0.0%		
near roads and buildings in forest	11	68.8%		
open landscape			**27**	**10.8%**
cropland and orchards	0	0.0%		
grassland	5	18.5%		
disused quarry	11	40.7%		
near roads and buildings in open landscape	8	29.6%		
near water in open landscape	0	0.0%		
river or canal dykes	3	11.1%		
coast			**1**	**0.4%**
total			**251**	

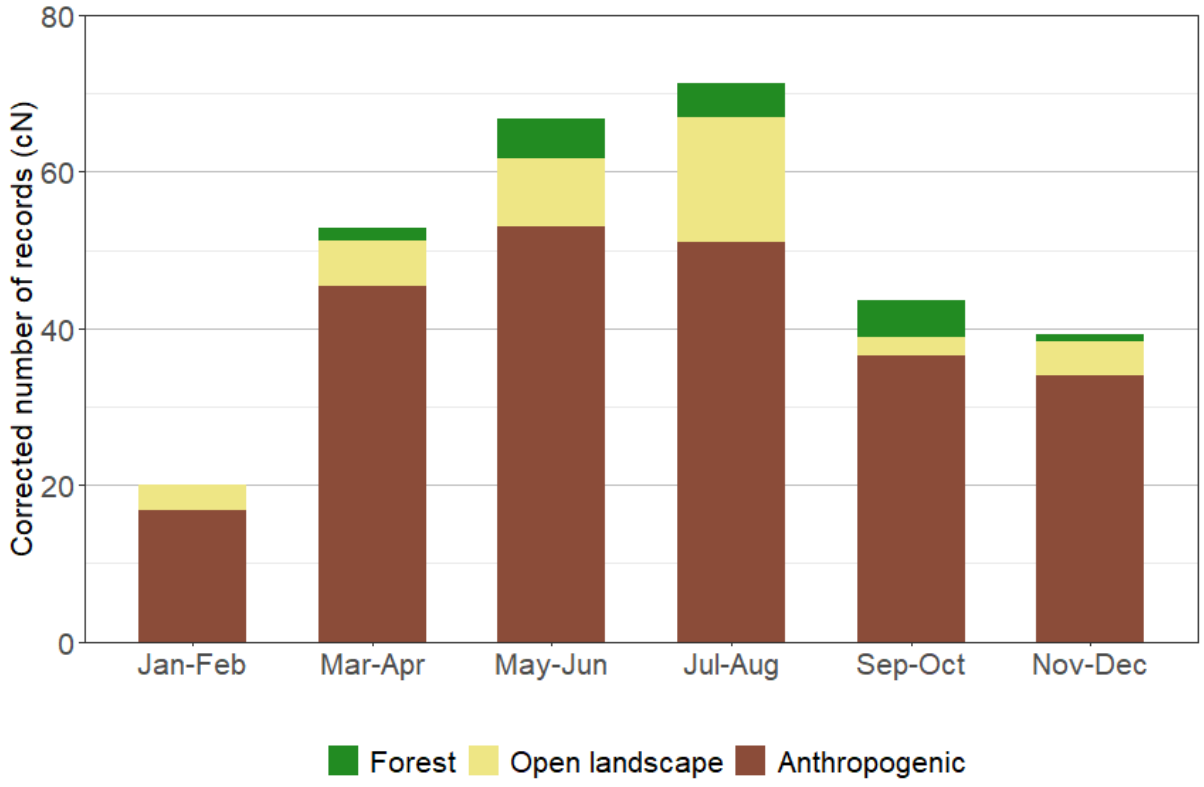
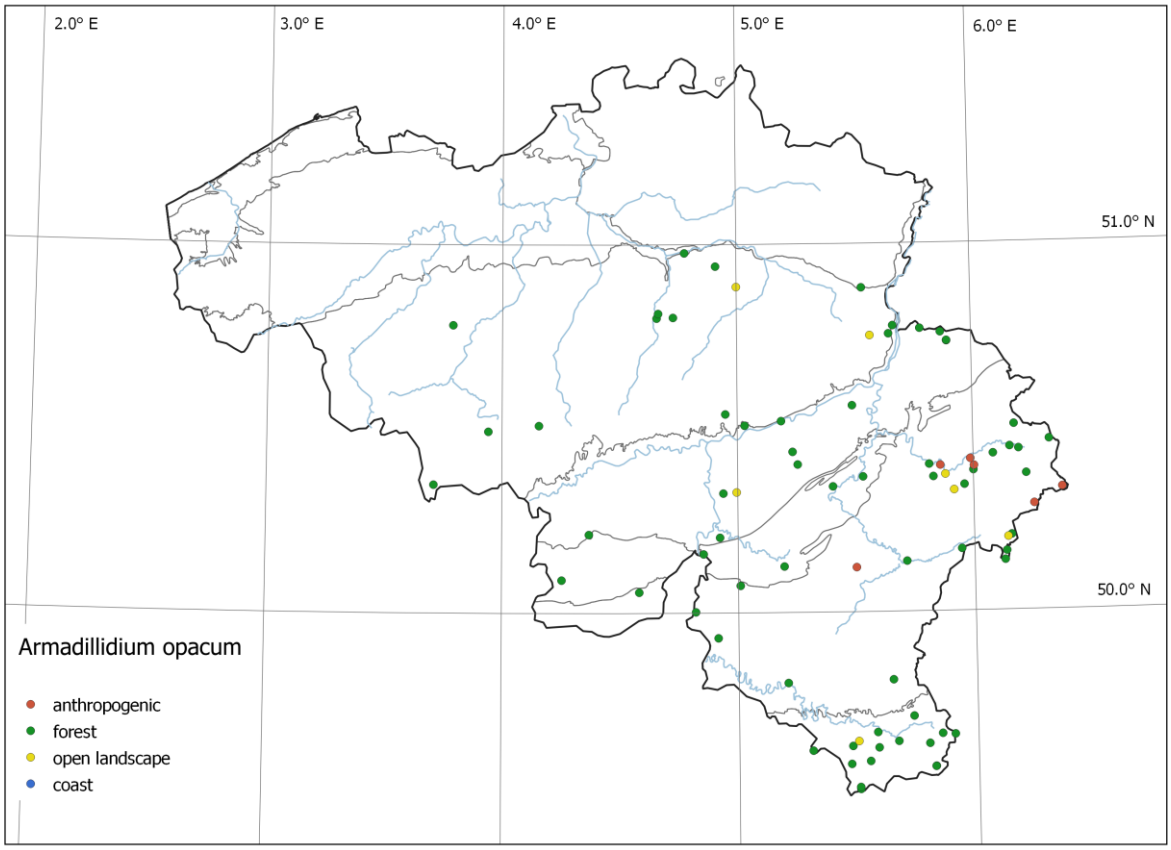


Fig. 26. Corrected number of observations per two-month period for *Armadillidium nasatum* (N = 287).

23. *Armadillidium opacum* (C. Koch, 1841)
(Fig. 19 g, Fig. 27, Map 23, Table 25)



Map 23. Distribution map for *Armadillidium opacum*.

The vast number of records of *Armadillidium opacum* is situated in forest habitat (83.1% of the records, see table 25). Across the country it is characterised as a species with a strong forest affinity (DE SMEDT *et al*., 2020b) and in the north it is a characteristic species from ancient woodland and closed forest habitat (DE SMEDT & VANDEKERKHOVE, 2020). In the south and east of the country, the species is more common and more frequently found in other habitat types. Especially in the east of the country, the species can be found outside forest where it replaces *A. vulgare* as most common *Armadillidium*-species in (semi-)natural habitat. The species has been found in grasslands but always in close vicinity to ancient woodland. The correct number of records strongly peaks in May–June (Fig. 27), coinciding with the species breeding period (DEVAERE, 1999).

Table 25. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Armadillidium opacum*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**6**	**7.6%**
farm	0	0.0%		
gardens and parks	2	33.3%		
near water in urban area	0	0.0%		
near roads and buildings in urban area	1	16.7%		
graveyard	3	50.0%		
forest			**66**	**83.5%**
coniferous forest	0	0.0%		
deciduous forest	32	48.5%		
near water in deciduous forest	26	39.4%		
near roads and buildings in forest	8	12.1%		
open landscape			**7**	**8.9%**
cropland and orchards	0	0.0%		
grassland	4	57.1%		
disused quarry	2	28.6%		
near roads and buildings in open landscape	1	14.3%		
near water in open landscape	0	0.0%		
river or canal dykes	0	0.0%		
coast			**0**	**0.0%**
total			**79**	

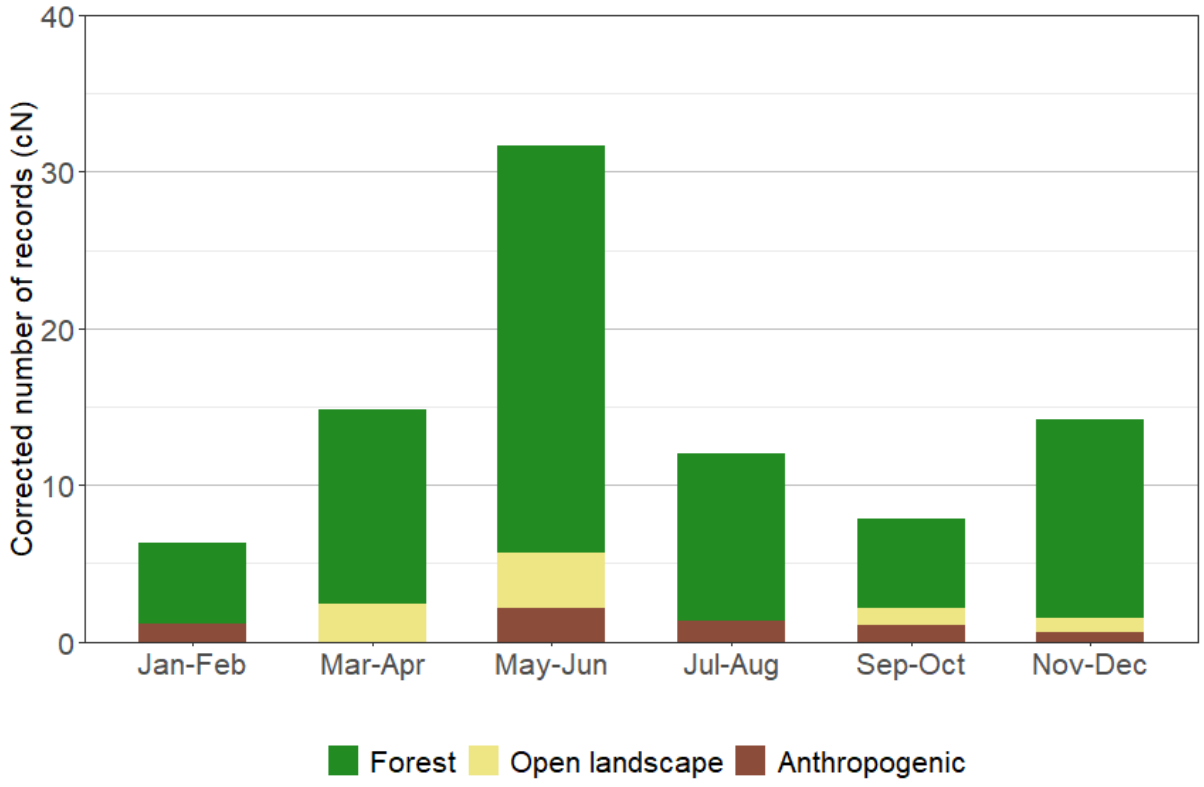
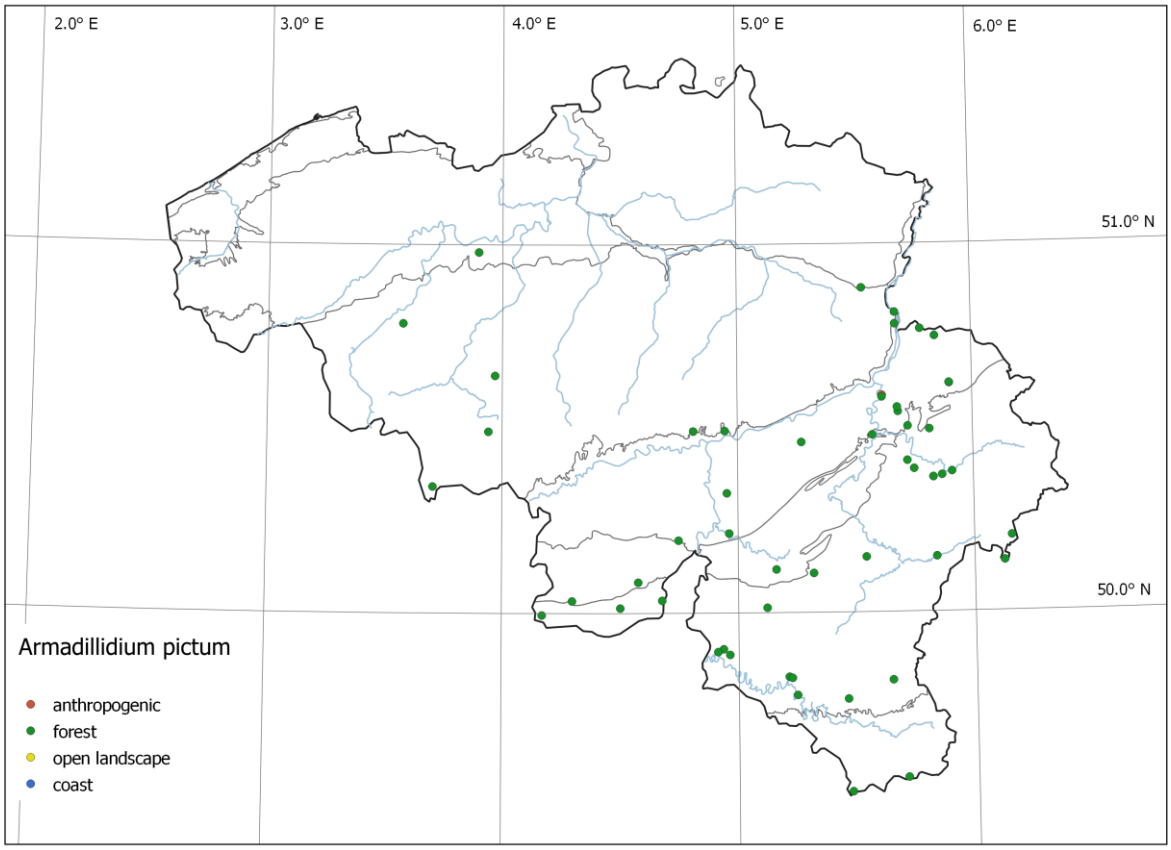


Fig. 27. Corrected number of observations per two-month period for *Armadillidium opacum* (N = 89).

24. *Armadillidium pictum* Brandt, 1833
(Fig. 2 e, Fig. 28, Map 24, Table 26)



Map 24. Distribution map for *Armadillidium pictum*.

Armadillidium pictum is almost exclusively found in forests (96.3 % of habitat records, see table 26). The species is common south of the rivers Sambre and Meuse but rare to the north (Map 24). It shows comparable habitat preferences as *A. pulchellum*, however both species rarely occur together and the reason for this is not known. This species is regularly found on the bark of trees where it hides during daytime between fissures, mosses and cracks.

The phenology diagram shows a remarkably low number of records in May–June (Fig. 28); although the species has a relatively high drought tolerance (DIAS *et al.*, 2013). The phenology pattern is therefore difficult to explain and more data is needed.

Table 26. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Armadillidium pictum.*

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**2**	**3.7%**
farm	0	0.0%		
gardens and parks	1	50.0%		
near water in urban area	0	0.0%		
near roads and buildings in urban area	0	0.0%		
graveyard	1	50.0%		
forest			**52**	**96.3%**
coniferous forest	1	1.9%		
deciduous forest	30	57.7%		
near water in deciduous forest	18	34.6%		
near roads and buildings in forest	3	5.8%		
open landscape			**0**	**0.0%**
cropland and orchards	0	0.0%		
grassland	0	0.0%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	0	0.0%		
near water in open landscape	0	0.0%		
river or canal dykes	0	0.0%		
coast			**0**	**0.0%**
total			**54**	

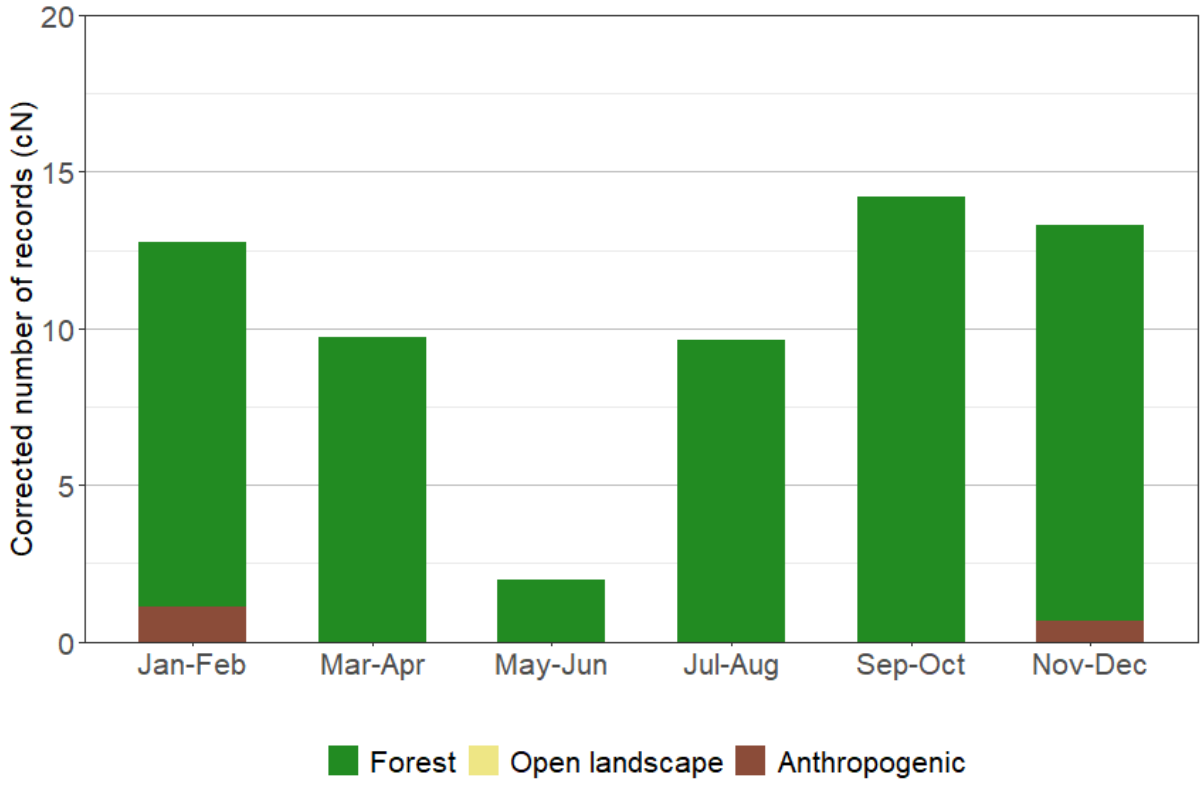
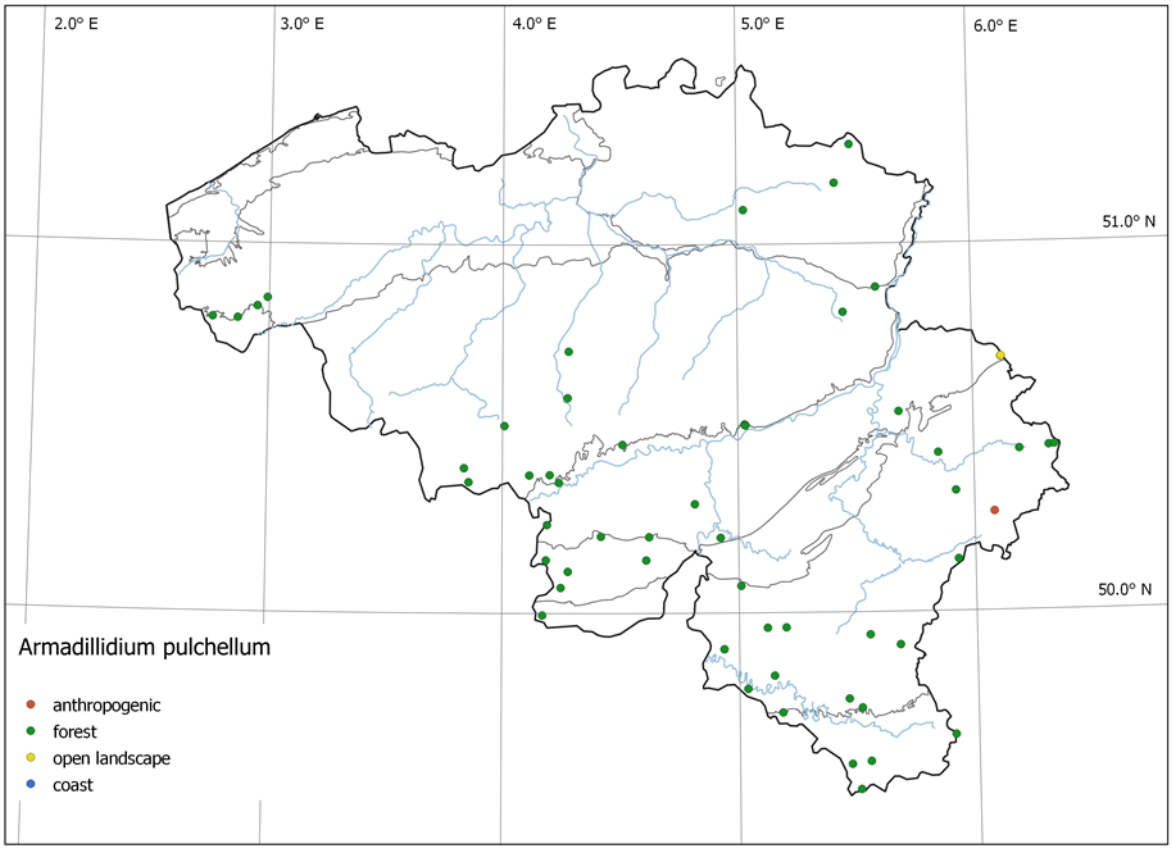


Fig. 28. Corrected number of observations per two-month period for *Armadillidium pictum* (N = 62).

25. ***Armadillidium pulchellum*** (Zencker, 1798)
(Fig. 19 h, Fig. 29, Map 25, Table 27)



Map 25. Distribution map for *Armadillidium pulchellum*.

Armadillidium pulchellum is almost exclusively found in forests (96.4 % of habitat records, see table 27) with observations widespread throughout the country (Map 25). Most isolated populations in the north of the country are in large ancient forest patches and therefore the species could be a good indicator for old and relatively undisturbed forest habitat (DE SMEDT & VANDEKERKHOVE, 2020). Some isolated populations are on sandy soils, where no other rare species are present. This species is commonly found on the bark of trees where it hides during daytime between fissures, mosses and cracks.

The corrected number of records shows a high peak in May–June (Fig. 29), which could be explained by the high drought tolerance of the species (DIAS *et al.*, 2013) but it is unclear whether this is a real peak in activity or rather a coincidental effect due to the relatively low number of records.

Table 27. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Armadillidium pulchellum*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**1**	**1.8%**
farm	0	0.0%		
gardens and parks	0	0.0%		
near water in urban area	0	0.0%		
near roads and buildings in urban area	0	0.0%		
graveyard	1	100.0%		
forest			**53**	**96.4%**
coniferous forest	0	0.0%		
deciduous forest	38	71.7%		
near water in deciduous forest	15	28.3%		
near roads and buildings in forest	0	0.0%		
open landscape			**1**	**1.8%**
cropland and orchards	0	0.0%		
grassland	0	0.0%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	1	100.0%		
near water in open landscape	0	0.0%		
river or canal dykes	0	0.0%		
coast			**0**	**0.0%**
total			**55**	

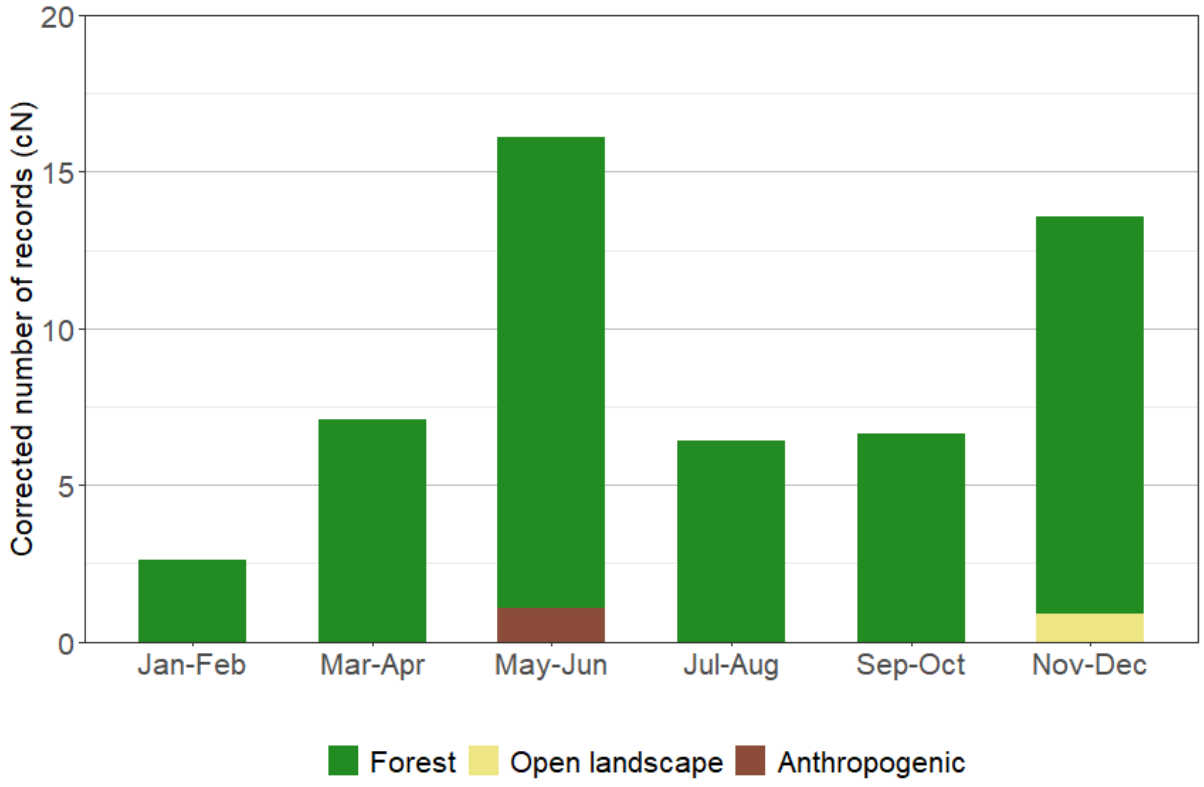
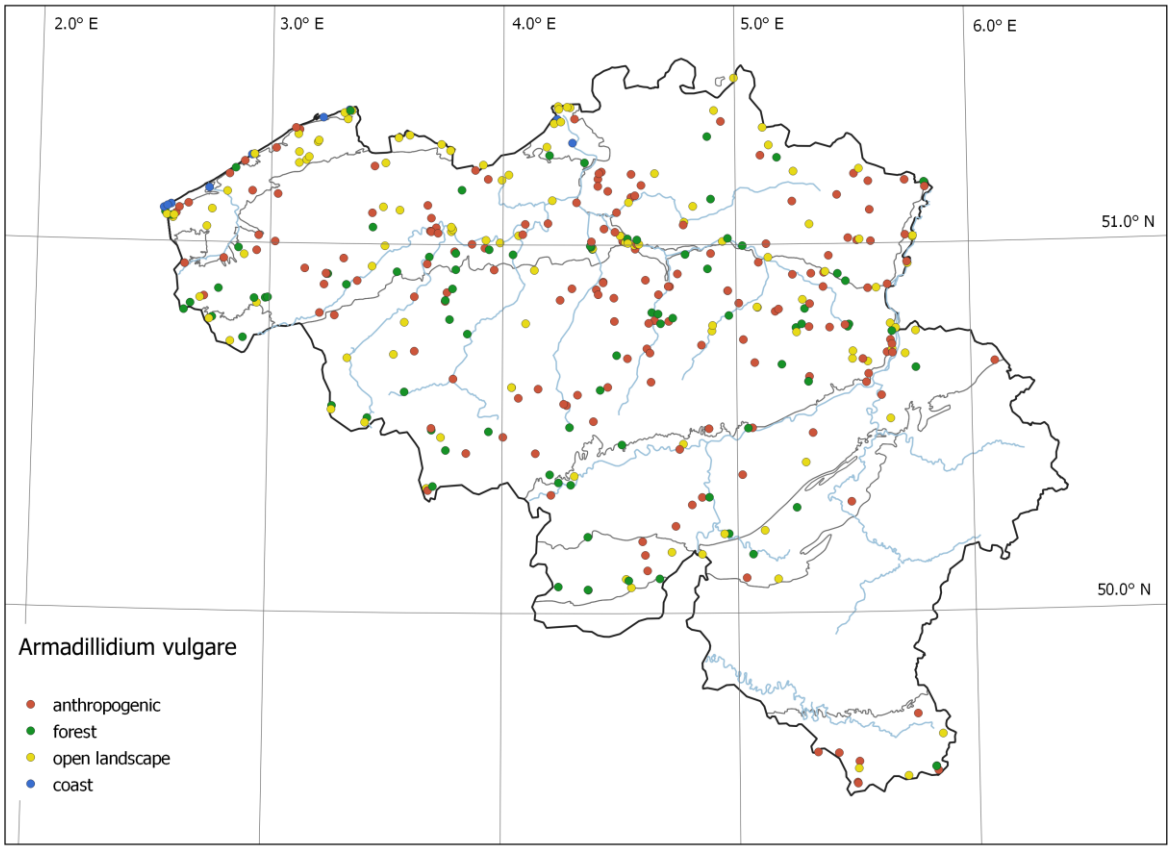


Fig. 29. Corrected number of observations per two-month period for *Armadillidium pulchellum* (N = 54).

26. ***Armadillidium vulgare*** (Latreille, 1804)
(Fig. 2 f, Fig. 30, Map 26, Table 28)



Map 26. Distribution map for *Armadillidium vulgare*.

Armadillidium vulgare is a very common species that can be found in a wide variety of habitats in Belgium (Table 28). The species is absent in the Ardennes ecological region and rare or absent in large parts of the Campine region (Map 26), which may be explained by acidic soil types in those regions and low temperatures in the Ardennes ecological region. *A. vulgare* shows a marked preference for a higher soil pH (VAN STRAALEN & VERHOEF, 1997). *Armadillidium vulgare* has a high desiccation resistance (DIAS *et al.*, 2013) and it is one of the few species that can be found running around exposed in full sunlight. The species is common on graveyards and near all kinds of roads and buildings where it hides under stones and wood. It can be very common on dry and rough grasslands if sufficient cover like stones and dead wood is present (see also DE SMEDT *et al.*, 2021). As eurytopic species, it is also commonly found in gardens and parks. Compared to other eurytopic species *A. vulgare* occurs less in forests compared to anthropogenic habitats and open landscape habitats. In forests, the species shows its highest abundances in the drier and warmer forest edges while it is almost absent from forest interior habitat (DE SMEDT *et al.*, 2018a).

As other drought-resistant species, it is most often recorded during summer months in all kind of habitat types with a peak in the number of records from May until August (Fig. 30). This is supported by pitfall trap data from DE SMEDT *et al.* (2021) where the species shows the strongest summer peak of eight common terrestrial isopod species in an abandoned sand quarry.

Table 28. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Armadillidium vulgare*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**166**	**44.0%**
farm	5	3.0%		
gardens and parks	34	20.5%		
near water in urban area	13	7.8%		
near roads and buildings in urban area	32	19.3%		
graveyard	82	49.4%		
forest			**88**	**23.3%**
coniferous forest	0	0.0%		
deciduous forest	52	59.1%		
near water in deciduous forest	19	21.6%		
near roads and buildings in forest	17	19.3%		
open landscape			**114**	**30.2%**
cropland and orchards	2	1.8%		
grassland	21	18.4%		
disused quarry	5	4.4%		
near roads and buildings in open landscape	41	36.0%		
near water in open landscape	22	19.3%		
river or canal dykes	23	20.2%		
coast			**9**	**2.4%**
total			**377**	

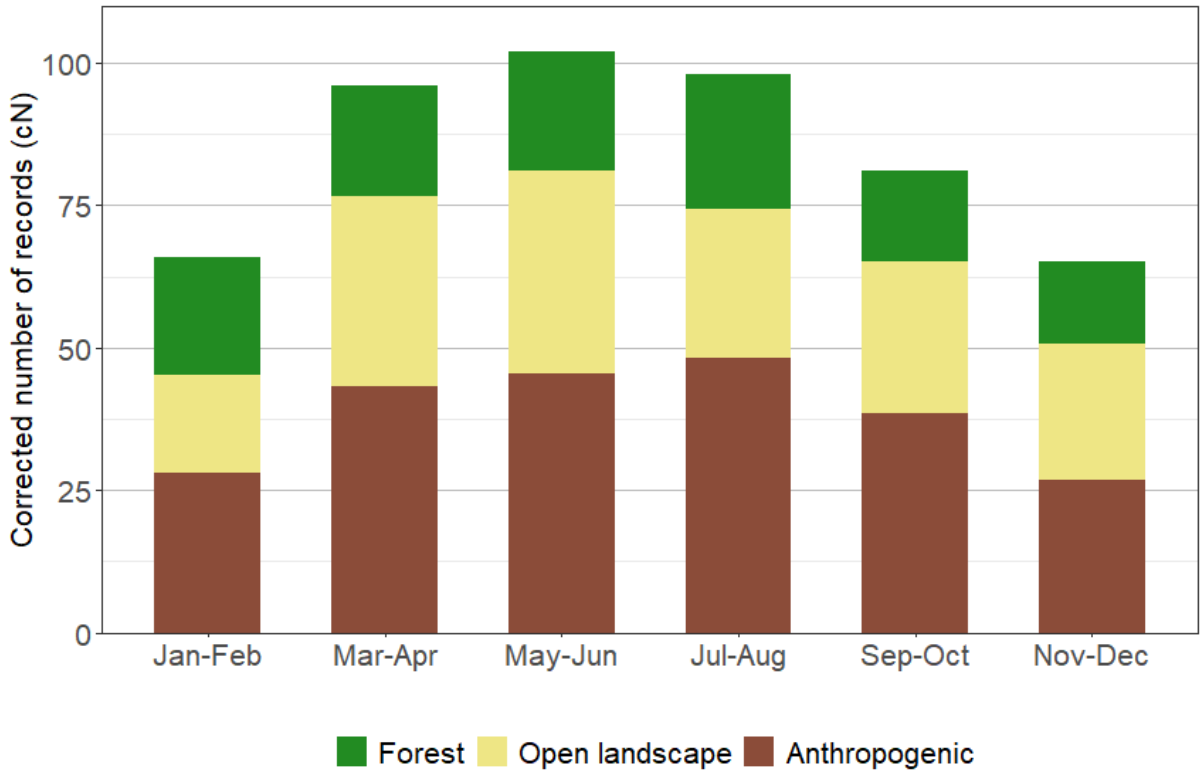
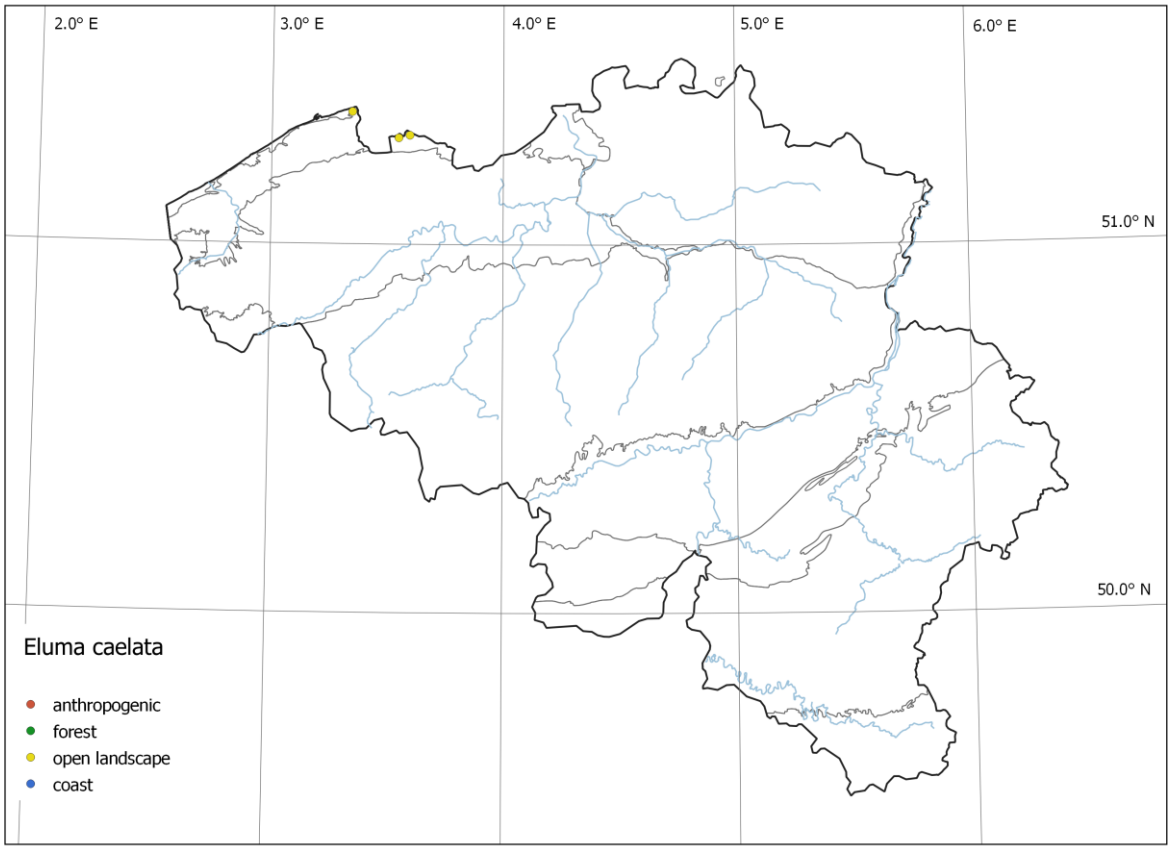


Fig. 30. Corrected number of observations per two-month period for *Armadillidium vulgare* (N = 502).

27. *Eluma caelata* (Miers, 1877)
(Fig. 20 a, Fig. 31, Map 27, Table 29)



Map 27. Distribution map for *Eluma caelata*.

Eluma caelata was for the first time recorded in Belgium in 2016 (DE SMEDT *et al.*, 2017). It is a very rare species with only three known localities in Belgium, all in open landscape (Table 29, Map 27). The first discovery was in a rough grassland habitat near the nature reserve het "Zwin". The other two observations were further away from the coast (10–15 km) in open landscape near a ditch with some trees in close vicinity. The species favours rather similar habitat in the Netherlands, where it occurs only in the province neighbouring the Belgian localities (BERG *et al.*, 2008). By contrast, in France *E. caelata* is found in forest on acidic soils but these localities are hundreds of kilometres south of the Belgian populations (SÉCHET & NOËL, 2015).

All Belgian observation are from the end of the season: October, November and December. However, because of the low number of records we cannot deduct conclusions based on the phenology diagram (Fig. 31).

Table 29. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Eluma caelata*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**0**	**0.0%**
farm	0	0.0%		
gardens and parks	0	0.0%		
near water in urban area	0	0.0%		
near roads and buildings in urban area	0	0.0%		
graveyard	0	0.0%		
forest			**0**	**0.0%**
coniferous forest	0	0.0%		
deciduous forest	0	0.0%		
near water in deciduous forest	0	0.0%		
near roads and buildings in forest	0	0.0%		
open landscape			**3**	**100.0%**
cropland and orchards	0	0.0%		
grassland	1	33.3%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	0	0.0%		
near water in open landscape	2	66.7%		
river or canal dykes	0	0.0%		
coast			**0**	**0.0%**
total			**3**	

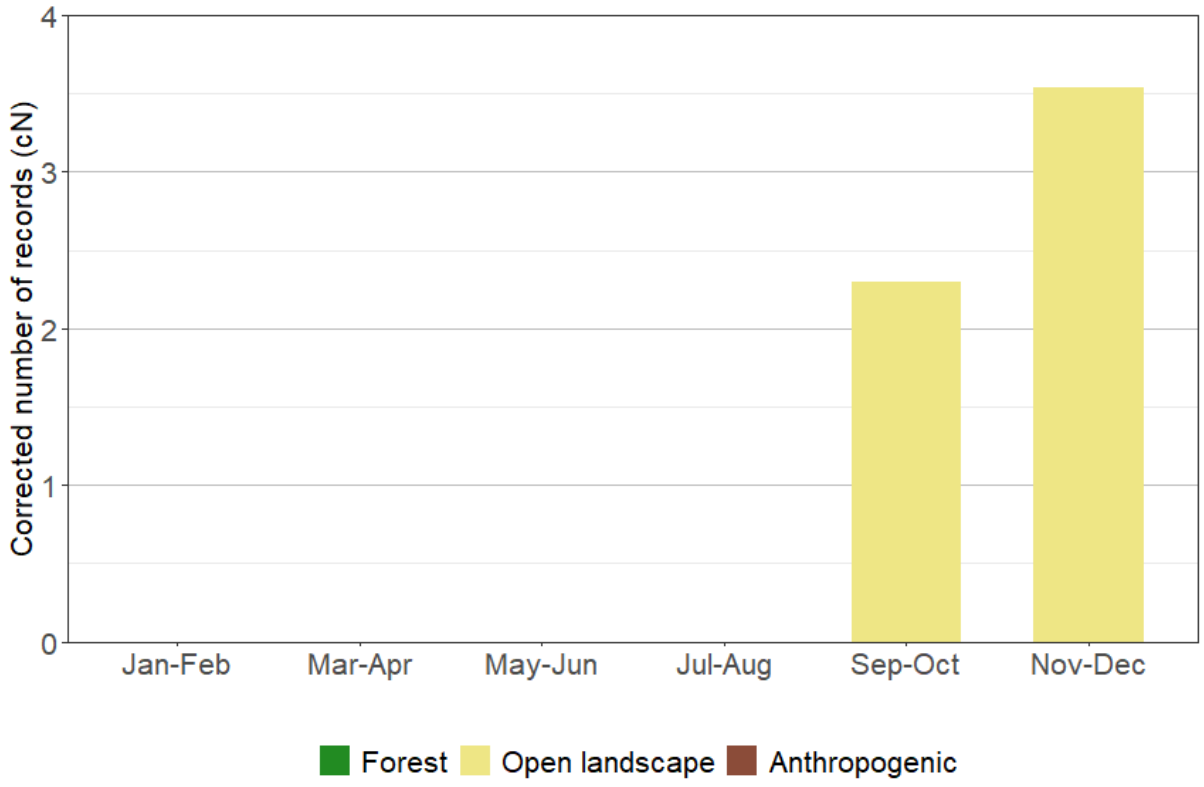
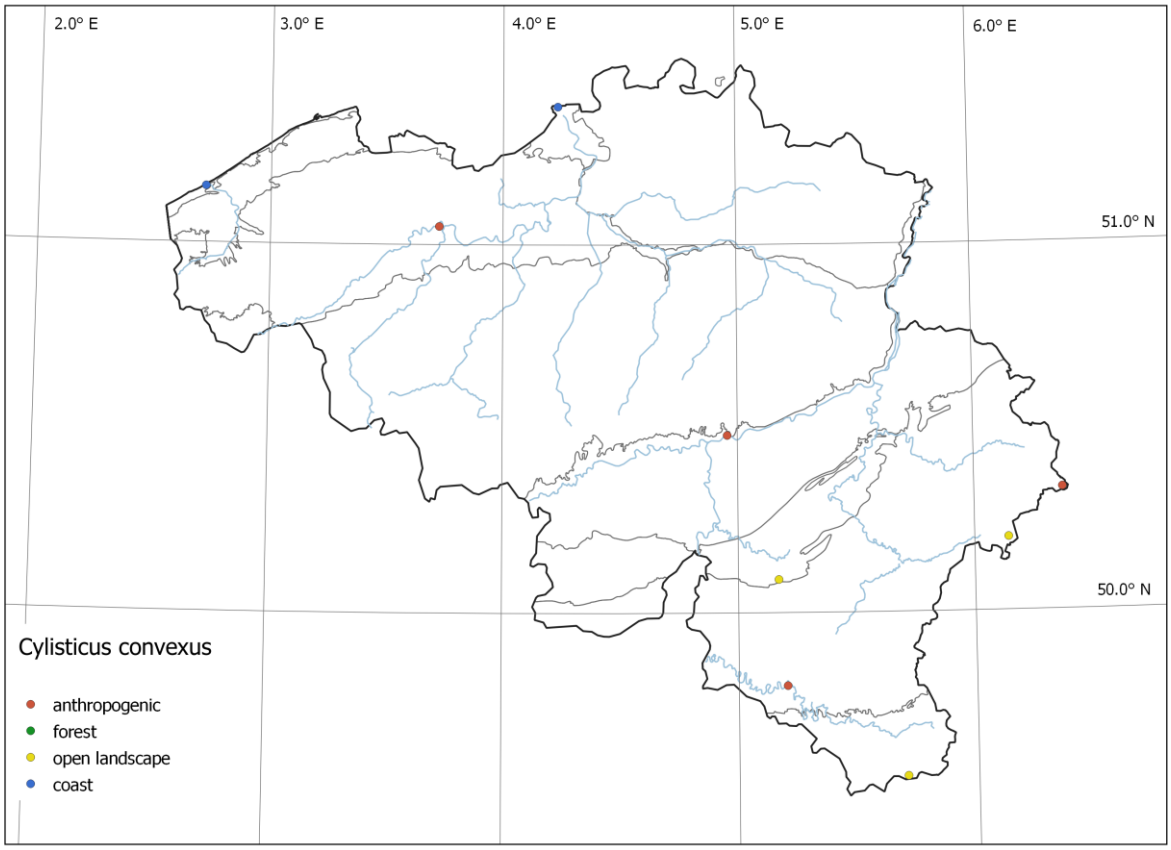


Fig. 31. Corrected number of observations per two-month period for *Eluma caelata* (N = 6).

28. *Cylisticus convexus* (De Geer, 1778)
(Fig. 20 b, Fig. 32, Map 28, Table 30)



Map 28. Distribution map for *Cylisticus convexus*.

Cylisticus convexus has recently been found in only nine locations but widely spread across the country (Map 28). The species is exclusively found in habitat with some degree of anthropogenic influence. Two observations were made in coastal habitat under stones from dykes and riverbank reinforcements. Inland, there is an observation in a city garden, one at an old railway station, two on farms and three observations were made in old quarries. Most observations report only one or a few specimens. Only in some quarries, the city garden and one of the farms, larger numbers were found. Probably this species is transported very often via human activity and can be expected to appear everywhere in the country in random locations. It is a thermophilic species (VANDEL, 1962), which can only establish populations in warm microsites. The habitat in Belgium corresponds to the habitat in Great Britain, where the species is more often recorded (HARDING & SUTTON, 1985; GREGORY, 2009).

There is only a limited number of observations which does not allow conclusions based on the phenology diagram (Fig. 32). Although, *C. convexus* is a thermophilic species we expect it to be more active during summer months, especially in open landscape habitats.

Table 30. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Cylisticus convexus*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**4**	**44.4%**
farm	1	25.0%		
gardens and parks	1	25.0%		
near water in urban area	0	0.0%		
near roads and buildings in urban area	2	50.0%		
graveyard	0	0.0%		
forest			**0**	**0.0%**
coniferous forest	0	0.0%		
deciduous forest	0	0.0%		
near water in deciduous forest	0	0.0%		
near roads and buildings in forest	0	0.0%		
open landscape			**3**	**33.3%**
cropland and orchards	0	0.0%		
grassland	0	0.0%		
disused quarry	3	100.0%		
near roads and buildings in open landscape	0	0.0%		
near water in open landscape	0	0.0%		
river or canal dykes	0	0.0%		
coast			**2**	**22.2%**
total			**9**	

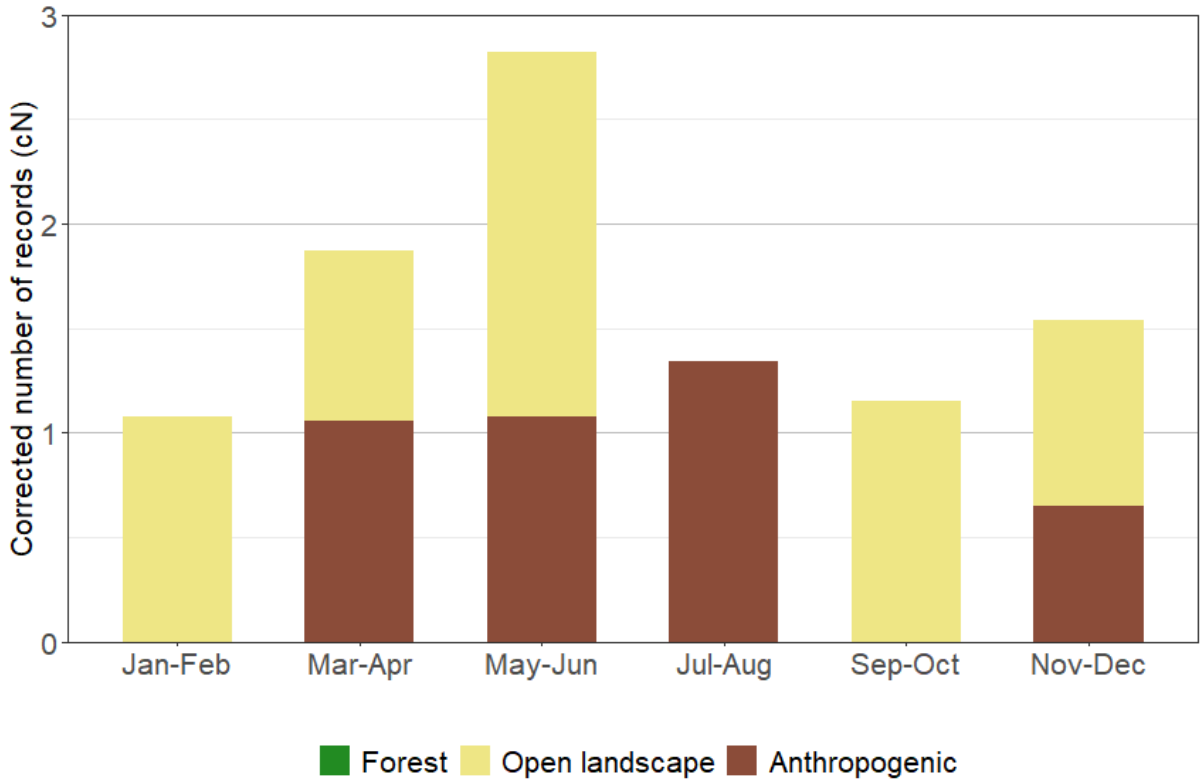
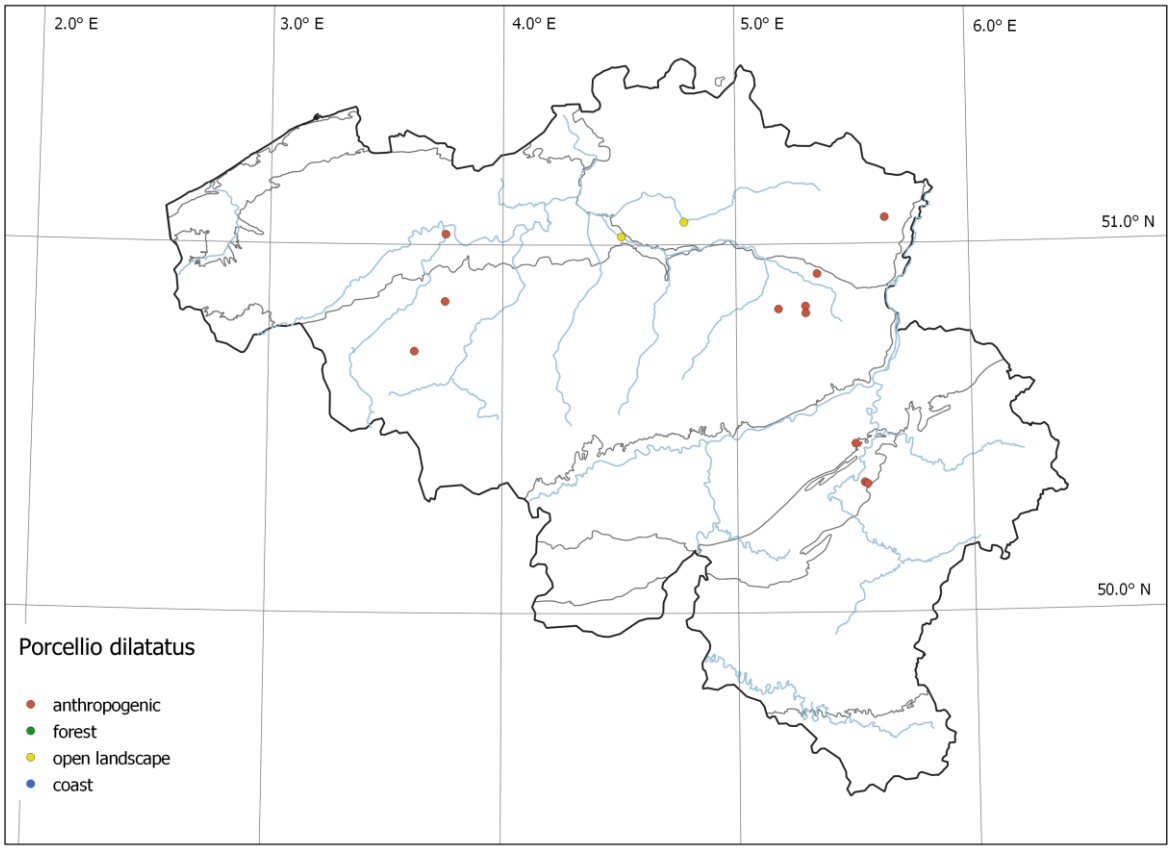


Fig. 32. Corrected number of observations per two-month period for *Cylisticus convexus* (N = 10).

29. *Porcellio dilatatus* Brandt, 1833
(Fig. 2 g, Fig. 33, Map 29, Table 31)



Map 29. Distribution map for *Porcellio dilatatus*.

Porcellio dilatatus has only been recorded in anthropogenic habitats or in open landscape in places with clear human influence (Table 31). Records of the species in gardens and parks concern mostly only one or a few individuals whereas in stables and barns on farms *P. dilatatus* is regularly observed in high numbers. Since *P. dilatatus* is a thermophilic species, we assume that constant warm and moist conditions in stables and barns are the optimal climate for a thriving population. Due to the continuing disappearance of old, small-scale farms the species is declining in Belgium (DE SMEDT *et al.*, 2020a). The species was not found under semi-natural conditions, which is the case in the south of the Netherlands, were the species is also known from calcareous grasslands (BERG *et al.*, 2008).

Due to the low number of records, it is difficult to draw conclusions based on the phenology diagram (Fig. 33). The species is probably active year-round inside stables and barns on farms. Outside buildings, the species is rarer and probably inactive during winter months (personal observations).

Table 31. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Porcellio dilatatus*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**11**	**84.6%**
farm	5	45.5%		
gardens and parks	4	36.4%		
near water in urban area	0	0.0%		
near roads and buildings in urban area	1	9.1%		
graveyard	1	9.1%		
forest			**0**	**0.0%**
coniferous forest	0	0.0%		
deciduous forest	0	0.0%		
near water in deciduous forest	0	0.0%		
near roads and buildings in forest	0	0.0%		
open landscape			**2**	**15.4%**
cropland and orchards	0	0.0%		
grassland	0	0.0%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	2	100.0%		
near water in open landscape	0	0.0%		
river or canal dykes	0	0.0%		
coast			**0**	**0.0%**
total			**13**	

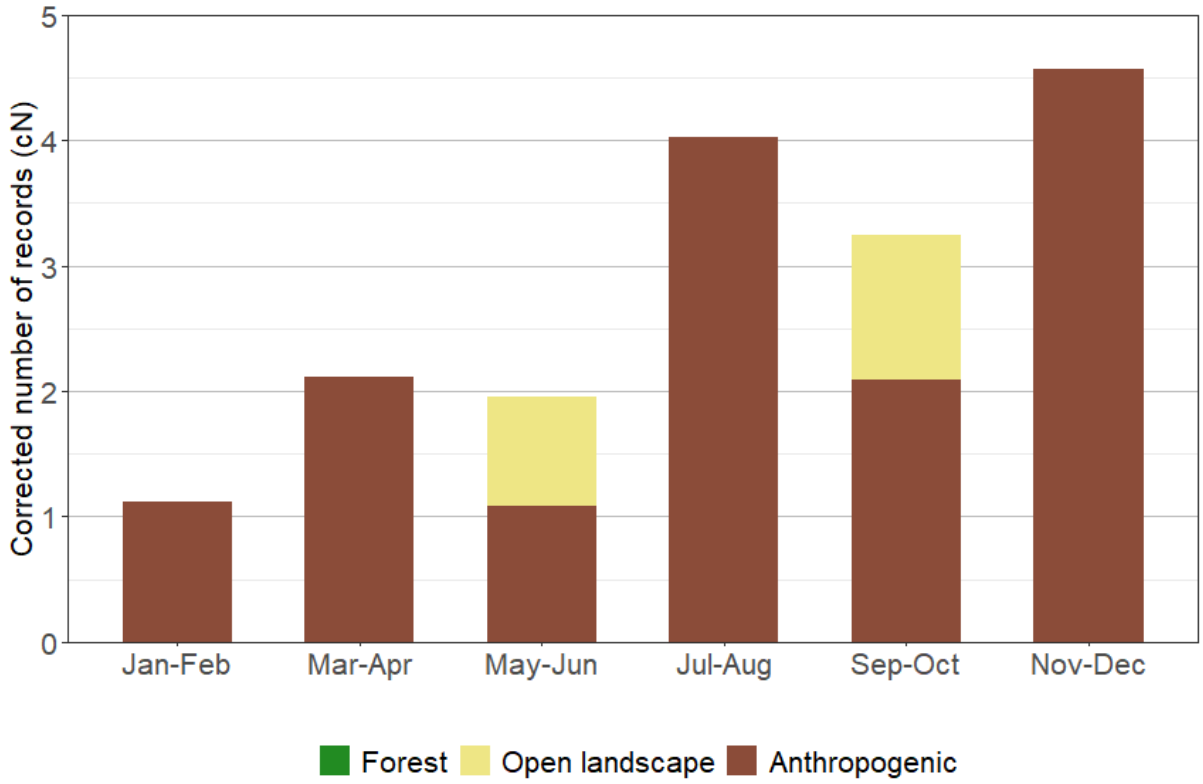
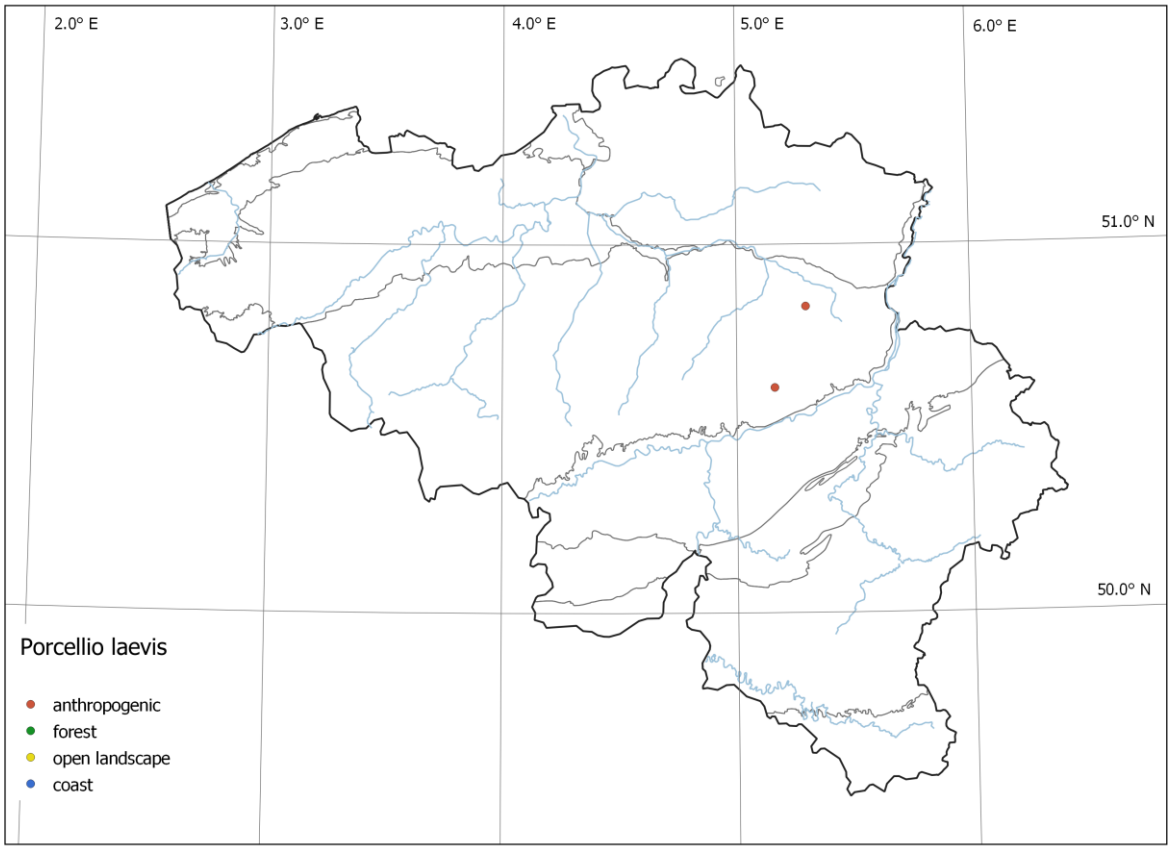


Fig. 33. Corrected number of observations per two-month period for *Porcellio dilatatus* (N = 18).

30. *Porcellio laevis* Latreille, 1804
(Fig. 2 h, Fig. 34, Map 30, Table 32)



Map 30. Distribution map for *Porcellio laevis*.

Recent records of *Porcellio laevis* in Belgium are restricted to old farms. It has a much narrower niche compared to *P. dilatatus.* The two only recent records are from active horse stables. The species was recorded underneath hay, stones and dung in a corner of the stable. When a resurvey of old locations from the early 1990's (BOON *et al.*, 1993) was undertaken, it turned out that in most locations the species was not present anymore, but also the farms were not active anymore. Probably, as a thermophilic species, it needs the constant warmer temperatures caused by livestock like cows and horses. It is one of the rarest species in Belgium and according to DE SMEDT *et al.* (2020a) it risks disappearing in Belgium, a trend that is also reported from the UK (HARDING, 2016).

The two recent records are from May 2015 and November 2019. Like *P. dilatatus*, *P. laevis* is probably year-round active in (horse) stables with livestock but because of the few observations, no conclusions can be drawn from the phenology diagram (Fig. 34).

Table 32. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Porcellio laevis*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**2**	**100.0%**
farm	2	100.0%		
gardens and parks	0	0.0%		
near water in urban area	0	0.0%		
near roads and buildings in urban area	0	0.0%		
graveyard	0	0.0%		
forest			**0**	**0.0%**
coniferous forest	0	0.0%		
deciduous forest	0	0.0%		
near water in deciduous forest	0	0.0%		
near roads and buildings in forest	0	0.0%		
open landscape			**0**	**0.0%**
cropland and orchards	0	0.0%		
grassland	0	0.0%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	0	0.0%		
near water in open landscape	0	0.0%		
river or canal dykes	0	0.0%		
coast			**0**	**0.0%**
total			**2**	

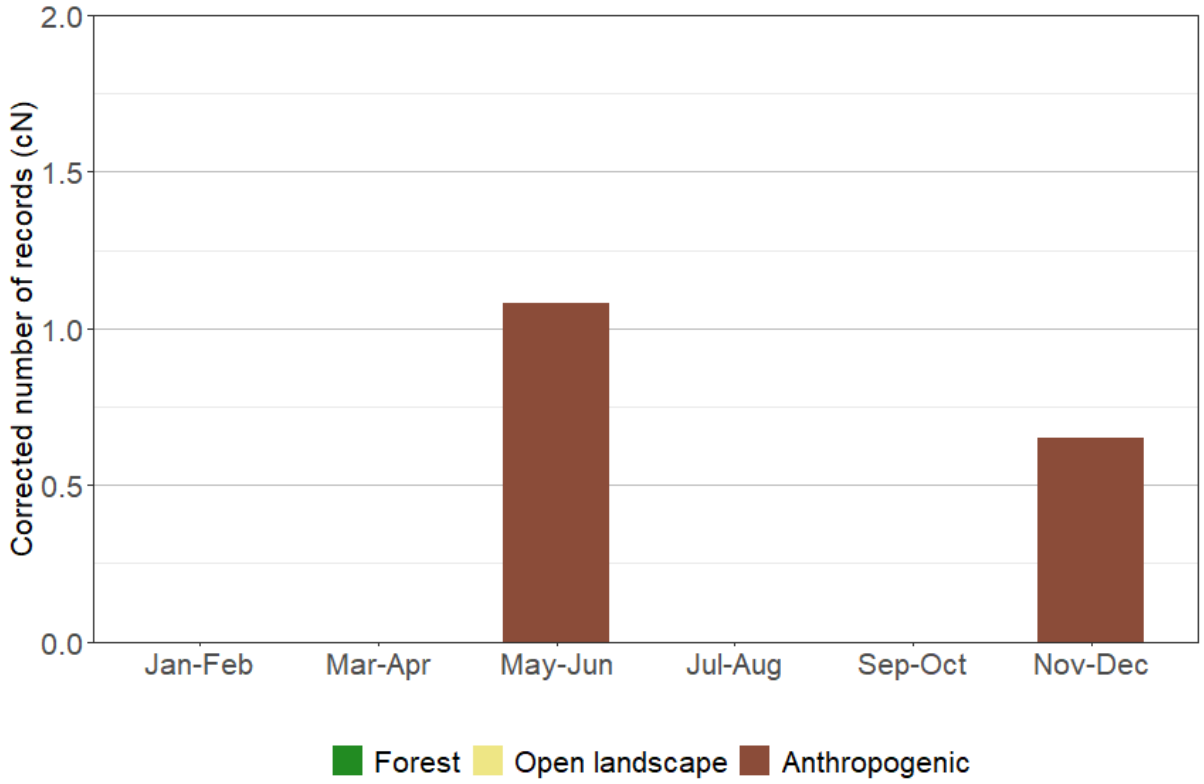
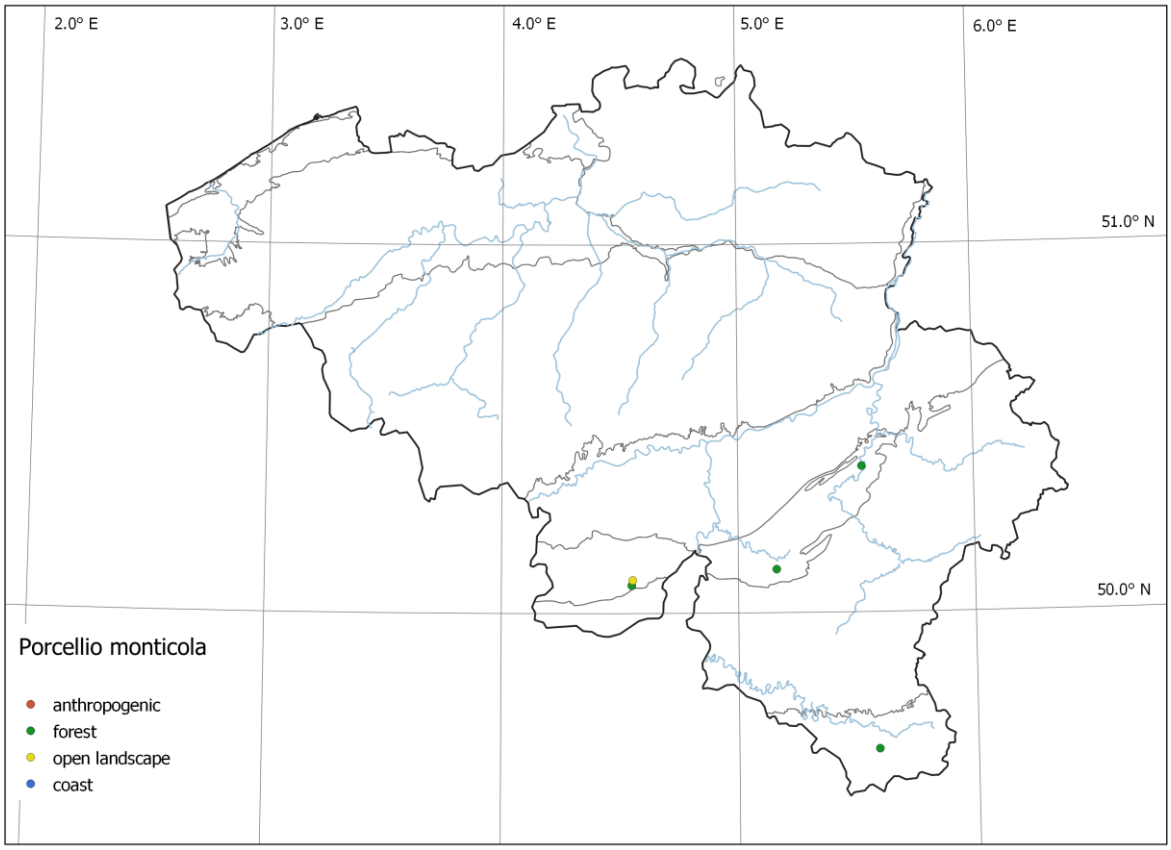


Fig. 34. Corrected number of observations per two-month period for *Porcellio laevis* (N = 2).

31. *Porcellio monticola* Lereboullet, 1853
(Fig. 20 c, Fig. 35, Map 31, Table 33)



Map 31. Distribution map for *Porcellio monticola*.

Porcellio monticola was just recently discovered for the first time in Belgium in 2014 (DE SMEDT *et al.*, 2015). Most observations were done in ancient deciduous forests on calcareous soil, where the species was sometimes found in large numbers. The dominant tree species were always Oak (*Quercus petraea/robur*) and Hornbeam (*Carpinus betulus*). There is one record from a calcareous grassland, but the location was close to ancient forest.

The limited number of records (Fig. 35) does not allow for any conclusions on possible seasonal activity patterns.

Table 33. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Porcellio monticola*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**0**	**0.0%**
farm	0	0.0%		
gardens and parks	0	0.0%		
near water in urban area	0	0.0%		
near roads and buildings in urban area	0	0.0%		
graveyard	0	0.0%		
forest			**4**	**80.0%**
coniferous forest	0	0.0%		
deciduous forest	3	75.0%		
near water in deciduous forest	1	25.0%		
near roads and buildings in forest	0	0.0%		
open landscape			**1**	**20.0%**
cropland and orchards	0	0.0%		
grassland	1	100.0%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	0	0.0%		
near water in open landscape	0	0.0%		
river or canal dykes	0	0.0%		
coast			**0**	**0.0%**
total			**5**	

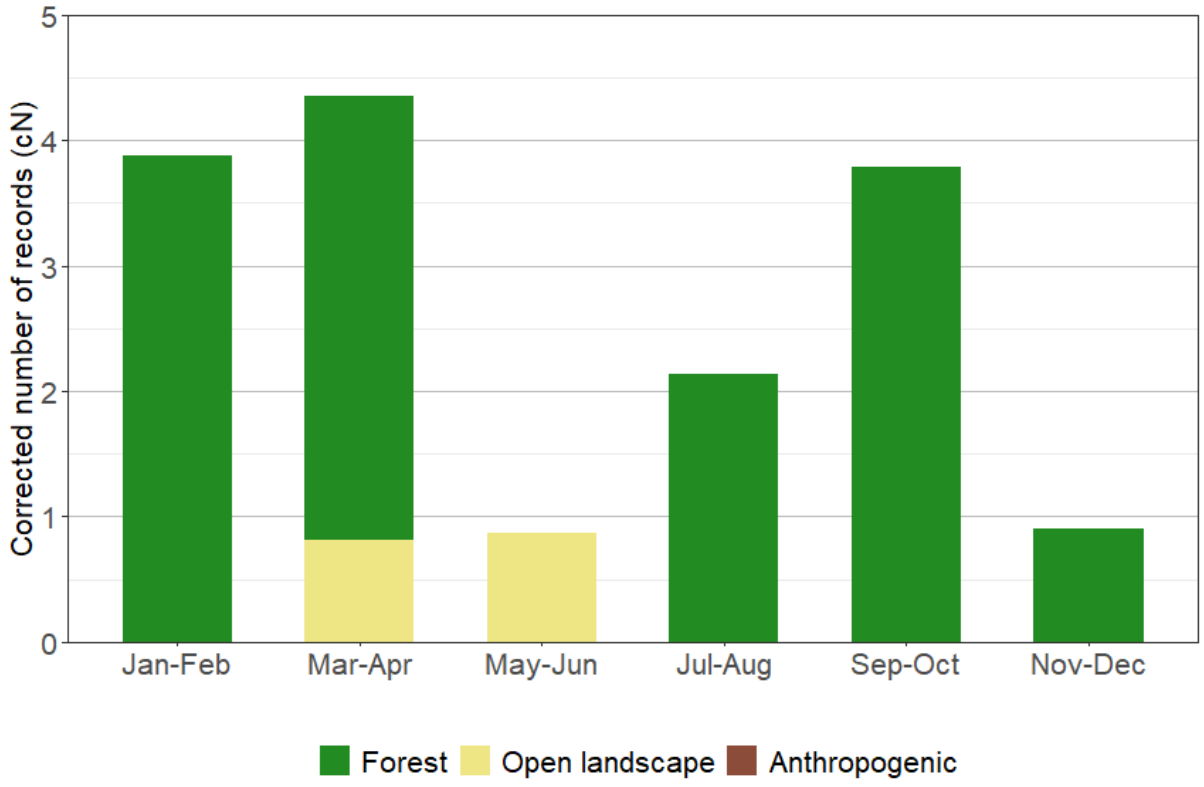
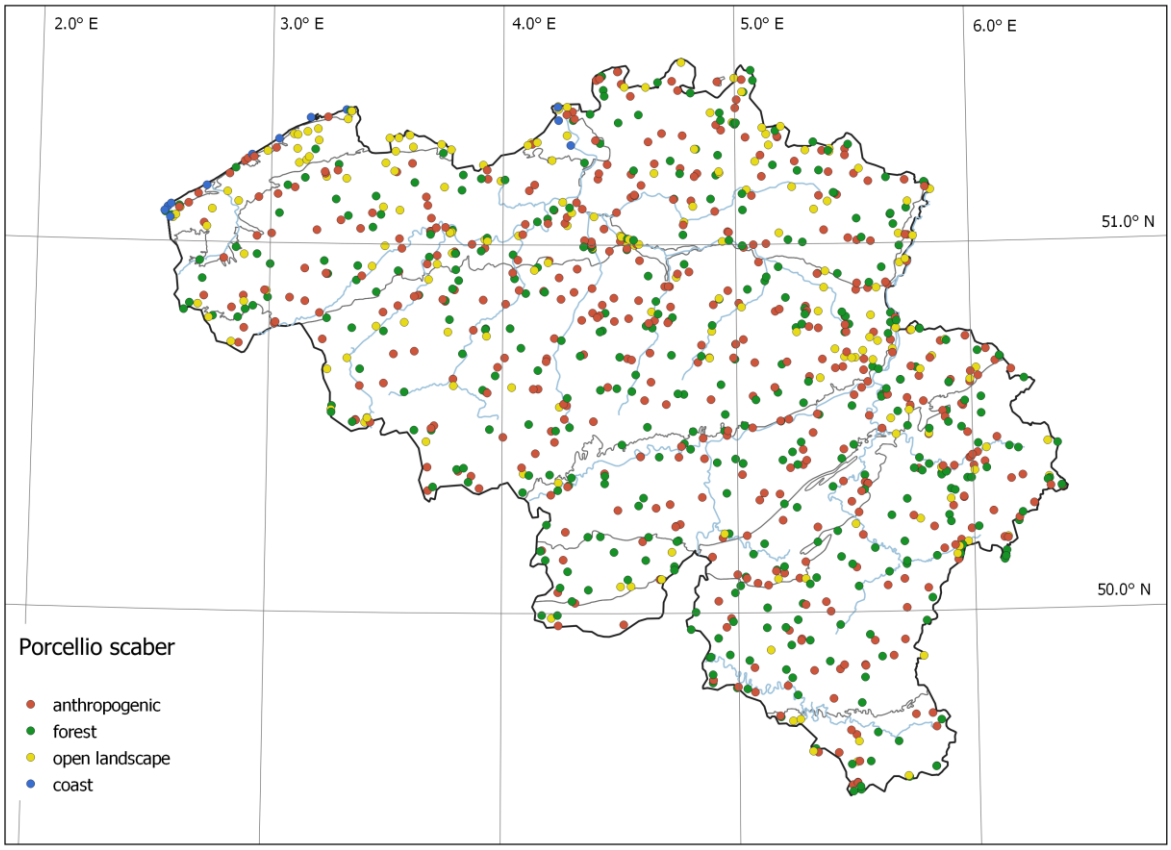


Fig. 35. Corrected number of observations per two-month period for *Porcellio monticola* (N = 16).

32. *Porcellio scaber* Latreille, 1804
(Fig. 20 d, Fig. 36, Map 32, Table 34)



Map 32. Distribution map for *Porcellio scaber*.

Porcellio scaber is probably the most abundant, widespread and most eurytopic species in Belgium. It can be found in a wide array of habitats across the whole country (Map 32). However, compared to other eurytopic species like *Oniscus asellus* and *Philoscia muscorum* it occurs less in forests and more in anthropogenic habitats. In forest habitat, the species can reach very high numbers in forest edges, but numbers are generally lower in closed interior forest habitat (DE SMEDT *et al.*, 2016b, 2018d). It is one of the few species that can also be abundant in coniferous forest in the Campine ecoregion. Due to its high drought resistance (DIAS *et al.*, 2013) it can also be found higher up in the vegetation or on the bark of living trees. In open landscapes, the species occurs in similar numbers as other eurytopic species. Together with *P. spinicornis*, *P. scaber* is one of the few species that is also regularly found inside buildings and houses.

The corrected number of records for *P. scaber* throughout the year is rather constant (Fig. 36). A slight drop appears in March–April in anthropogenic habitats and in September–October in forests. Generally speaking, *P. scaber* is observed at constant levels throughout the year whereas *Armadillidium vulgare* is found more during summer months and *O. asellus* less. This corresponds with the drought resistance for *P. scaber* lying in between the values for *A. vulgare* and *O. asellus* (DIAS *et al.*, 2013). DE SMEDT *et al.* (2021) however, found a peak during the summer months in different habitat types, but this peak was less pronounced compared to the more drought resistant *A. vulgare*.

Table 34. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Porcellio scaber*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**444**	**43.4%**
farm	14	3.2%		
gardens and parks	96	21.6%		
near water in urban area	25	5.6%		
near roads and buildings in urban area	90	20.3%		
graveyard	219	49.3%		
forest			**382**	**37.3%**
coniferous forest	10	2.6%		
deciduous forest	224	58.6%		
near water in deciduous forest	101	26.4%		
near roads and buildings in forest	47	12.3%		
open landscape			**185**	**18.1%**
cropland and orchards	0	0.0%		
grassland	45	24.3%		
disused quarry	13	7.0%		
near roads and buildings in open landscape	66	35.7%		
near water in open landscape	35	18.9%		
river or canal dykes	26	14.1%		
coast			**12**	**1.2%**
total			**1023**	

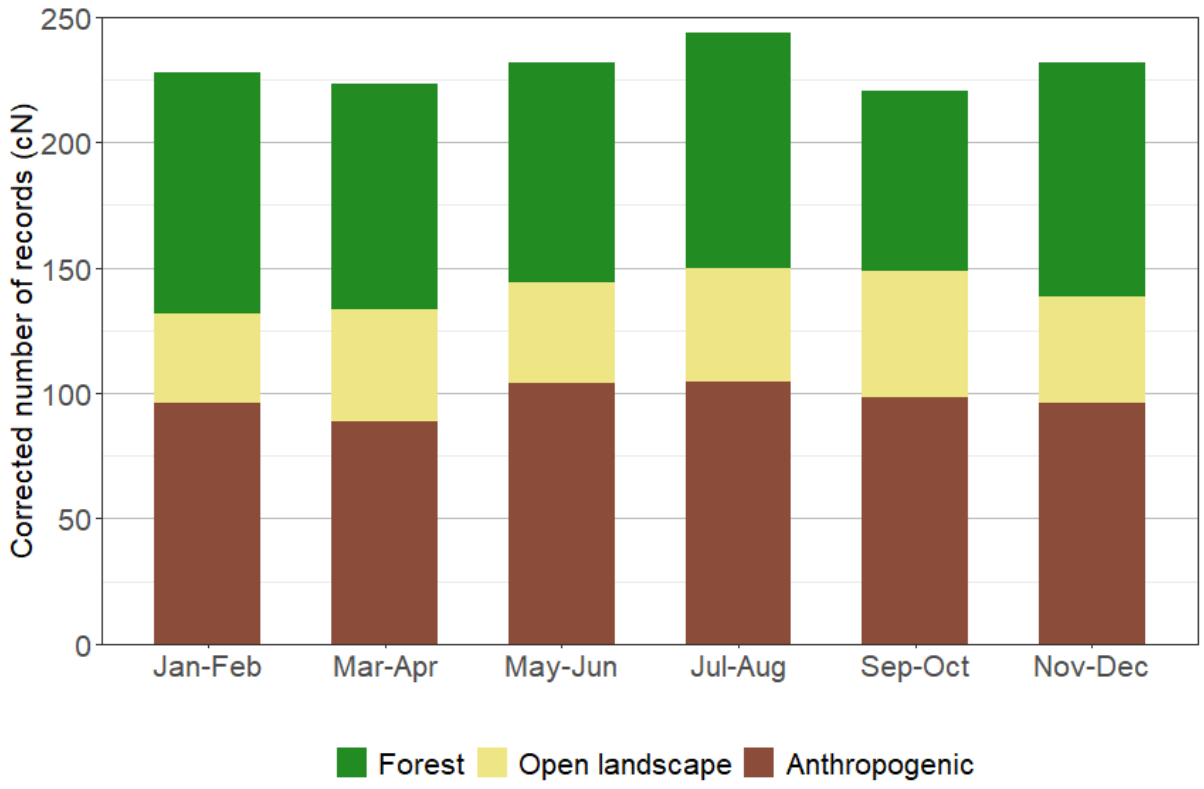
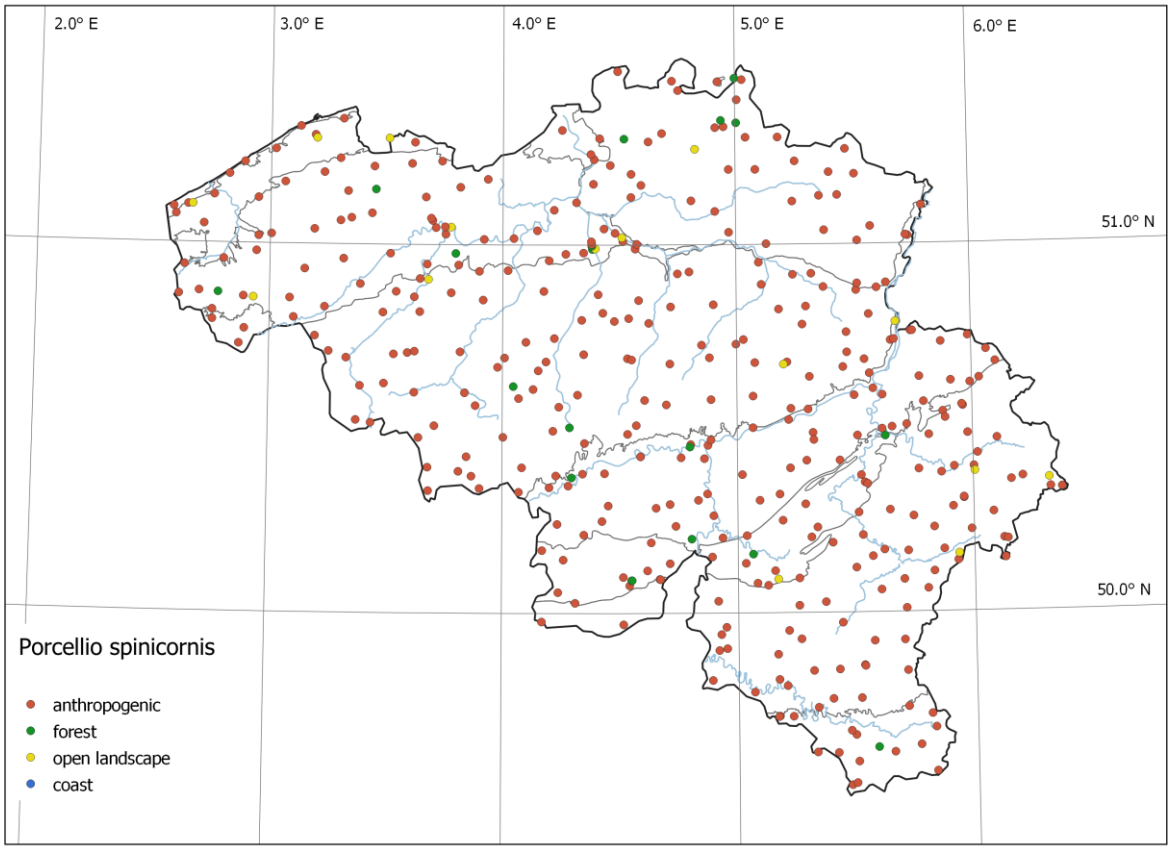


Fig. 36. Corrected number of observations per two-month period for *Porcellio scaber* (N = 1373).

33. ***Porcellio spinicornis*** Say, 1818
(Fig. 20 e, Fig. 37, Map 33, Table 35)



Map 33. Distribution map for *Porcellio spinicornis*.

Porcellio spinicornis is found in anthropogenic habitats all across the country (Map 33). It is a typical species from old walls, old buildings and graveyards. It is mostly found above ground level in crevices and under loose stones in walls. Together with *P. scaber*, it is one of the few species that can also be found inside buildings. The species is also rather common in old gardens, where it can be found between stacked stones and on old walls. The few observations in open landscape habitat or in forest are all near roads and buildings (Table 35). Like most species, *P. spinicornis* is nocturnal and can easily be found at night, foraging on old walls.

The corrected number of records are higher during the months May until August and November–December (Fig. 37). *P. spinicornis* has a very high desiccation resistance (DIAS *et al.*, 2013) and therefore we could assume that the species' activity peaks in summer. It is unclear why the species was recorded more during November–December than in other winter months.

Table 35. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Porcellio spinicornis*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**366**	**91.7%**
farm	9	2.5%		
gardens and parks	24	6.6%		
near water in urban area	3	0.8%		
near roads and buildings in urban area	62	16.9%		
graveyard	268	73.2%		
forest			**18**	**4.5%**
coniferous forest	0	0.0%		
deciduous forest	5	27.8%		
near water in deciduous forest	0	0.0%		
near roads and buildings in forest	13	72.2%		
open landscape			**15**	**3.8%**
cropland and orchards	0	0.0%		
grassland	1	6.7%		
disused quarry	2	13.3%		
near roads and buildings in open landscape	12	80.0%		
near water in open landscape	0	0.0%		
river or canal dykes	0	0.0%		
coast			**0**	**0.0%**
total			**399**	

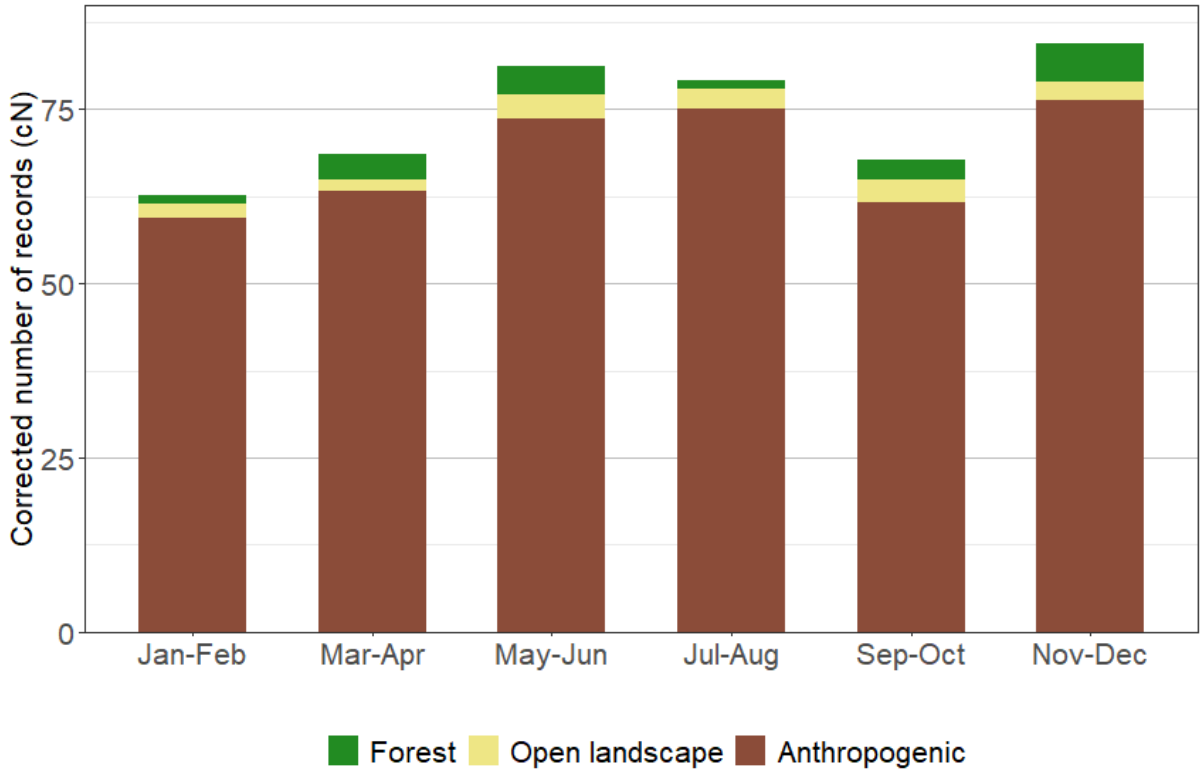
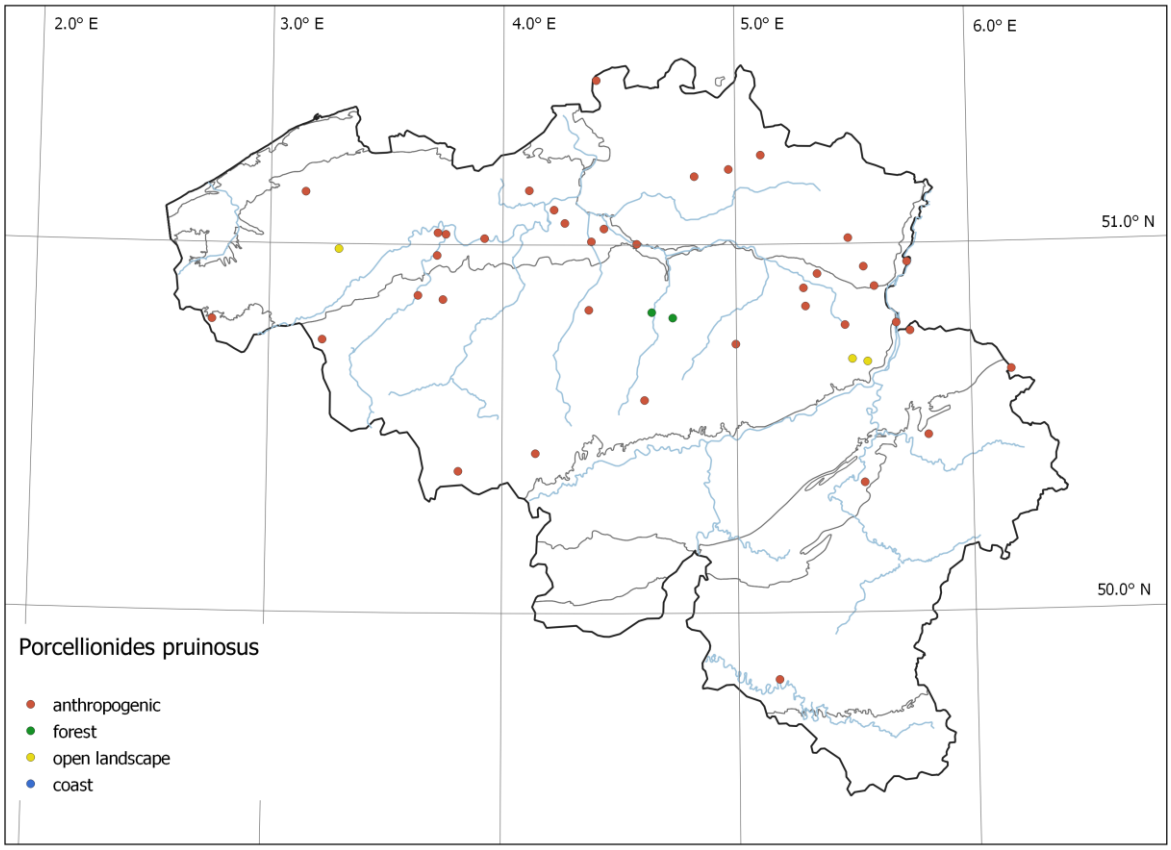


Fig. 37. Corrected number of observations per two-month period for *Porcellio spinicornis* (N = 448).

34. ***Porcellionides pruinosus*** (Brandt, 1833)
(Fig. 20 f, Fig. 38, Map 34, Table 36)



Map 34. Distribution map for *Porcellionides pruinosus*.

Porcellionides pruinosus is strongly bound to anthropogenic conditions in Belgium. It can most easily be found in compost heaps in gardens and allotments. The species prefers compost heaps composed of a good mix of kitchen waste (fruits and vegetable waste) and tree leaves, with the largest numbers found on the boundary between dry and wet material. It has also rather commonly been found on farms (often in dung of farm animals), on graveyards (often between waste of potted plants), but also sometimes a few tens of meters away from places with an accumulation of organic material. The locations in forest habitat are from warm forest edges where mown hay or other organic waste was dumped. However, since these forest edges are warmer compared to interior forest the species can probably persist here for several years. In open landscape habitat, the species has only been found next to manmade structures. *P. pruinosus* originates from the Mediterranean region (VANDEL, 1962), in Belgium it can possibly establish populations in (semi-) natural habitat if climate gets warmer. Dispersion via human transportation is presumably the most important way of dispersion for this species.

The number of records of *P. pruinosus* peaks during summer months (Fig. 38) as we can expect for a thermophilic species. However, the vast number of records in May–June is difficult to explain. Probably the species is active year-round in anthropogenic places with rather high temperatures across the year like for instance stables with livestock.

Table 36. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Porcellionides pruinosus*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**38**	**88.4%**
farm	8	21.1%		
gardens and parks	13	34.2%		
near water in urban area	2	5.3%		
near roads and buildings in urban area	6	15.8%		
graveyard	9	23.7%		
forest			**2**	**4.7%**
coniferous forest	0	0.0%		
deciduous forest	1	50.0%		
near water in deciduous forest	1	50.0%		
near roads and buildings in forest	0	0.0%		
open landscape			**3**	**7.0%**
cropland and orchards	0	0.0%		
grassland	0	0.0%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	3	100.0%		
near water in open landscape	0	0.0%		
river or canal dykes	0	0.0%		
coast			**0**	**0.0%**
total			**43**	

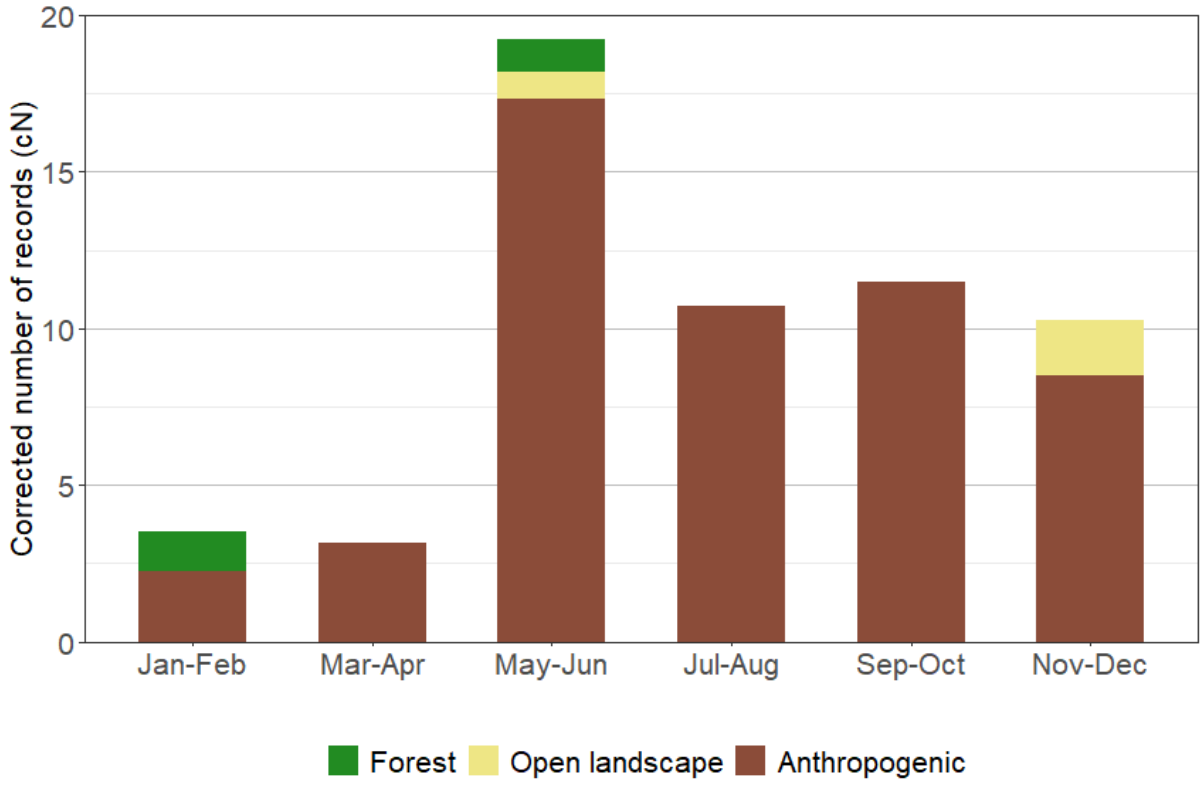
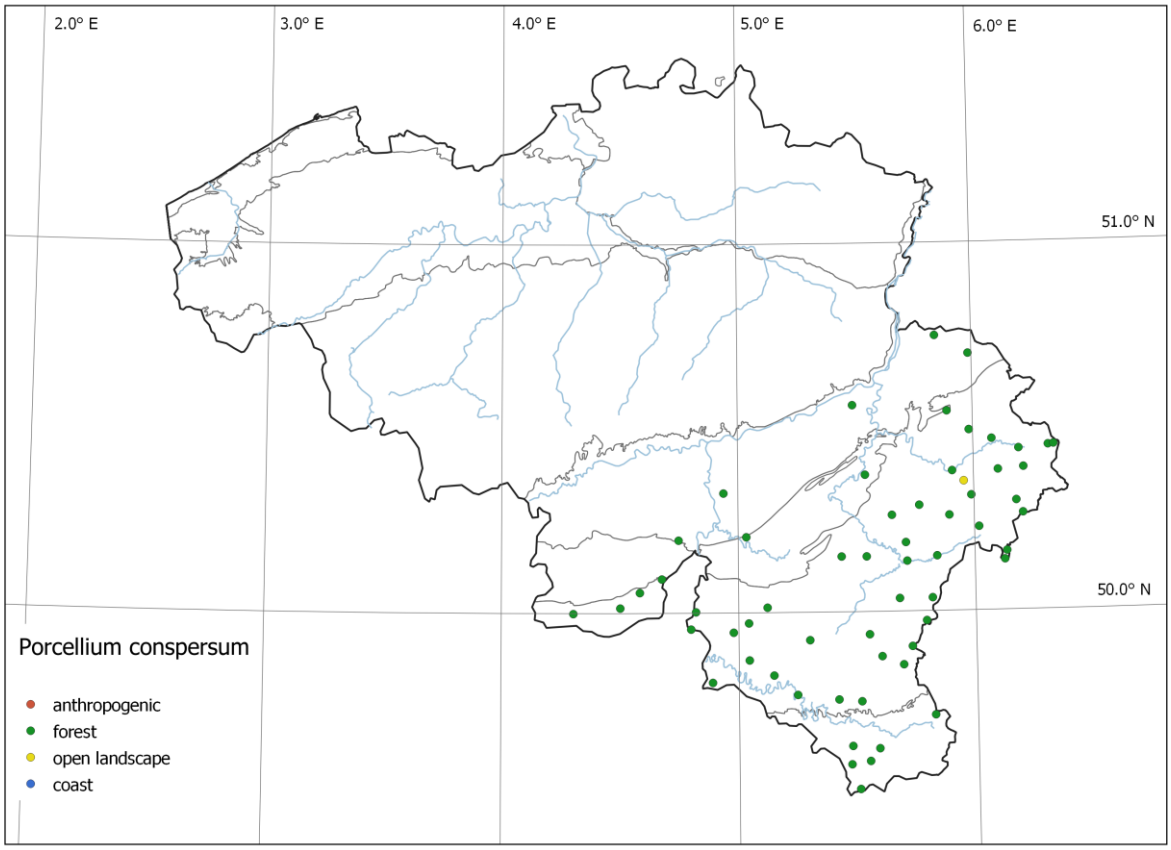


Fig. 38. Corrected number of observations per two-month period for *Porcellionides pruinosus* (N = 58).

35. ***Porcellium conspersum*** (C. Koch, 1841)
(Fig. 20 g, Fig. 39, Map 35, Table 37)



Map 35. Distribution map for *Porcellium conspersum*.

Porcellium conspersum occurs commonly in forests south of the rivers Sambre and Meuse (Map 35), with only one record (1.7%) registered in open landscape (Table 37). Most records in forests were near water (83.1%) with banks of small streams and rivers in deciduous forest as the main habitat for this species (Table 37). *P. conspersum* is together with *Ligidium hypnorum* and *Oniscus asellus* one of the few species in Belgium that can be found in locations with a high soil acidity.

The corrected number of records is highest from May until August and in November–December (Fig. 39). The species seems to be less commonly found at the beginning of the year (January–April). It is unclear if this is a real pattern or if this is due to random effects or the species' reproduction cycle.

Table 37. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Porcellium conspersum*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**0**	**0.0%**
farm	0	0.0%		
gardens and parks	0	0.0%		
near water in urban area	0	0.0%		
near roads and buildings in urban area	0	0.0%		
graveyard	0	0.0%		
forest			**59**	**98.3%**
coniferous forest	0	0.0%		
deciduous forest	8	13.6%		
near water in deciduous forest	49	83.1%		
near roads and buildings in forest	2	3.4%		
open landscape			**1**	**1.7%**
cropland and orchards	0	0.0%		
grassland	1	100.0%		
disused quarry	0	0.0%		
near roads and buildings in open landscape	0	0.0%		
near water in open landscape	0	0.0%		
river or canal dykes	0	0.0%		
coast			**0**	**0.0%**
total			**60**	

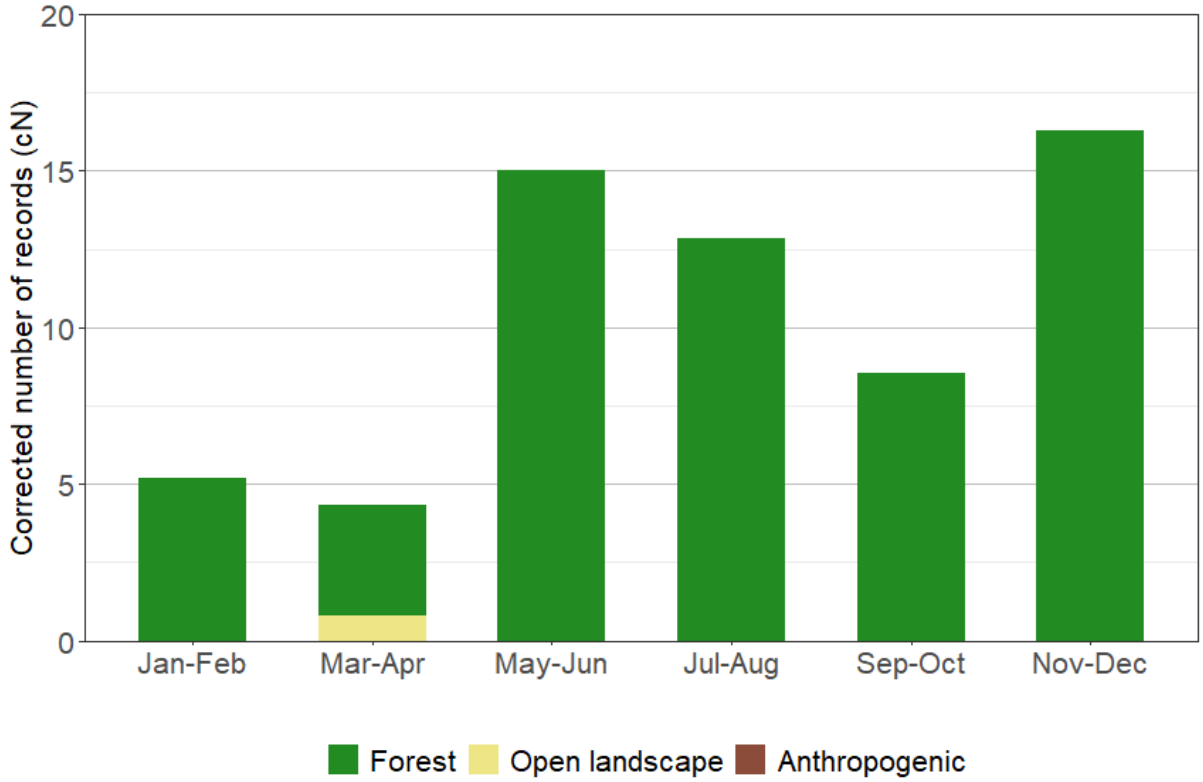
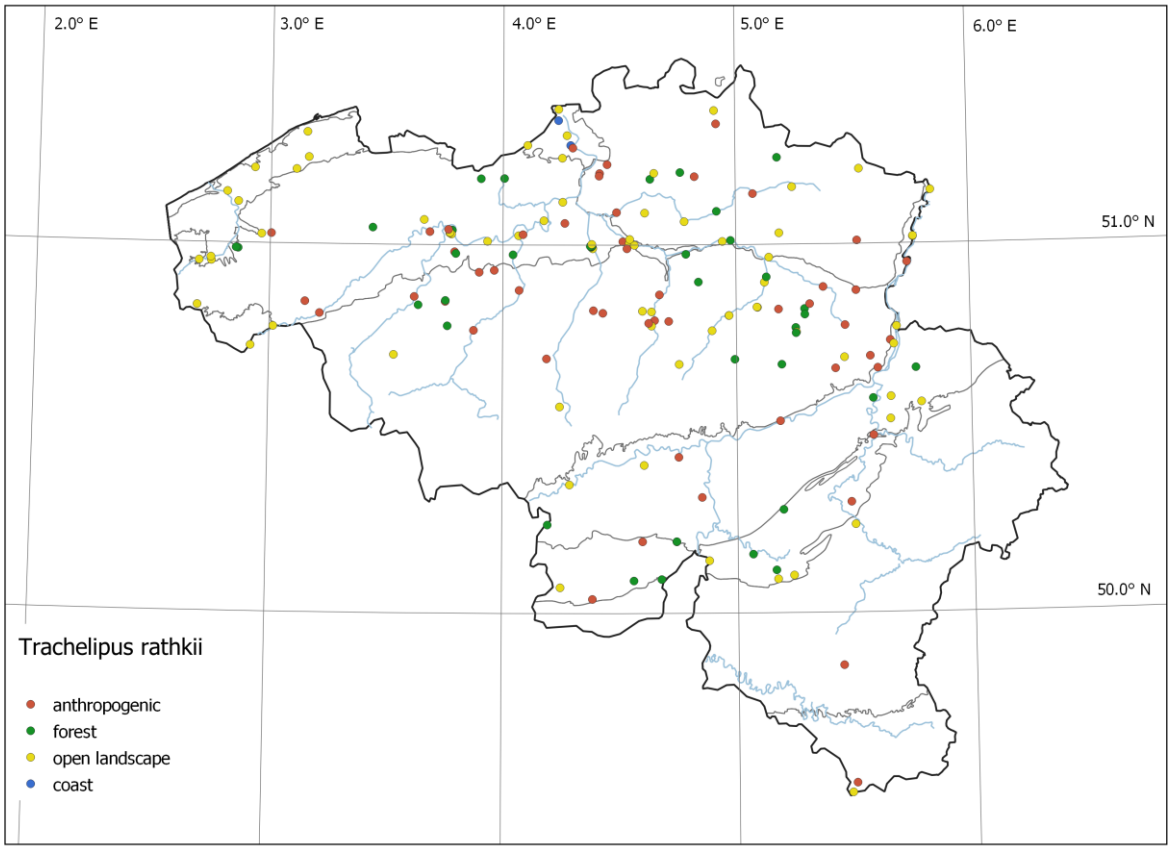


Fig. 39. Corrected number of observations per two-month period for *Porcellium conspersum* (N = 63).

36. *Trachelipus rathkii* (Brandt, 1833)
(Fig. 20 h, Fig. 40, Map 36, Table 38)



Map 36. Distribution map for *Trachelipus rathkii*.

Trachelipus rathkii occurs in a wide range of habitats and is common across the country except in the south, more specifically in the ecological regions of the Ardennes and the Lorraine (Map 36). *T. rathkii* withstands inundation very well (OOMS *et al.*, 2020) and appears frequently near streams and rivers in open landscapes, forests and anthropogenic habitats. A relatively high number of records (43.2%) are registered in open landscape habitats (Table 38). In particularly for grasslands, *T. rathkii* can be considered as a characteristic species, next to the very common species *Armadillidium vulgare* and *Philoscia muscorum. T. rathkii* occurs in forest, but is mostly confined to forest edges; however, this can be different in other regions in Europe (DE SMEDT *et al.*, 2018a).

T. rathkii is less commonly found in open landscape and anthropogenic habitat during summer months (Fig. 40). *T. rathkii* has a relatively low desiccation resistance (DIAS *et al.*, 2013) and this might explain the observed pattern. In forests is the corrected number of records remarkably higher in January–February, for which we do not have a clear explanation. Using pitfall traps, DE SMEDT *et al.* (2021) found however an activity peak in late summer compared to other seasons.

Table 38. Number of records and relative number of records per habitat type (N, rel. N) and per synthesis habitat (N_s, rel. N_s) for *Trachelipus rathkii*.

	N_s	Rel. N_s	N	Rel. N
anthropogenic			**51**	**31.5%**
farm	1	2.0%		
gardens and parks	23	45.1%		
near water in urban area	8	15.7%		
near roads and buildings in urban area	14	27.5%		
graveyard	5	9.8%		
forest			**39**	**24.1%**
coniferous forest	0	0.0%		
deciduous forest	16	41.0%		
near water in deciduous forest	18	46.2%		
near roads and buildings in forest	5	12.8%		
open landscape			**70**	**43.2%**
cropland and orchards	0	0.0%		
grassland	21	30.0%		
disused quarry	4	5.7%		
near roads and buildings in open landscape	12	17.1%		
near water in open landscape	20	28.6%		
river or canal dykes	13	18.6%		
coast			**2**	**1.2%**
total			**162**	

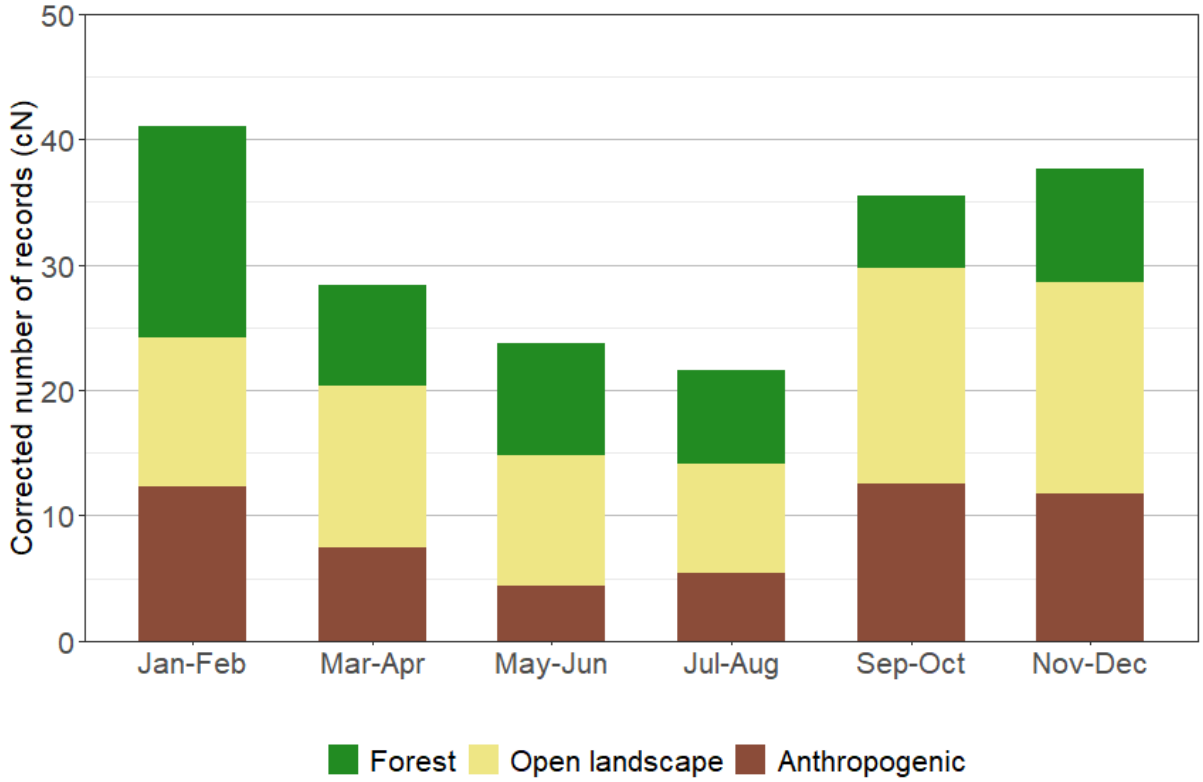


Fig. 40. Corrected number of observations per two-month period for *Trachelipus rathkii* (N = 189).

RESULTS OF ORDINATION ANALYSIS

The ordination of species according to the main habitat type (Fig. 41) shows characteristic species for all three main habitat types. The first axis is mainly a forest gradient with forest species to the left and non-forest species to the right and represents most of the variation (68%). The second axis separates species with a large proportion of records in open landscape from species most frequently recorded in anthropogenic habitat. Species like *A. pictum, P. affinis, A. pulchellum, P. conspersum, L. hypnorum* and *A. opacum* are mostly observed in forest habitat. These species have deciduous forest as their main habitat type and are rare or even absent outside forests. Species like *T. sarsi and T. rathkii* are, compared to other species, more frequently recorded in open landscapes. A large share of species is located near the open landscape "corner" but in between two habitat types i.e. *H. mengii, T. albidus* and *T. provisorius* between open landscape and forest and *P. hoffmannseggii, A. vulgare* and *M. leydigii* between open landscape and anthropogenic habitat. Although these species have an important share of their observations in open landscapes, open landscape records never exceed 50% of the corrected number records (Fig. 42). Anthropogenic habitat on the other hand has many characteristic species like *P. spinicornis, P. pruinosus, A. nasatum, P. dilatatus* and *A. dentiger*. In the middle of the ordination diagram we find a collection of species without a strong habitat preference. These are *P. scaber, O. asellus, P. muscorum, H. danicus* and *H. riparius*.

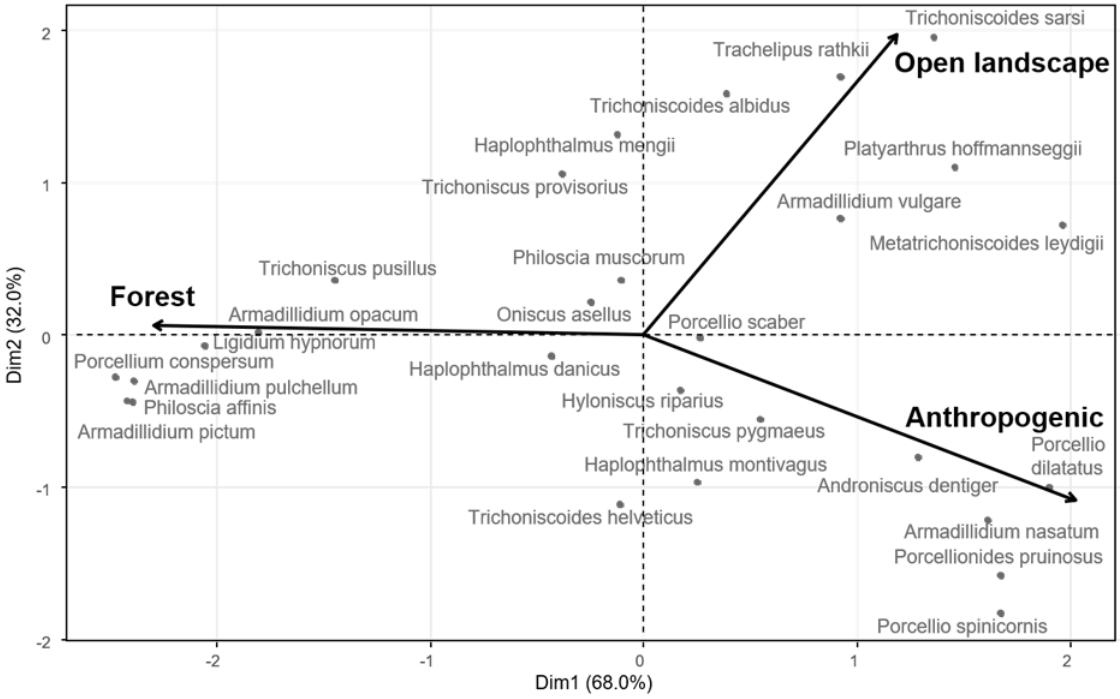


Fig. 41. Principal component analysis of species according to their relative abundance in the different main habitat types.

The ordination of species according to the two-month period of observation (Fig. 43) show some clear preferences of species for different seasons. The two-month periods are ordinated clockwise indicating an overall seasonal pattern. The first two axis represent 77.9% of the variation in the species data. The first axis (56%) represents mainly the differences between winter (to the left) and summer (to the right). The second axis (21.9%) represents the difference between spring (lower part) and autumn (higher part). Small and drought-sensitive species like *T. sarsi, T. albidus, H. danicus* and *T. pygmaeus* are more commonly found during winter

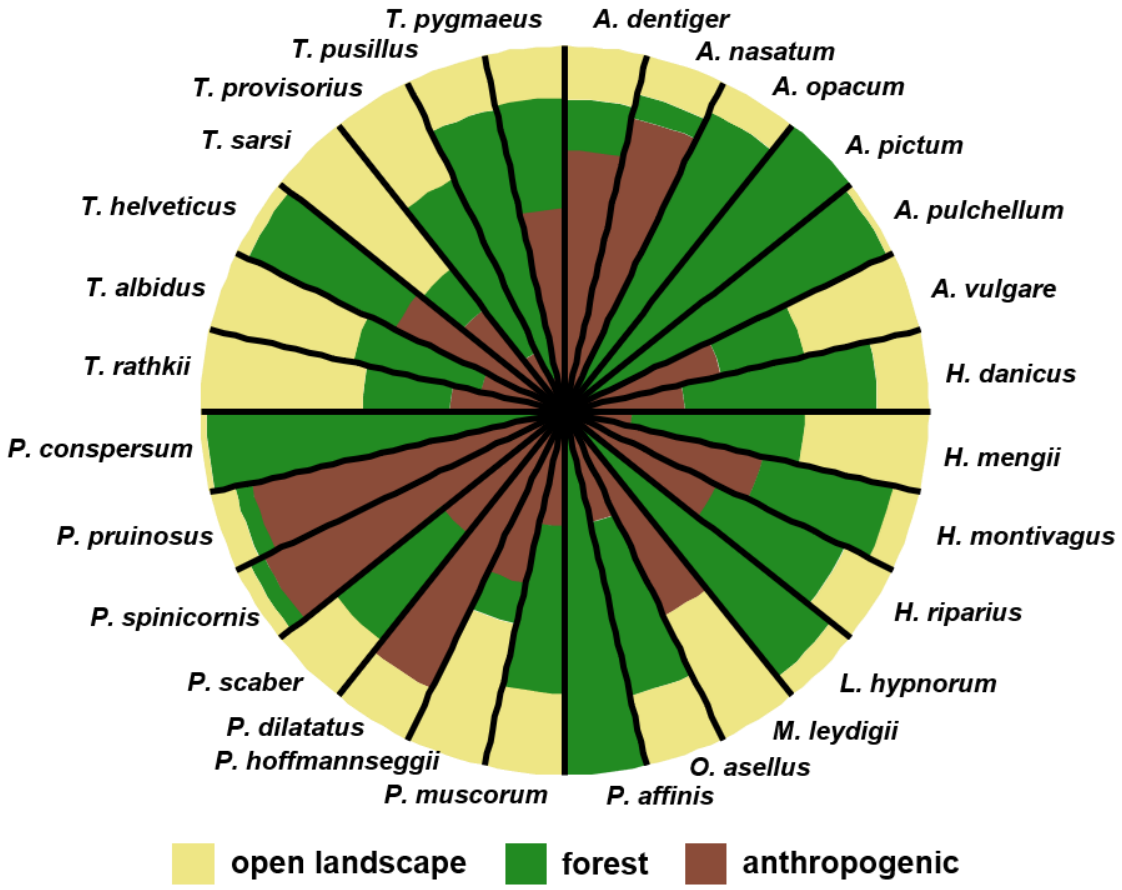


Fig. 42. Graphical representation of the species used in the PCA-ordination according to the species main habitat. Length of the coloured parts of the stacks represent the relative number of records for each species per habitat type.

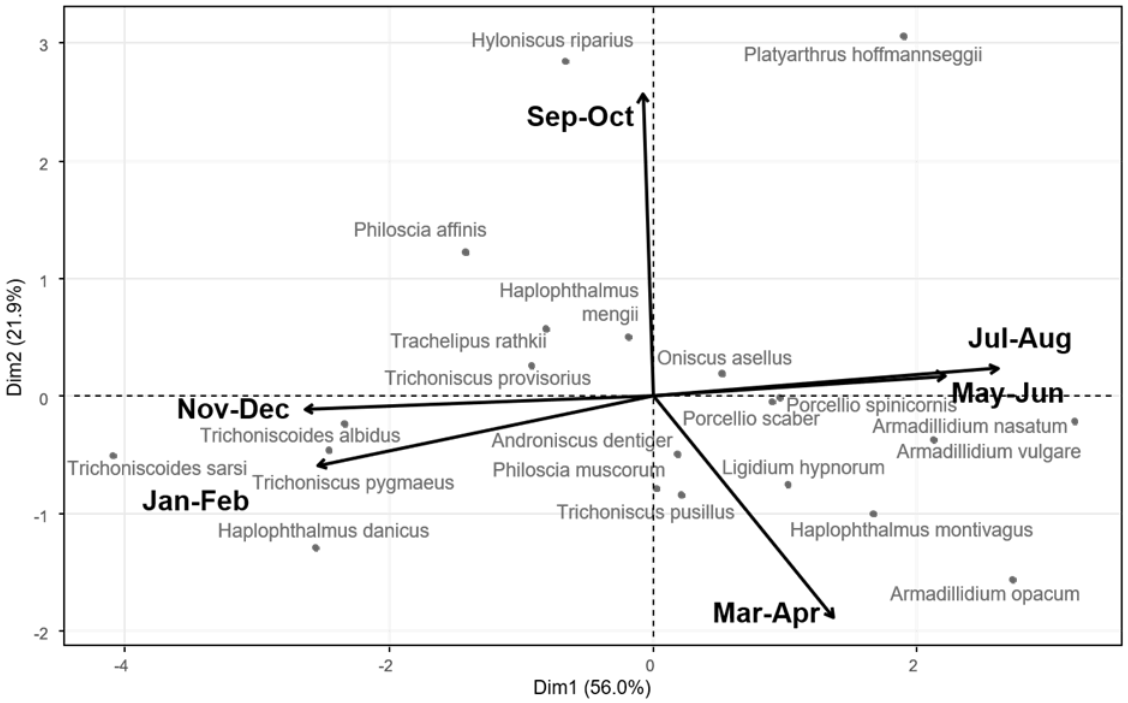


Fig. 43. Principal component analysis of species according to their relative abundance in the different two-month periods.

months while some large and drought-resistant species are more commonly found in summer such as *A. nasatum* and *A. vulgare*. Some species are most commonly found during spring and early summer like *A. opacum* and *H. montivagus*, while *H. riparius* is most commonly found in autumn. *P. hoffmanseggii* is most commonly found in summer and autumn and is the only species that prefers summer as well as autumn. Few species have no clear seasonal pattern.

Conclusion

The distribution and habitat are well known for most terrestrial isopod species in Belgium except for some enigmatic and very rare species like *M. leydigii, C. convexus, P. laevis, P. monticola* and *T. alemannicus.* The two very rare coastal species *A. album* and *M. patiencei* prove to be very difficult to observe in Belgium but their habitat is better known in neighboring countries (BERG *et al.*, 2008; GREGORY, 2009). For these seven species it is advised to thoroughly document all new observations in Belgium.

A number of species show a strong preference for forest or anthropogenic habitat but few species in Belgium show such preference for open landscape habitat. The high temporal fluctuations in temperature and moisture conditions in open landscapes are probably an important determinant for the lower numbers of records of terrestrial isopods in open landscapes. Multiple species are found in a variety of habitat types and a more detailed comparison of the species habitat preferences and distribution show remarkable differences in microhabitat use between the different general habitat types. We see for example that certain species, like *T. albidus* or *T. sarsi,* are more closely bound to water in open landscape compared to anthropogenic habitats, which gives interesting insights in the importance of small-scale habitat preferences between different habitat types. Geographical differences in habitat preference for a species are clearly seen in the distribution of *H. mengii*, which occurs in the northern part of the country mostly in open landscape habitats and in the southern part almost exclusively in forests. The mechanisms behind these observations are largely unknown and pose interesting future research questions. Presumably species traits like desiccation resistance and inundation resistance are key in answering these questions (see e.g. OOMS *et al.*, 2020). Additionally, the role of soil type, food quality and competition deserves extra attention in explaining distribution patterns of terrestrial isopods.

The data gathered with the purpose of creating distribution maps offers also opportunities to gain better insight in the seasonal activity patterns of terrestrial isopods. Drought-sensitive species of the Trichoniscidae family show a clear drop in number of records during the summer months. Very drought-resistant species or species from southern Europe origin show an opposite pattern with increased number of records during summer months, examples are *P. spinicornis, P. pruinosus, A. nasatum* and *A. vulgare*. Seasonal patterns can vary between different habitat types which can presumably be attributed to the microclimatic conditions. Activity patterns are e.g. less pronounced in forest habitat compared to open landscape habitat (e.g. for the species *A. vulgare, H. mengii, O. asellus, P. muscorum* and *T. albidus*). These patterns could be linked to the forest microclimate which is much more buffered throughout the year compared to open landscapes (DE FRENNE *et al.*, 2019). Species mainly living in forests have more irregular activity diagrams, further investigation is necessary to determine how reliable these patterns are. Examples are *P. affinis, A. opacum, A. pictum, A. pulchellum* and *P.conspersum*. Also, the effect of the urban heat island (PENG *et al.*, 2012) can be studied using terrestrial isopods as can be deducted from the seasonal activity of *P. hoffmannseggii*, for which the species' number of records peaks in different months in open landscape and in anthropogenic habitat. For species with a widespread distribution in anthropogenic habitats and increased activity during summer months, e.g. *A. nasatum, A. vulgare* and *P. spinicornis*, the

urban heat island effect may also be discernable when comparing the seasonal activity patterns from populations in urban centers to populations in small villages or hamlets in open landscape.

Lastly, we want to stress that the seasonal patterns are based on field observation by sieving and turning objects and whether the species was detected (presence) or not (absence). This dataset therefore reflects the species presence in the litter layer and mineral top soil. Presence of species can differ e.g. on tree trunks, old walls or deeper in the soil profile. Seasonal patterns on other substrates could therefore form an interesting topic for future investigation to understand species movement and ecology. Additionally, based on our seasonal data, few can be concluded about species abundances and reproductive cycles. These aspects of isopod phenology are crucial to truly understand species ecology and their functional role in different ecosystems. We therefore encourage research that assess abundance and reproductive status throughout the year using standardized methods, e.g. pitfall traps, bark traps, sieving and heat extraction via Tullgren-funnels.

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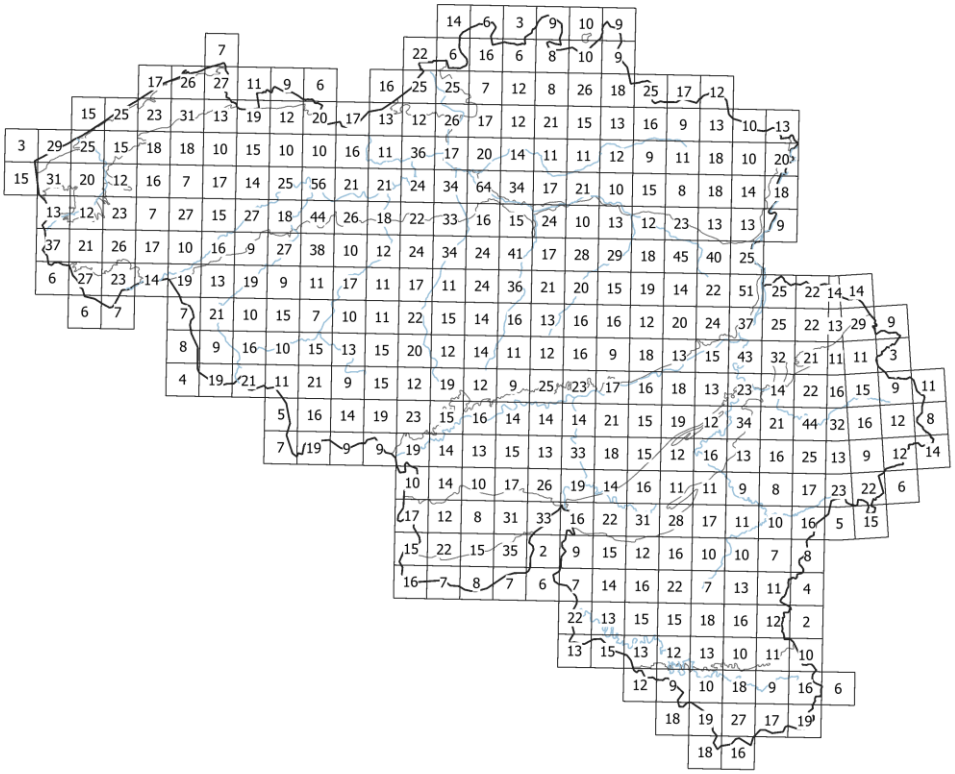
Appendices

APPENDIX A.

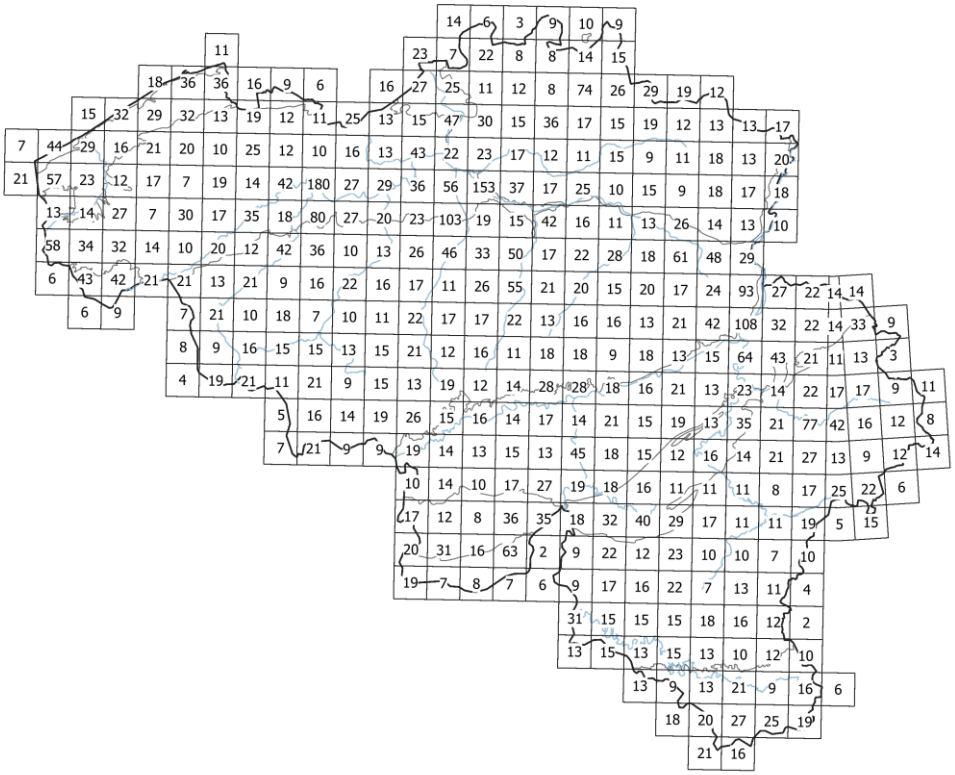
Table A. A detailed, general synthesis of habitats and landscapes linked to the records.

Detailed habitat	General habitat	Synthesis habitat	Landscape
orchard	open landscape	cropland and orchards	open landscape
constructions at the seaside	coast	coast	open landscape
fallow terrain - urban area	anthropogenic	near roads and buildings in urban area	anthropogenic
swampforest	forest	deciduous forest	forest
river or canal dykes - forest	open landscape	river or canal dykes	open landscape
river or canal dykes - open landscape	open landscape	river or canal dykes	open landscape
river or canal dykes - urban area	anthropogenic	near water in urban area	anthropogenic
dunes	coast	coast	open landscape
cropland - edges	open landscape	cropland and orchards	open landscape
grassland	open landscape	grassland	open landscape
glades	forest	deciduous forest	forest
farm	anthropogenic	farm	anthropogenic
hedgerows in grassland	open landscape	grassland	open landscape
graveyard	anthropogenic	graveyard	anthropogenic
deciduous forest	forest	deciduous forest	forest
coniferous forest	forest	coniferous forest	forest
near buildings - forest	forest	near roads and buildings in forest	forest
near buildings - open landscape	open landscape	near roads and buildings in open landscape	open landscape
near buildings - urban area	anthropogenic	near roads and buildings in urban area	anthropogenic
stream bank - forest	forest	near water in deciduous forest	forest
stream bank - open landscape	open landscape	near water in open landscape	open landscape
stream bank - urban area	anthropogenic	near water in urban area	anthropogenic
ditch - forest	forest	near water in deciduous forest	forest
ditch - open landscape	open landscape	near water in open landscape	open landscape
river bank - forest	forest	near water in deciduous forest	forest
river bank - open landscape	open landscape	near water in open landscape	open landscape
river bank - urban area	anthropogenic	near water in urban area	anthropogenic
shoreline pond or lake - forest	forest	near water in deciduous forest	forest
shoreline pond or lake - open landscape	open landscape	near water in open landscape	open landscape
disused quarry	disused quarry	disused quarry	open landscape
disused quarry - shoreline lake	disused quarry	disused quarry	open landscape
old farm	anthropogenic	farm	anthropogenic
park	anthropogenic	gardens and parks	anthropogenic
greenhouse	greenhouse	greenhouse	greenhouse
salt marsh	coast	coast	open landscape
garden	anthropogenic	gardens and parks	anthropogenic
roadside - forest	forest	near roads and buildings in forest	forest
roadside - forest - stream bank	forest	near roads and buildings in forest	forest
roadside - open landscape	open landscape	near roads and buildings in open landscape	open landscape
roadside - urban area	anthropogenic	near roads and buildings in urban area	anthropogenic

APPENDIX B.



Map B 1. Number of records per UTM 10 x 10 km square in the dataset for the analysis of the habitat preferences.



Map B 1. number of records per UTM 10 x 10 km square in the dataset for the analysis of the phenology.

APPENDIX C.

Table C. Species list with number of records per two-month period. The numbers of records are divided according to the three habitat types with records in anthropogenic habitats before the first slash, in forests between the two slashes and in open landscape after the second slash.

	Jan-Feb	**Mar-Apr**	**May-Jun**	**Jul-Aug**	**Sep-Oct**	**Nov-Dec**	**Total**
Androniscus dentiger	8 / 4 / 4	22 / 2 / 3	13 / 2 / 0	11 / 3 / 1	18 / 5 / 0	32 / 2 / 11	141
Armadillidium album	0 / 0 / 1	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	1
Armadillidium nasatum	15 / 0 / 3	43 / 2 / 7	49 / 5 / 10	38 / 4 / 11	35 / 5 / 2	52 / 1 / 5	287
Armadillidium opacum	1 / 4 / 0	0 / 14 / 3	2 / 26 / 4	1 / 10 / 0	1 / 6 / 1	1 / 14 / 1	89
Armadillidium pictum	1 / 9 / 0	0 / 11 / 0	0 / 2 / 0	0 / 9 / 0	0 / 15 / 0	1 / 14 / 0	62
Armadillidium pulchellum	0 / 2 / 0	0 / 8 / 0	1 / 15 / 0	0 / 6 / 0	0 / 7 / 0	0 / 14 / 1	54
Armadillidium vulgare	25 / 16 / 16	41 / 22 / 41	42 / 21 / 41	36 / 22 / 18	37 / 17 / 23	41 / 16 / 27	502
Cylisticus convexus	0 / 0 / 1	1 / 0 / 1	1 / 0 / 2	1 / 0 / 0	0 / 0 / 1	1 / 0 / 1	10
Eluma caelata	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 2	0 / 0 / 4	6
Haplophthalmus danicus	9 / 19 / 3	10 / 16 / 3	2 / 10 / 1	0 / 6 / 2	6 / 13 / 3	21 / 29 / 10	163
Haplophthalmus mengii	2 / 4 / 4	2 / 6 / 9	1 / 7 / 2	3 / 7 / 0	4 / 8 / 4	4 / 9 / 11	87
Haplophthalmus montivagus	8 / 3 / 0	16 / 15 / 4	10 / 8 / 2	13 / 11 / 1	17 / 5 / 1	26 / 14 / 3	157
Hyloniscus riparius	7 / 3 / 2	5 / 4 / 5	4 / 15 / 4	3 / 7 / 1	17 / 7 / 4	25 / 14 / 5	132
Ligia oceanica	0 / 0 / 2	0 / 0 / 2	0 / 0 / 1	0 / 0 / 0	2 / 0 / 3	0 / 0 / 3	13
Ligidium hypnorum	2 / 31 / 1	1 / 70 / 5	0 / 45 / 5	3 / 47 / 3	2 / 51 / 2	5 / 71 / 1	345
Metatrichoniscoides leydigii	0 / 0 / 1	0 / 0 / 1	0 / 0 / 1	0 / 0 / 0	3 / 0 / 2	7 / 0 / 1	16
Oniscus asellus	58 / 78 / 34	59 / 115 / 51	42 / 103 / 36	45 / 98 / 19	68 / 114 / 31	95 / 127 / 48	1221
Philoscia affinis	0 / 14 / 0	0 / 9 / 0	0 / 11 / 0	0 / 10 / 0	2 / 13 / 0	0 / 22 / 0	81
Philoscia muscorum	65 / 68 / 38	63 / 93 / 51	37 / 84 / 32	25 / 75 / 22	51 / 74 / 31	99 / 111 / 52	1071
Platyarthrus hoffmannseggii	3 / 0 / 6	8 / 4 / 9	22 / 5 / 10	10 / 4 / 10	21 / 1 / 14	17 / 4 / 15	163
Porcellio dilatatus	1 / 0 / 0	2 / 0 / 0	1 / 0 / 1	3 / 0 / 0	2 / 0 / 1	7 / 0 / 0	18
Porcellio laevis	0 / 0 / 0	0 / 0 / 0	1 / 0 / 0	0 / 0 / 0	0 / 0 / 0	1 / 0 / 0	2
Porcellio monticola	0 / 3 / 0	0 / 4 / 1	0 / 0 / 1	0 / 2 / 0	0 / 4 / 0	0 / 1 / 0	16
Porcellio scaber	86 / 74 / 33	84 / 102 / 55	96 / 88 / 46	78 / 88 / 31	94 / 76 / 44	147 / 103 / 48	1373
Porcellio spinicornis	53 / 1 / 2	60 / 4 / 2	68 / 4 / 4	56 / 1 / 2	59 / 3 / 3	117 / 6 / 3	448
Porcellionides pruinosus	2 / 1 / 0	3 / 0 / 0	16 / 1 / 1	8 / 0 / 0	11 / 0 / 0	13 / 0 / 2	58

Porcellium conspersum	0 / 4 / 0	0 / 4 / 1	0 / 15 / 0	0 / 12 / 0	0 / 9 / 0	0 / 18 / 0	63
Trachelipus rathkii	11 / 13 / 11	7 / 9 / 16	4 / 9 / 12	4 / 7 / 6	12 / 6 / 15	18 / 10 / 19	189
Trichoniscoides albidus	3 / 4 / 10	1 / 11 / 5	0 / 4 / 4	1 / 2 / 2	6 / 5 / 4	11 / 8 / 16	97
Trichoniscoides helveticus	3 / 2 / 0	1 / 4 / 0	1 / 2 / 0	1 / 1 / 0	4 / 0 / 0	6 / 6 / 1	32
Trichoniscoides sarsi	5 / 1 / 12	2 / 1 / 7	2 / 2 / 1	0 / 1 / 1	5 / 4 / 1	14 / 3 / 17	79
Trichoniscus alemannicus	1 / 0 / 0	0 / 1 / 0	0 / 1 / 0	0 / 1 / 0	0 / 0 / 0	1 / 2 / 0	7
Trichoniscus provisorius	7 / 9 / 11	4 / 15 / 7	1 / 10 / 8	2 / 10 / 4	7 / 17 / 3	8 / 20 / 14	157
Trichoniscus pusillus	9 / 29 / 9	5 / 45 / 11	0 / 47 / 5	2 / 36 / 6	6 / 35 / 4	6 / 59 / 12	326
Trichoniscus pygmaeus	20 / 10 / 3	8 / 9 / 3	8 / 5 / 5	5 / 3 / 2	13 / 4 / 3	38 / 17 / 6	162
Total	**405 / 406 / 207**	**448 / 600 / 303**	**424 / 547 / 239**	**349 / 483 / 142**	**503 / 504 / 202**	**814 / 715 / 337**	**7628**