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INFLUENCE OF SMALL- AND LARGE-SCALE ECOLOGICAL FACTORS ON THE CENTIPEDE (CHILOPODA) ASSEMBLAGES OF ARMORICAN FORESTS (NW FRANCE)

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MYRIAPODA
LITTER
SOIL
QUADRAT SAMPLING
COMPETITION

ABSTRACT. – Despite their high functional role as abundant predators, the drivers of centipede assemblages remain poorly known in forests, especially in France. Using replicated depletion quadrats, we sampled five forests distributed over the Armorican Massif. A total of 5209 individuals belonging to 20 species was collected between 2015 and 2017. Assemblage composition was surprisingly constant across parcels, with only different dominant species in the oldest parcel (Bercé, Pays-de-Loire) and in the forest of Cerisy (Normandy). The latter hosted two exclusive species, likely because of both biogeographic and abiotic conditions, *Geophilus truncorum* and *Lithobius aeruginosus*. Species richness was overall close among sites and parcels, and therefore little influenced by tree age or dominant species. Individual densities varied between site pair-matched parcels, probably because of differences in temporal forest continuity rather than differences in tree ages. In quadrats, the presence of numerous ants strongly affected the number of centipedes, with global densities divided by an average factor of 7. Also at small spatial scale, we did not find a strong vertical stratification of centipede species in terms of presence-absence, with only 2 species exclusive of soil and none for litter, but with important differences in the relative abundance of dominant species. This study suggests that centipedes are important components of the forest soil and litter fauna, should be more frequently studied in French forests and have a potential of bio-indicators of local conditions in these habitats, as well as of temporal forest continuity.

INTRODUCTION

Centipedes are predators, mainly feeding upon other invertebrates living in or on the soil, or under above-ground shelters (Demange 1981, Iorio 2014). There are more than 550 centipede species known from Europe (Zapparoli 2003, Bonato & Minelli 2014, Simaiakis & Strona 2015), including 149 currently reported from metropolitan France (Iorio 2014, Iorio & Geoffroy 2019). Behind Italy, France is the second country with the highest species diversity in Europe (Zapparoli & Minelli 2006, Simaiakis & Strona 2015). Since twenty years, and even more during the last 10 years, basic knowledge on centipedes is highly increasing in France because of numerous qualitative inventories in various regions and ecosystems (Iorio 2019). But on the other hand, these arthropods remain highly neglected in broad ecological studies in France, especially in forests. Some forest studies have sometimes taken considered centipedes together with various other invertebrate groups (*e.g.* Geoffroy *et al.* 1981, Blandin *et al.* 1985, Auclerc *et al.* 2012, De Smedt *et al.* 2019), but fully dedicated studies to forest centipedes or myriapods are very rare (Geoffroy 1979).

The ecological importance of centipedes in forest ecosystems is yet widely recognized elsewhere in Europe. They represent indeed one of the most abundant groups of soil predators in terms of density of individuals in temperate forests (Albert 1979, Poser 1988, Scheu *et al.* 2003), with many species restricted to forest habitats (Voigtländer 2009, 2011). In several countries, authors have investigated variation in centipede assemblage and diversity in forests (*e.g.* Leśniewska 2000, Wytwer 2000, Lock *et al.* 2001, Kula & Lazorík 2015, Peretti & Bonato 2018). More precisely, the effects of reforestation (Baini & Zapparoli 2015), fragmentation (Fründ *et al.* 1997, Grinvald 2011, Distribution of Myriapods in Forest Mosaic. Master Sci Nature Protection, Dept Ecol Environ Sci Fac Sci Palacky), succession (Grgič & Kos 2003, 2005, Leśniewska *et al.* 2005, Lock *et al.* 2005) and the influence of various environmental factors (*e.g.* moisture, temperature, exposition, litter mass, openings caused by a windstorm) on the distribution of centipedes were studied over the last decades, showing the potential importance of this group in French forests (Poser 1990, Tuf 2002, Jabin 2008, Leśniewska & Skwierczyński 2018). Finally, some studies focused on the efficiency of sampling methods, showing that the pitfall trapping is not the most reliable for assessing centipede diversity and number of individuals (Gerlach *et al.* 2009, Tuf 2015). Despite this recent literature, centipedes are still considered less known than other groups of predators (*e.g.* spiders and carabid beetles: Bonato *et al.* 2018).

To increase our knowledge of forest centipedes in France, we characterized both litter and soil assemblages of Chilopoda over five forests of the Armorican Massif, a wide homogenous geologic area in North-Western France. More precisely, we aimed at assessing how assemblages (in terms of numbers of species and individuals, species composition) changed at different spatial scales, *i.e.* between sites, habitats and micro-habitats. Thanks to our sampling design, we especially could test for the effects of (i) biogeographic conditions (forest scale), (ii) dominant tree species and age (parcel scale, although they were sometimes confounded) and (iii) the vertical distribution and the presence of ants (quadrat scale).

MATERIAL AND METHODS

Sampling sites and their characteristics: Five forests were selected in the Armorican Massif area or its margins in western France: four in the Pays de la Loire region and one in the west of the Normandy region (Fig. 1). In each forest, two distinct and geographically close parcels, from 300 m to 5 km between almost all paired parcels (only those of Bercé are more distant: 16 km), were chosen (Table I). The following environmental variables were taken:

– The dominant tree species and the age of forest stands (data from "Office National des Forêts" and private owners, or from our personal observations: Table I). The forest of Cerisy was the only forest mainly dominated by beech (*Fagus sylvatica*). Dominant tree species and climatic factors such as annual temperature were closely linked (Table I).

– The temporal forest continuity (data from the French National Geographic Institute: https://www.geoportail.gouv.fr; https://remonterletemps.ign.fr), which shows that one of the parcels (BE2) was clear-cut in 1972, when all the others were ancient.

– The mean annual rainfall (mm) and mean annual temperature (°C), with quotation of the mean summer temperature (*i.e.* the season with the highest differences between the forests), data from Météo-France (2012), Artélia (2013) and Cantat *et al.* (2015) (Table I).

Field sampling: In each parcel, we collected ten leaf-litter and soil samplings in a 0.25 m² metallic square from 10 cm of depth; each sampling being spaced with a minimum of three metres to the other, but without criterion of choice. Leaf-litter and soil were systematically separated on the field in each 0.25 m² square: collection of the leaf-litter horizons L and F in one bag; collection of below horizons (H and A) in a second bag; both being numbered with indelible felt. The specimens trying to escape were immediately captured and placed in the corresponding bag. All the contents of the bags were placed in Berlèse apparatus to extract centipedes. The litter and soil sampling has been used with success by various authors to study this group (*e.g.* Geoffroy 1979, Leśniewska *et al.* 2005, Auclerc 2012). Because quadrats with many (> 50) ants had few centipedes (1 in BE1, BE2 and VI1, and 2 in VI2), five quadrats were excluded from analyses, except when testing the effects of ants.

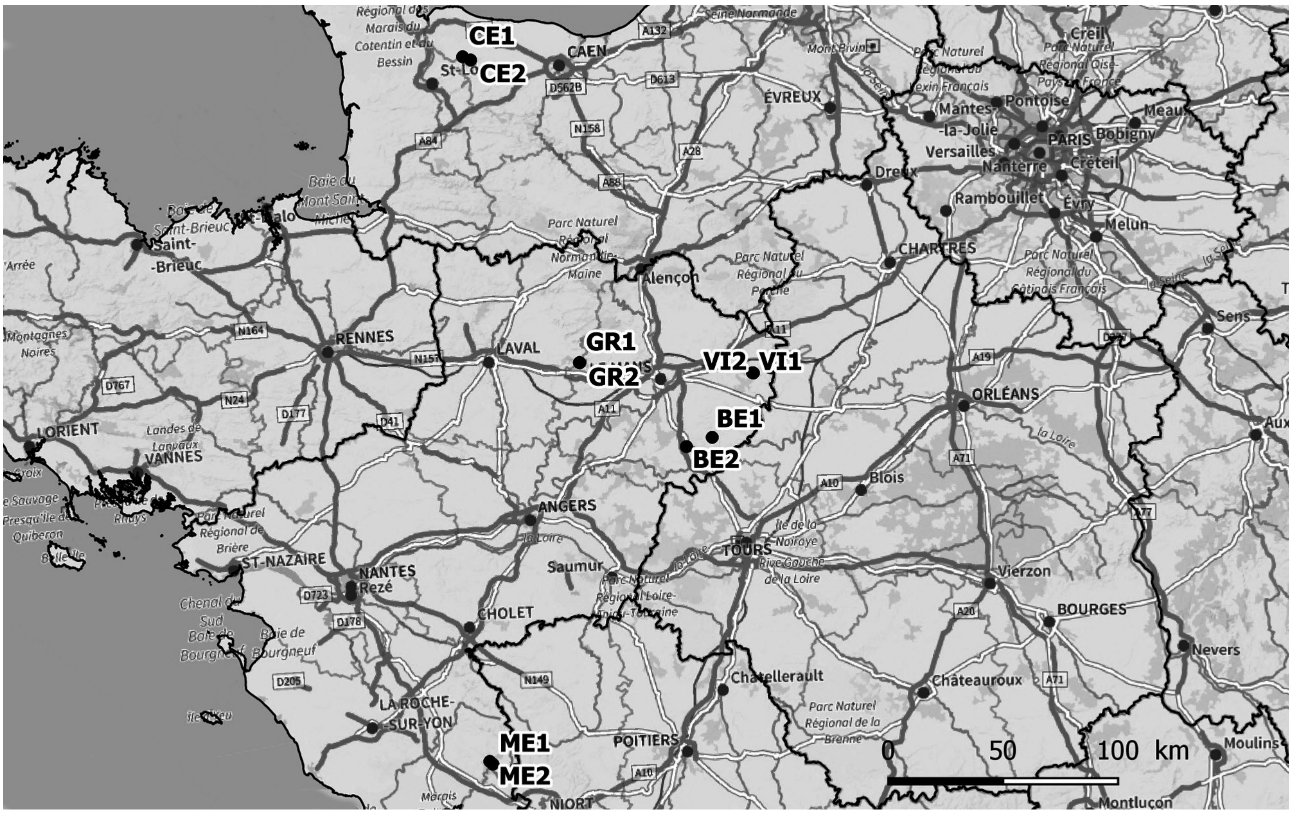

Fig. 1. – Map showing the studied forest parcels in western France (base: IGN FranceRaster).

Table I. – Main characteristics of the five studied forests. * Oak = *Quercus* sp. (both *Q. petraea* and *Q. robur* are present; almost only *Q. petraea* in Grande Charnie and BE1).

Name of the forest	Bercé		Grande Charnie		Mervent		Vibraye		Cerisy	
Parcel	BE1	BE2	GR1	GR2	ME1	ME2	VI1	VI2	CE1	CE2
Altitude	143	150	212	197	90	78	179	169	97	119
Dominant tree species*	Oak	Oak	Oak	Oak	Oak	Oak	Oak	Oak	Alder	Beech
Age of the forest stand	> 300 years	> 100 years	> 120 years	> 120 years	> 180 years	40 years	> 120 years	> 120 years	> 80 years	> 140 years
Mean annual rainfall	700-800	700-800	800-900	800-900	900-1000	900-1000	700-800	700-800	800-900	800-900
Mean annual temperature (mean summer temperature)	11-12 (18-19)	11-12 (18-19)	11-12 (18-19)	11-12 (18-19)	12-13 (19-20)	12-13 (19-20)	11-12 (18-19)	11-12 (18-19)	10-11 (15-17)	10-11 (15-17)

Most forests were sampled in spring (Mervent: 05/05/2015; Grande Charnie: 05/04/2016; Vibraye: 01/06/2016; Bercé: 06/04/2017), except for Cerisy that sampled in autumn (03/11/2017). Because of time and logistic constraints, sampling was carried over different years, but assemblages of forest centipedes have few inter-annual variations (Albert 1979, Geoffroy 1979). In temperate forests, centipedes have their highest activity in spring, but also are very active in autumn (Geoffroy 1979, Voigtländer 2009, 2011). In North-Western France and adjacent regions, all species included in the present paper are much found in both seasons (*e.g.* Iorio 2005a, b, 2007, 2014, Racine & Iorio 2017, Iorio & Racine 2018, Tillier 2018) as well as in United Kingdom for those which are also present in this country (Barber & Keay 1988). Dominant species are consequently similar between spring and autumn (Geoffroy 1979). We consequently argue that assemblages of Cerisy can still be compared with the others despite a difference in sampling periods.

Data analysis: Compositions were compared between parcels and forests using an analysis of similarity based on Pearson correlations and average links on the occurrence matrix.

To test whether numbers of individuals and species differed among spatially pair-matched parcels (for testing the effects of dominant tree species and parcel age) Wilcoxon tests were used.

Results were analyzed with PAST and Mintab softwares. We have taken into account the data of the centipede atlas of the Pays de la Loire region in progress (6707 data and 20976 centipedes identified in this region at the end of May 2018) (Iorio & Racine, 2018), in addition of other references, to support some parts of our discussion.

RESULTS

A total of 5209 specimens belonging to 20 species was collected (Table SI), including 166 immature individuals of the genus *Lithobius*.

Forest-scale analysis

Species richness ranged between 13 to 16 species between forests (Table SI). Assemblages were constant

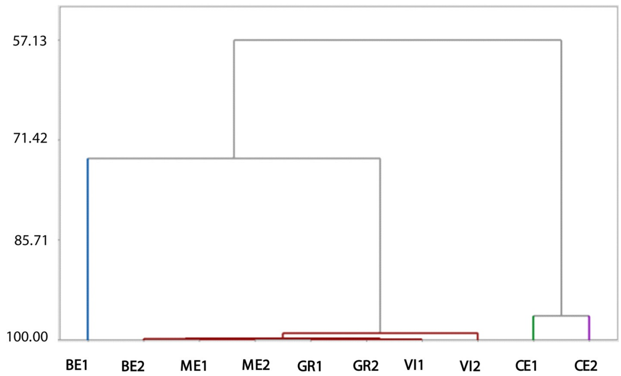

Fig. 2. – Dendrogram based on correlation coefficients of centipede assemblages (complete link).

between sites with high degrees of similarity in species composition, but also between parcels of a given forest (Fig. 2). Only the forest of Cerisy strongly differed from the other sites, and that was mostly explained by the high abundance of *Geophilus truncorum* and the low abundance of *Schendyla nemorensis*, while the oldest parcel (Bercé) was quite different from the other parcels and sites due to the high abundance of *Cryptops hortensis* (Fig. 3). *Geophilus truncorum* was an exclusive species from Cerisy, with a relative abundance of 48.8 % in this forest. On the other way, the density of *Schendyla nemorensis* was lowest in Cerisy (28 % of total numbers) when in all the other forests it dominated assemblages (from 56.5 % until 86.7 % in Bercé and Grande Charnie, respectively).

Because of this high similarity, we did not check for differences in species composition between pair-matched parcels, but only in numbers of species and individuals (both total and for dominant species).

Parcel-scale analysis

The mean densities of centipedes ranged from 118.4 specimens/m² to 350.4 specimens/m² per parcel, with extreme densities from the same forest (forest of Mervent, parcels ME2 and ME1, respectively) (Fig. 4). The species richness was rather constant between parcels,

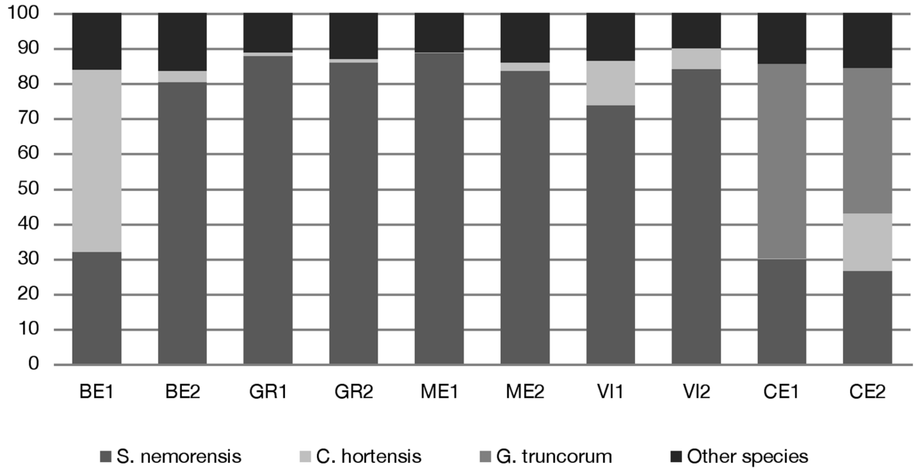

Fig. 3. – Relative abundance (%) of dominant species in at least one forest parcel.

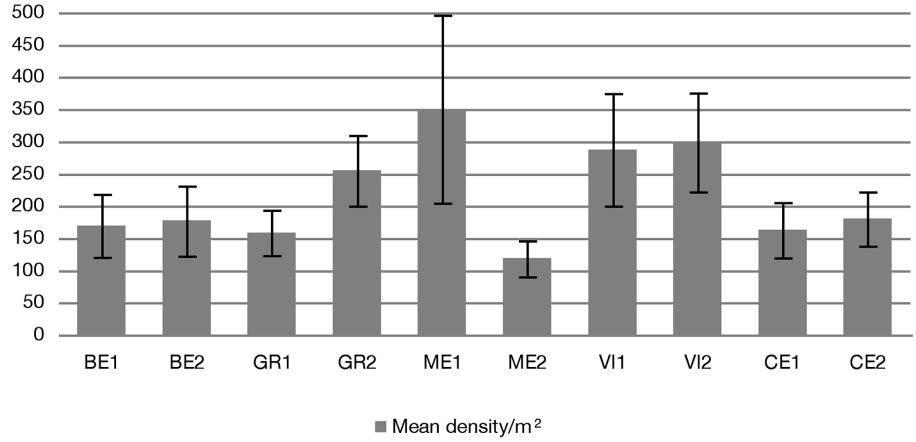

Fig. 4. – Mean density (± standard deviation) of centipedes (all species confounded) per forest parcel.

between 6 and 14 species, with some important variations (*e.g.* Bercé).

In Cerisy, between CE1 and CE2 parcels having different age and dominant tree species, the difference in centipede densities was not significant (Wilcoxon & Mann-Whitney test, Qobs = 35, P = 0.272), and the same goes for the densities of dominant species *Geophilus truncorum* (Qobs = 58, P = 0.570). *Lithobius aeruginosus* was an exclusive species to CE1, the younger parcel dominated by the alder (*Alnus glutinosa*). On the other way around, *Strigamia acuminata* was more abundant in CE2, the older parcel dominated by the beech (56.5 % of its total numbers).

Comparisons of pair-matched oak parcels with different ages (ME1 *vs* ME2; BE1 *vs* BE2) show a significant difference in centipede densities in one case (ME1 *vs* ME2) with more individuals in the older parcel, but not in the other (BE1 and BE2) (Wilcoxon & Mann-Whitney tests, Qobs = 100, P < 0.001 and Qobs = 40.5, P = 1, respectively).

Quadrat-scale analysis

1915 specimens were collected in the litter *vs* 3294 individuals in the upper soil samples. Two species were exclusive from the soil samples: *Geophilus electricus* and *Stigmatogaster subterraneus*, while all litter species were found in the soil samples. However, *G. electricus* and *S. subterraneus* were present by few specimens (n = 11 and 8 respectively). Most of other species were better represented in the upper soil than in the litter, but for some species the opposite pattern was found, like *e.g. Strigamia acuminata* (80.4% of relative abundance in the litter), *Geophilus easoni* (71.4 %) or *Lithobius piceus* (64.1 %) (Fig. 5).

Centipede were on an average 7 times less abundant when ants are numerous (> 50 individuals per quadrat) compared to quadrats where they are not, or few, present (Table II).

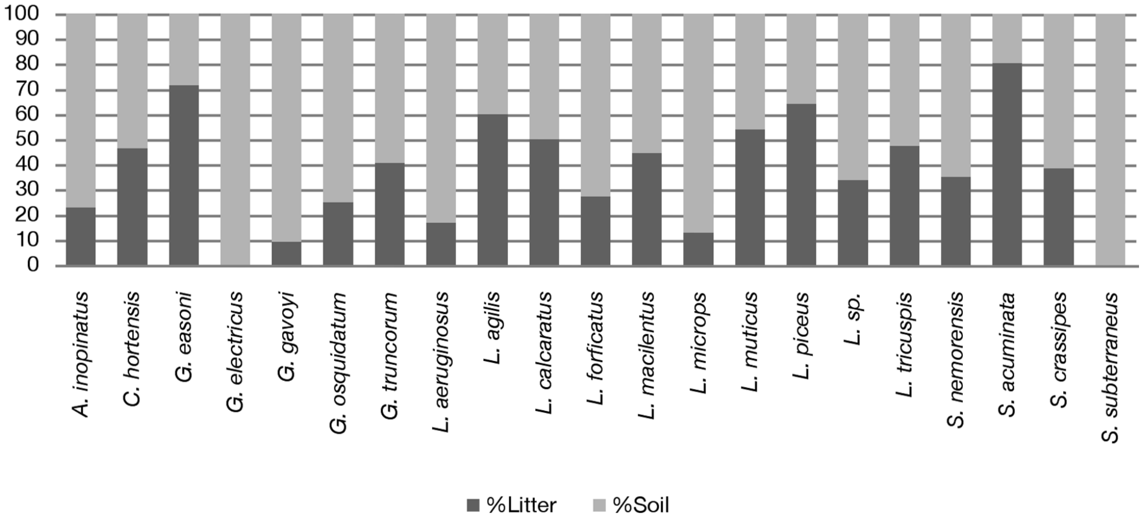

Fig. 5. – Relative abundance (%) of centipede species in litter *vs* soil samples.

Table II. – Proportion of mean centipede densities per parcel without or with few (< 10) ants *vs* with many (> 50) ants (± standard deviation, number of quadrats is given between brackets).

Parcel	Square samplings without ants	Square samplings with numerous ants	Proportion
BE1	42.3 ± 12.2 (9)	6 (1)	7.05
BE2	44.2 ± 13.5 (9)	6 (1)	7.37
VI1	71.8 ± 21.8 (9)	10 (1)	7.18
VI2	74.75 ± 19.3 (8)	9.75 ± 4.9 (2)	7.67

DISCUSSION

Biogeographic conditions

The forest of Cerisy strongly differs of those of Pays de la Loire because of the presence and dominance of *Geophilus truncorum*. This is a North-Western European species found in Normandy and elsewhere in forests of North-Western France, but that becomes very rare southern, as in Pays de la Loire region (Iorio 2014, Racine & Iorio 2017, Iorio & Racine 2018). In this region, it is almost only present in the most northern parts of the northern departments (Sarthe and Mayenne departments) (Iorio & Racine 2018). We also found in Cerisy *Lithobius aeruginosus*, a Central European species which reaches its western limit of distribution in very few localities of the Armorican region. It was found in the coldest forest of the five forests studied: mean annual and summer temperatures differences between Pays de la Loire forests only vary of 1 °C at most (Mervent *vs* others), but the mean annual and summer temperatures of Cerisy are respectively lower of 1 °C and 2.5 °C than three of the Pays the la Loire forests, and of 2 °C and 3.5 °C of the fourth. The mean temperatures of Cerisy seem low enough to lead to a different species composition, getting closer to the assemblages of more northern or continental European forests (Fründ *et al*. 1997, Lock *et al*. 2001, Iorio 2014).

In terms of species richness, the studied forests were slightly richer (by a difference from 1 to 4 species) than a Francilian forest like the forest of Commanderie (south of Fontainebleau, Ile-de-France: n = 12 species); this last being however considered as fairly poor because of its suburban location (Geoffroy 1979). The forest of Commanderie has had a much higher pressure of sampling than ours, thus the difference is potentially higher in favour of our cases. Species richness is yet overall similar to other Northern European forests, but the Lithobiomorpha are more numerous in the latter when continental (*e.g*. Leśniewska 2000, Lock *et al*. 2001, Leśniewska *et al*. 2005, 2011, Jabin 2008, Voigtländer 2009). The Southern European or Alpine forests are obviously richer than Armorican forests, until two times (*e.g*. Grgič & Kos 2005, Kula & Lazorík 2015, Peretti & Bonato 2018).

The superdominant centipede species of Commanderie and of Pays the la Loire forests is the same (*i.e*. *Schendyla nemorensis*), but it is different from more continental forests. *Lithobius mutabilis* and *Strigamia acuminata* are indeed over-dominating the latter, yet sometimes co-dominating with *S. nemorensis* and *G. truncorum* (Leśniewska 2000, Jabin 2008, Voigtländer 2009, Grinvald 2011). Differences in species composition are getting larger when leaving French Atlantic for the continental area, with *e.g*. *Arctogeophilus inopinatus* and *Geophilus easoni* in the first area, and *Lithobius dentatus* and *Strigamia* *transsilvanica* in the second (Spelda 1999, Wytwer 2000, Jabin 2008, Voigtländer 2009, Grinvald 2011, Iorio 2014, Racine & Iorio 2017, Iorio & Racine 2018). The centipede assemblages of Atlantic forests thus show some clear biogeographic particularities compared to other regions, as well as inside its area according to finer climatic conditions (northern location of Cerisy).

Dominant tree species and stand age

Seemingly, tree species, all deciduous, only had a weak influence on centipede densities and assemblages in the Armorican Massif. The densities of both Cerisy parcels, respectively dominated by the alder (CE1) and the beech (CE2), are in the mid-range of those observed in oak parcels. Also, there was no significant difference between alder and beech parcels in terms of centipede numbers, as well as for the superdominant species *Geophilus truncorum*. Although *Lithobius aeruginosus* was exclusive to CE1, we cannot assume that its presence is linked to the alder because this species is also reported from forest parcels dominated by other deciduous trees in France and elsewhere (Spelda 1999, Lock 2000, Jabin 2008, Iorio 2014). In the parcel CE1, the dominance of the alder reflect of the more humid soil of this parcel. It must be underlined that the three other known Armorican localities of *L. aeruginosus* are from parcels dominated by other tree species (beech, oak) but also under particular abiotic conditions, *e.g.* fairly high altitude for this area (from 200 m a.s.l. to > 300 m a.s.l.) or in shaded and humid valleys with small streams and mesohygrophile to hygrophile flora species like *Paris quadrifolia* and *Chrysosplenium* sp. (Racine & Iorio 2017, Iorio & Racine 2018, Franck Noël pers. com.). The assumption of Racine & Iorio (2017) and Iorio & Racine (2018) that *L. aeruginosus* only inhabits cold and humid forest habitats in the Armorican Massif tends to be confirmed here. Also, as already reported for several centipede species, both humidity and temperature are important factors shaping population dynamics (Tuf 2002, Jabin 2008, Voigtländer 2009, 2011). The presence of *L. aeruginosus* in Cerisy is thus likely due to both biogeographic and parcel abiotic conditions.

In this study only *Strigamia acuminata* seemed to favour a parcel dominated by a specific tree species, with differences between the beech-dominated parcel (CE2) and the alder-dominated parcel (CE1) in Cerisy. This tendency is broadly in accordance with the knowledge in other areas (Iorio 2014, Kula & Lazorík 2015).

The age of parcels was not acting significantly on centipede densities in both Bercé & Cerisy, but was highly significant in Mervent. Not only ME2 was younger than ME1 but, to the difference of other young parcels, was clear-cut in 1972 (https://remonterletemps.ign.fr). The parcel ME1 has never been clear-cut (as far back as we can go in time); nor the other studied forest parcels. The lower density of centipede in ME2 could therefore be the result of interrupted forest continuity (by a clear-cutting of the parcel). Openings in forest habitats, even if resulting of a natural phenomenon like windstorm, are indeed known to have a strong impact on centipede assemblages (Leśniewska & Skwierczyński 2018). Lock *et al.* (2005) showed that, in forest extensions on former pastures or agricultural lands, it takes more than 23 years to have some typical woodland species, yet not reaching the population density of old forests for these species. Pontégnie *et al.* (2005) also stated that large clearings in forests have a negative effect on centipedes. Jabin (2008) also demonstrated that centipede density was much higher in primeval forests than in recently or historically managed forests of Central Europe (> 400 individuals/m^2 *vs* rarely more than 200 individuals/m^2). Abundance of forest species such as *L. mutabilis* were also reduced according to the same author. Baini & Zapparoli (2015) finally showed that centipede assemblages were different between native forests and reforestations in Central Italy. Thus the factor which had an importance here was more probably the temporal forest continuity (*i.e.* interrupted or not by a clear-cutting) than age tree, at least for trees a few decades old.

Other important factors not studied here, like small-scale heterogeneity in forest stands, can also play an important role in driving local densities, species richness and to support populations of specialised species. It has indeed been shown that too homogeneous even-aged parcels contain poorer centipede assemblages than uneven-aged parcels (Grgič & Kos 2003, 2005). This could be another reason why the very regular and even-aged parcel of BE1 had much lower and more variable densities than the second oldest forest stand of ME1, also lacking some forest-specialized species like *Arctogeophilus inopinatus* and conversely the surprising overdominance of the eurytopic *Cryptops hortensis* in the first (Table SI).

Small-scale distribution patterns

Our observations on the vertical distribution of centipedes are in accordance with other studies in European forests. The majority of the Geophilomorpha is indeed considered having a preference for the upper horizons of soil, thus euedaphic; but several species such as *Strigamia acuminata* and several *Lithobius* spp. prefer the litter layers (F and L-layers) (Geoffroy 1979, Poser 1990, Voigtländer 2009, 2011). It is interesting to note that *Geophilus easoni* had its highest relative abundance in the litter and not in the upper soil, contrary to other studied *Geophilus* spp. on this aspect.

Ants are known to feed upon centipedes as well as on many other ground- and litter-dwelling animals (Cerdá & Dejean 2011), but their interspecific relations with centipedes in Western Europe are poorly known. The slow-moving geophilomorphs have glandular ventral secretions to defend against predators; however, even a large European species like *Henia vesuviana* cannot defend itself against swarms of ants (Hopkin & Anger 1992). The very reduced centipede densities in quadrats with numerous ants tends to confirm that the presence of ants (probably near their nest) is antagonistic with most centipedes.

As a conclusion, this first work on forest centipedes on the Armorican Massif, and more widely on Western France, show that, even if species richness is quite low, centipedes are important components of the soil and litter fauna of local deciduous forests, especially in terms of density. Thus this group should be more studied in French forests. Centipedes probably have the potential of being accurate bio-indicator at a large scale to study the effects of temporal forest continuity, and at a finer scale to study the effect of local abiotic like temperature and local humidity and biotic factors like interspecific competition factors.

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Appendix

Table SI. – Taxonomic list of centipede species, and total numbers per parcel.

	BE1	BE2	GR1	GR2	ME1	ME2	VI1	VI2	CE1	CE2	Total
Geophilomorpha	136	352	361	562	829	260	542	542	384	347	4315
Arctogeophilus inopinatus	0	21	0	0	33	4	11	6	31	12	118
Geophilus easoni	0	7	0	1	7	6	0	0	0	0	21
Geophilus electricus	0	0	7	4	0	0	0	0	0	0	11
Geophilus gavoyi	2	0	0	0	7	2	0	0	0	0	11
Geophilus osquidatum	0	0	2	5	0	0	0	0	0	1	8
Geophilus truncorum	0	0	0	0	0	0	0	0	226	186	412
Schendyla nemorensis	123	324	347	547	775	247	529	535	121	119	3667
Strigamia acuminata	9	0	1	3	1	0	1	1	4	26	46
Strigamia crassipes	2	0	3	1	1	0	1	0	2	3	13
Stigmatogaster subterraneus	0	0	1	1	5	1	0	0	0	0	8
Lithobiomorpha	50	39	31	69	45	29	85	58	22	29	457
Lithobius aeruginosus	0	0	0	0	0	0	0	0	6	0	6
Lithobius agilis	0	0	0	0	1	0	3	1	0	0	5
Lithobius calcaratus	3	8	4	1	0	3	6	14	2	1	42
Lithobius forficatus	1	0	0	0	2	4	2	2	0	0	11
Lithobius macilentus	7	0	0	1	6	2	0	2	0	0	18
Lithobius microps	9	0	3	8	30	11	0	4	3	2	70
Lithobius muticus	0	0	5	10	0	1	0	1	9	0	26
Lithobius piceus	3	0	4	7	0	2	3	1	2	17	39
Lithobius sp.	13	11	15	33	4	3	52	29	0	6	166
Lithobius tricuspis	14	20	0	9	2	3	19	4	0	3	74
Scolopendromorpha	201	13	4	7	2	7	91	37	1	74	437
Cryptops hortensis	201	13	4	7	2	7	91	37	1	74	437
Total number of individuals (parcel)	387	404	396	638	876	296	718	637	407	450	5209
Number of species (parcel)	11	6	11	14	13	13	10	12	11	12	20
Total number of individuals (forest)	791		1034		1172		1355		857		5209
Number of species (forest)	13		14		16		13		13		20