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Habitat characteristics of Aradidae (Insecta: Heteroptera) in two french deciduous forests

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Abstract Forest management can have a strong negative effect on biodiversity, especially for saproxylic species. To protect this biodiversity, we must understand the specific requirements of the concerned species. However, information on mycetophagous Aradidae in temperate forests is scarce, and the factors influencing their abundance are poorly known. We studied the habitat requirements of the Aradidae (Heteroptera) *Aneurus avenius* and *Aneurus laevis* in two french deciduous forests. We first defined their habitat preferences at the piece-of-wood scale; we compared the effects of tree species, degree of decay, bark dehiscence and surface area. At a larger (stand) scale, we tested the effects of surface area and volume of standing or fallen dead wood, and the presence of fungi. Three other species, i.e. *Aradus brenskei*, *A. conspicuus* and *A. versicolor* were encountered during our study, but their occurrences were too rare to perform statistical tests, so only descriptive data are given for these species. We concluded that the two *Aneurus* species have slightly different habitat requirements, with *A. avenius* being more abundant on oak and under dehiscent bark, and favoured in stands with small branches and the presence of fungi, while *A. laevis* is more abundant on decayed wood and under various types of bark in stands with small branches. All species of Aradidae vary in their habitat preferences, and can be sensitive to different types of exploitation. Some species need large senescent trees, while others, like the *Aneurus* species, depend on small fresh deadwood and are therefore more sensitive to woodfuel harvesting.

Keywords *Aneurus* · *Aradus* · Saproxylic insects · Mycetophagous · Dead wood · Woodfuel harvesting

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Introduction

The Aradidae Brullé, also called bark bugs or flat bugs, are a family of Heteroptera containing about 2000 known species worldwide. Following Speight's (1989) definition, Aradidae are saproxylic and depend on wood-inhabiting fungi for at least a part of their life cycle. One species, *Aradus cinnamomeus* Panzer, which is the only one in Europe with economic importance (Heliövaara 2000), feeds on living trees. However, Aradidae live in dead wood, on the surface or between the bark and wood, where they feed on wood decaying fungi (Usinger and Matsuda 1959; Heiss and Péricart 2007). Several bark bugs species are known to live on small-diameter branches (Heiss and Péricart 2007) where fungi are generally more diversified (Heilmann-Clausen and Christensen 2004; Nordén et al. 2004), but ecological and habitat preferences remain unknown for many species. The most comprehensive study on habitat requirements (continuity, host and resource availability, shade tolerance) was published by Gossner et al. (2007) and concerns four species of Aradidae (*Aneurus avenius* (Dufour), *Aradus betulae* (Linnaeus), *Aradus depressus* (Fabricius), and *Aradus conspicuus* Herrich-Shaeffer). Most of the available information is based on occasional observations (Heiss and Péricart 2007) and scientific studies on habitat requirements are still lacking. In particular, the species' dependence on surface

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area of the deadwood piece or on deadwood volume per hectare is poorly understood.

Most of the scientific publications on Aradidae ecology concern boreal forests and focus on pyrophilous species in the genus *Aradus* Fabricius which occur after a forest fire and feed on fungi growing on burned wood (Wyniger et al. 2002; Deyrup and Jackson 2004; Hjälten et al. 2006). Aradidae may also be sensitive to forestry and human activities: five species among the 17 known have virtually disappeared from Finland since the last century, and three of the remaining species seem to be in decline (Heliövaara and Väisänen 1983). Simov (2005) looked for Aradidae in protected old coniferous forest in Bulgaria and concluded that *Aradus* diversity was poor compared with Central and Northern European countries. Several Aradidae species are red-listed in some European countries; for example, *Aradus truncatus* Fieber is critically endangered in Germany, endangered in Sweden and near threatened in Finland (Ministerium für Umwelt 2005; Gärdenfors 2010; Rassi et al. 2010). Moreover, some species have even been proposed as bio-indicators of site quality, for example *A. conspicuus* Herrich-Shaeffer or *A. truncatus* Fieber in Europe (Speight 1989). In temperate ecosystems, forest dynamics and management are different from the boreal biome and the effect of the available amount of deadwood on Aradidae populations may vary (as it is the case for other saproxylic groups, see Lassauce et al. 2011). The demand for fuelwood may increase the pressure on saproxylic species (Grove 2002; Nordén et al. 2004; Robertson et al. 2008; Lassauce et al. 2012).

In this context, the aim of this study is to improve the knowledge of the habitat requirements of some Aradidae species living in two deciduous forests in France. First, we observed the characteristics of dead or senescent wood in which they mostly occur. This included the qualities of the deadwood pieces such as degree of decay, the available surface area and bark dehiscence. Second, we determined the effect of stand characteristics such as total deadwood amount or presence of fungi on the abundance of the species. We compare our results at the two different scales and discuss the potential effects of forest management on Aradidae diversity, with particular attention to slash harvesting.

Materials and methods

Study sites

We studied two deciduous lowland forests located in the northern part of France: the state forests of Rambouillet (around 1°55′E, 48°37′N) and Fontainebleau (around 2°41′E, 48°24′N). The Rambouillet forest covers 14,550 ha on moderately acidic to neutral sandy to loamy soils. The mean annual temperature and rainfall are 10 °C and 650 mm, respectively. The forest is dominated by deciduous species (75 % of the forest cover of which 90 % are oaks: *Quercus petraea* (Matt.) and *Q. robur* L.). Two conifers (*Pinus sylvestris* L. and *P. nigra* Arnold) make up the remaining 25 %. The Fontainebleau forest covers 17,073 ha on acidic sandy soils. The mean annual temperature and rainfall are 10.6 °C and 760 mm, respectively. The forest is dominated by deciduous species (60 % of the forest cover of which 70 % are oaks: *Q. petraea* and *Q. robur*; and 18 % are beech: *Fagus sylvatica* L.). The conifer *P. sylvestris* covers 30 %, and the remainders are mixed stands. The Fontainebleau forest includes around 1,000 ha of strict forest reserves, including some that have not been managed for more than 150 years.

The study area was made of 30 plots of 50 m radius in the Rambouillet forest and 26 plot of 50 m radius in Fontainebleau (13 in managed stands and 13 in forest reserves).

Plot dendrometric and mycological data

The dendrometric protocols used to measure deadwood volumes were designed in two independent research projects and differ between the two forests (Table 1). Deadwood volume estimations are probably better for the Rambouillet than for Fontainebleau. Despite these differences, the data were included in the same analyses to preserve sufficient statistical power.

Mycological data came from the same two research projects as the dendrometric protocols. Fungi were counted on the pieces of wood recorded during the dendrometric studies.

Aradidae sampling and characteristics for individual pieces of wood

Aradidae were hand collected during springtime (May 31 to June 23, 2010). This method was preferred over

Table 1 Protocols used in deadwood measurements for the two study sites (length or surface area sampled)

Deadwood type	Rambouillet forest	Fontainebleau forest
Lying deadwood $D < 7.5$ cm	LIS = 40 m	LIS = 60 m
Lying deadwood $7.5 \text{ cm} < D < 30$ cm	3,534 m^2	LIS = 60 m
Standing deadwood $7.5 \text{ cm} < D < 30$ cm	3,534 m^2	314 m^2
Lying and standing deadwood $D > 30$ cm	4,084 m^2	1,256 m^2

LIS line intersect sampling (Van Wagner 1968), the other figures correspond to the surface areas sampled interception traps which appear to be less effective (personal observations, and, in Gossner et al. (2007) only 1.5 % of total Aradidae encountered were caught with interception traps).

Within each sample plot (50 m radius), two observers searched for Aradidae on standing or fallen, dead or senescent pieces of wood for 1 h for standardization. We counted the number of individuals per piece and noted the presence or absence of larvae. A few specimens were collected each time for identification.

For each piece of wood where individuals were found, we noted the tree species (oak, hornbeam, beech, and undetermined species), the status (dead or senescent), the position (standing or fallen), the degree of decay according to the "knife test" ("Fresh": the knife tip penetrates < 1/4 of the diameter, the wood is hard; "Decayed": moderately to strongly decayed wood, form is still apparent but soft or partly destroyed wood appears, the knife tip penetrates > 1/4 the diameter), the length, the diameter where insects were present, bark dehiscence (1: dehiscent, easy to remove in large pieces; 2: moderately dehiscent, can be removed with a knife but in small pieces; 3: hard to remove, not dehiscent). The pieces of wood where no individuals were found were not measured, so we adapted the statistical methods accordingly (see below).

Statistical analyses

All statistic analyses were performed with R.2.12.2 (R core Team 2011)

We considered the abundance of each species as the response variable, and distinguished two datasets. The first set of data includes all the specimens encountered. The second dataset (hereafter called "reproduction site subset") includes only pieces of wood where larvae were present, and then excludes all pieces of wood where only adult were present. For this subset, all individuals are counted, adults and larvae. This allows us to determine more specifically factors favouring the reproduction of the species.

As zeros were not recorded during the sampling, we used the "vglm" function in the VGAM package and positive error distributions (Yee 2008, 2010) to model the response of abundance per piece of wood to individual piece-of-wood characteristics. Thus, depending on the data distribution for each Aradidae species, we used either the positive negative binomial family or the positive Poisson family. Different models were compared on the basis of their Akaike Information Criterion (AIC), the best model being the one with the lowest AIC value. If two models had a similar AIC (less than two points higher), we chose the simplest one. The sample size here was large enough to use the AIC rather than de AICc. We tested the null model, and the following explanatory variables: forest (Fontainebleau vs. Rambouillet), degree of wood decay (fresh vs. decayed), bark dehiscence (1: easy to remove, 2: moderately dehiscent, 3: hard to remove), tree species (beech, oak, hornbeam or undetermined tree species) and surface area of the pieces of wood. To prevent over-parametrization, we tested only the simple models, and two-factor models with and without their interaction (summarized in Table 2). The effect of an explanatory variable was considered significant when the absolute value of the "t" statistic was greater than 2 (Yee 2010). We did not correct for autocorrelation between plots as random effect is not implemented in VGAM package.

To study the effects of factors at the plot scale on the abundance of each species, and according to distribution data, we first used the negative binomial generalised linear model (glm.nb) of the MASS package (Venables and Ripley 2002) to test one-factor models.

The explanatory variables used in the models were: Site (FBL = Fontainebleau, RBO = Rambouillet); volume per hectare of fallen dead wood of different sizes (V.FDW.inf7.5 = small, less than 7.5 cm diameter; V.FDW.inf30 = medium, between 7.5 and 30 cm diameter; V.FDW.sup30 = large : more than 30 cm diameter); surface area per hectare of fallen dead wood (small: S.FDW.inf7.5, medium: S.FDW.inf30 and large: S.FDW.sup30); volume per hectare of standing dead wood (medium: V.SDW.inf30 and large: V.SDW.sup30); surface area per hectare of standing dead wood (medium: S.SDW.inf30 and large: S.SDW.sup30); number of small pieces of fallen dead wood (=nb.SFDW); number of tree species (=nb.tree.sp); number of different genera of fungi where Aradidae can typically be encountered (*Fomes* (Fr.), *Stereum* (Hill), *Trametes* Fr., *Hypoxylon* Bull.); total number of Ascomycetes on the plot (=T.Asco); and total number of "Aphyllophorales" (=T.Aphyllo, saprophytic fungi with shelf-like bodies, including in our case *Stereum* (Hill), *Trametes* Fr. and *Fomes* (Fr.), but also other genera such as *Botryobasidium* Donk, *Hyphoderma* (Wallr), *Hyphodontia* Eriksson, *Phanerochaete* P.Karst., *Phellinus* (Quel.), *Sistotrema* Fr., *Tomentella* (Pers.), *Trechispora* (P.Karst.), etc.).

The models were ranked with the Akaike Information Criterion corrected for small samples (AICc) and Akaike weights to identify the best models (Burnham and Anderson 2002). However, several models showed similar AICcs (i.e. less than two points higher than the lowest value), so the R package "MuMIn" was used for model selection and model averaging (Burnham and Anderson 2002; Barton 2009). Model averaging makes it possible to calculate parameter estimates when models are very close to one another (Grueber et al. 2011). An effect was considered significant whenever the 95 % confidence interval did not bracket zero.

Table 2 Akaike Information Criterion of the models tested on the abundance of Aradidae species

No.	Explanatory variables	Complete dataset		Reproduction sites	
		A. avenius	*A. laevis*	*A. avenius*	*A. laevis*
0	Null	1,381.97	995.89	351.99	647.67
1	Forest	1,377.00	995.14	353.89	648.06
2	Decay	1,383.48	995.53	353.93	648.45
3	Bark dehiscence	1,345.12	989.73	354.33	644.29
4	Surface area	1,378.46	994.82	352.77	646.76
5	Tree species	1,289.69	1,000.19	354.19	652.37
6	Decay + surface area	1,380.16	995.08	354.76	647.94
7	Decay + surface + decay:surface area	1,330.93	996.79	354.82	649.51
8	Decay + tree species	1,290.14	996.50	355.41	651.73
9	Decay + tree species + decay:tree species	–	996.18	**348.40**	644.36
10	Decay + dehiscence	1,346.60	989.12	356.29	643.92
11	Decay + dehiscence + decay:dehiscence	1,340.51	**985.97**	359.28	**641.15**
12	Tree species + surface area	1,279.23	999.40	355.01	651.18
13	Tree species + surface + tree species:surface area	–	1,003.65	358.68	655.53
14	Tree species + dehiscence	**1,270.50**	993.30	356.93	649.01
15	Tree species + dehiscence + tree species:dehiscence	–	990.92	–	–
16	Dehiscence + surface area	1,334.22	988.63	355.09	643.22
17	Dehiscence + surface area + dehiscence:surface	1,282.97	991.43	357.22	646.14

A Positive Poisson Error Distribution was used for *A. avenius* and a Positive Negative Binomial for all the other tests, including subsets with larvae only. The lowest log-likelihoods are in bold characters. Models without value failed to converge. *Aneurus avenius*: n = 77, reproduction site subset n = 48; *Aneurus laevis*: n = 119, reproduction site subset n = 67

Results

In the study site of Rambouillet, a total of 2,707 specimens belonging to only two species (368 *A. avenius* (Dufour), 2,339 *Aneurus laevis* (Fabricius) were recorded on 105 pieces of wood (Table 3). In the study site of Fontainebleau, 1,672 individuals of five different species were recorded on 108 pieces of wood (502 *A. avenius* (Dufour), 1,101 *A. laevis* (Fabricius), 27 *A. brenskei* Reuter, 32 *A. conspicuus* Herrich-Schaeffer, and 10 *Aradus versicolor* Herrich-Schaeffer).

Species' habitat preferences

The results of species abundance depending on the degree of wood decay and surface area are summarized in Table 3. Because of the low abundance of the other species, the different models were applied to two species only: *A. avenius*, and *A. laevis*. Some models failed to converge and were excluded: model 09, model 13 and model 15 for *A. avenius*, and model 15 for the subsets of reproduction site (Table 2).

Table 3 Abundances of *A. brenskei, A. conspicuus*, *A. versicolor*, *A. avenius* and *A. laevis* as a function of diameter (D) and degree of decay (*F* fresh, *D* decayed)

	A. avenius		*A. brenskei*		*A. conspicuus*		*A. laevis*		*A. versicolor*		Total
	F	D	F	D	F	D	F	D	F	D	
Deadwood D < 7.5 cm	645	119	0	0	20	0	1,309	1,327	9	0	3,429
Deadwood 7.5 cm ≤ D < 30 cm	105	1	11	0	11	0	576	189	1	0	894
Deadwood D ≥ 30 cm	0	0	3	13	0	1	39	0	0	0	56
Total	750	120	14	13	31	1	1,924	1,516	10	0	4,379

Moreover, among the 14 specimens of *A. brenskei* on fresh wood, 13 were in fact on senescent wood where the bark had become dehiscent. All specimens on decayed wood were found on a senescent tree partially decayed on one side

Table 4 Model parameters relating abundance of Aradidae and characteristics of wood pieces

Response variable	Model	Parameters	Value	SE	*t* value
A. avenius	[14]	Intercept	2.65	0.07	36.81
n = 77		Oak	0.66	0.11	5.96
		Undetermined	−0.38	0.10	−3.90
		Beech	−0.19	0.09	−2.14
		Dehiscence:moderate	−0.23	0.08	−3.10
		Dehiscence:not dehiscent	−0.70	0.19	−3.69
A. avenius (reproduction sites)	[09]	Intercept:1	0.72	1.19	0.60
n = 48		Intercept:2	0.09	0.30	0.31
		Decay:fresh	2.02	1.23	1.64
		Oak	1.31	1.40	0.94
		Undetermined	2.68	1.32	2.03
		Beech	0.00	1.69	0.00
		Oak × decay:fresh	0.55	1.72	0.32
		Undet. × decay:fresh	−3.58	1.38	−2.60
		Beech × decay:fresh	−0.13	1.73	−0.08
A. laevis	[11]	Intercept:1	3.90	0.34	11.37
n = 119		Intercept:2	−0.87	0.22	−3.96
		Decay:fresh	−1.26	0.42	−2.99
		Dehiscence:moderate	−0.82	0.53	−1.54
		Dehiscence:not dehiscent	−2.10	0.62	−3.39
		Decay:Fresh × dehiscence:moderate	1.65	0.65	2.55
		Decay:fresh × dehiscence:not dehiscent	1.47	0.77	1.90
A. laevis (reproduction sites)	[11]	Intercept:1	4.25	0.25	16.72
n = 67		Intercept:2	0.05	0.20	0.23
		Decay:fresh	−0.99	0.34	−2.93
		Dehiscence:moderate	−0.55	0.43	−1.26
		Dehiscence:not dehiscent	−1.54	0.57	−2.72
		Decay:fresh × dehiscence:moderate	1.46	0.55	2.66
		Decay:FRESH × dehiscence:not dehiscent	1.03	0.76	1.36

A Positive Poisson error distribution was used for all occurrence of *A. avenius*, and a Positive Negative Binomial for *A. laevis* and reproduction site subsets of both species. Response variables: degree of decay (fresh or decayed); bark dehiscence (dehiscent, moderately dehiscent, not dehiscent) tree species (hornbeam, oak, undetermined tree species, and beech). The effect was considered statistically significant if the absolute *t* value was higher than 2 (Yee 2010). *SE* standard error associated with the model

The best model for *A. avenius* is the one involving bark dehiscence and tree species (additive model 14—Table 2). There were significantly more individuals under dehiscent bark than under moderately or not dehiscent bark, and on oak and hornbeam than on beech, but less individuals on undetermined species than on all other tree species (Table 4).

For the reproduction site subset, the best model for *A. avenius* included the degree of decay, the tree species, and the interaction between these two factors (Model 09, Table 2). Abondances on fresh or decayed wood depended on the tree species. There were more individuals on oak or hornbeam, especially for fresh wood. There were approximately the same number of individuals on hornbeam and beech, but less than on oak and undetermined species for decayed wood (Table 4). Nevertheless, there were not significantly more individuals on fresh wood than on decayed wood in the overall (Table 4).

For *A. laevis,* the best model was the additive model involving the decay degree and the bark dehiscence, including the interaction between these two factors (model 11, Table 2). There were significantly fewer individuals on fresh wood (Table 4). There were slightly more individuals on dehiscent bark than on moderately dehiscent and non-dehiscent bark (Table 4). However when we considered the interaction, more individuals were found on fresh wood with moderately dehiscent bark.

When considering only the *A. laevis* reproduction site subset, the best model included the degree of decay, the bark dehiscence and the interaction between these two factors (model 11, Table 2). There were significantly more individuals on decayed wood, and under dehiscent bark (Table 4), but this order varied when considering the interaction with the degree of decay: e.g. the abundance was higher on fresh wood with moderately dehiscent bark.

Species from the genus *Aradus* occurred too rarely to perform tests. Some descriptive results for these species are summarized in Table 3.

Aradus conspicuus was only found on fresh dead beech, except for one occurrence. It was mostly encountered on wood with a small and medium diameter (less than 30 cm in diameter). *A. brenskei* was found exclusively on beech with a diameter greater than 20 cm, and 95 % of the individuals were found on senescent trees attacked by fungi; sometimes the part of the tree where the individuals were found was highly decayed.

Ninety percent of *A. versicolor* was found on standing dead beech and beech stumps, and always on fresh dead wood with a diameter ranging from 5 to 10 cm.

Stand level variables

Only abundance of *A. avenius* and *A. laevis* is used here. *A. brenskei, A. conspicuus* and *A. versicolor* were found only in the study site of Fontainebleau in less than five plots for each species, so no analysis could be performed.

The abundance of *A. avenius* depends mainly on the surface area of large fallen dead wood, with slightly fewer individuals on large than on small trees (weight = 0.17, estimate = −8.49e−04, Table 5). Other models within two points of AICc had a lower weight than the null model (0.15). Nevertheless the number of Ascomycetes and the surface area of medium-diameter standing dead wood tended to have a positive effect on the abundance of *A. avenius*, with a respective weight of 0.13 and 0.10.

For the reproduction site subset, the number of *Fomes* tended to have a positive effect on adults and larvae abundance (weight = 0.19) as did the total number of Ascomycetes and *Trametes* (weight = 0.13), and the surface area of standing dead wood of medium and large size (weight = 0.10). Only the number of different tree species seemed to have a negative effect on the abundance of *A. avenius* (weight = 0.10).

The abundance of *A. laevis* depended mainly on the surface area of fallen dead wood of medium (7.5–30 cm in diameter) and small size (less than 7.5 cm in diameter), with respective weights of 0.20 and 0.18 (Table 6). The surface area of large fallen dead wood also seemed to have

Table 5 Averaged model with Negative-Binomial error distribution parameters for abundance of *A. avenius* for all 56 plots (and a total of 979 insects) and for plots with larvae only (31 plots, and a total of 875 insects)

Data subset	Explanatory variables	Coefficient	SE	Lower CI	Upper CI	Relative weight
All plots	(Intercept)	2.89	0.31	2.28	3.49	
	S.FDW.sup30	−8.49e−04	2.13e−03	−5.04e−03	3.34e−03	0.17
	T.Asco	6.62e−03	0.02	−0.04	0.05	0.13
	S.FDW.inf30	−4.56e−05	1.83e−04	−4.08e−04	3.17e−04	0.10
	S.SDW.inf30	4.48e−04	2.11e−03	−3.74e−03	4.63e−03	0.09
	Fomes	1.15e−02	0.06	−0.10	0.12	0.08
	S.FDW.inf7.5	−5.42e−05	2.50e−04	−5.49e−04	4.40e−04	0.08
	SiteRBO	−2.03e−02	0.13	−0.29	0.25	0.07
	Stereum	−4.72e−03	0.03	−0.07	0.06	0.07
	V.SDW.inf30	5.91e−03	0.04	−0.07	0.08	0.07
Reproduction	(Intercept)	3.28	0.34	2.60	3.96	
Site subset	Fomes	4.14e−02	0.10	−0.17	0.25	0.19
	T.Asco	4.49e−03	0.02	−0.03	0.04	0.13
	Trametes	2.17e−02	0.09	−0.15	0.19	0.13
	nb.tree.sp	−1.98e−02	0.10	−0.23	0.19	0.10
	S.SDW.inf30	3.21e−04	1.60e−03	−2.90e−03	3.54e−03	0.10
	S.SDW.sup30	3.25e−04	1.74e−03	−3.19e−03	3.84e−03	0.10

SE standard error associated with the model, CI = 95 % confidence interval. Relative weight quantifies the evidence for each parameter across all of the models. Variables retained in the models: *Fomes* = number of fungi of the genus *Fomes* on plot; nb.tree sp. = number of different tree species on the plot; site = forest (*FBL* Fontainebleau, *RBO* Rambouillet); S.SDW.inf30 = surface area of standing dead wood between 7.5 and 30 cm diameter per hectare; S.SDW.sup30 = surface area of standing dead wood more than 30 cm diameter per hectare; S.FDW.inf30 = surface area of fallen dead wood between 7.5 and 30 cm diameter per hectare; S.FDW.sup30 = surface area of fallen dead wood more than 30 cm diameter per hectare; S.FDW.inf7.5 = surface area of fallen dead wood less than 7.5 cm diameter per hectare; *Stereum* = number of fungi of the genus *Stereum* on plot; *T.Asco* = total number of Ascomycetes on plot; *Trametes* = number of fungi of the genus *Trametes* on plot; V.SDW.inf30 = volume of standing dead wood between 7.5 and 30 cm diameter per hectare

Table 6 Averaged model with Negative-Binomial error distribution parameters for abundance of *A. laevis* for all 56 plots (n = 3,411 insects) and for plots with larvae only (40 plots, n = 3,342 insects)

Data subset	Coefficient	SE	Lower CI	Upper CI	Relative weight
All plots					
(Intercept)	3.91	0.36	3.20	4.62	
S.FDW.inf30	1.40e−04	3.21e−04	−4.92e−04	7.72e−04	0.20
S.FDW.inf7.5	1.70e−04	4.33e−04	−6.85e−04	1.02e−03	0.18
Hypoxylon	−0.09	0.25	−0.58	0.40	0.14
SiteRBO	0.08	0.26	−0.44	0.60	0.12
S.FDW.sup30	3.47e−04	1.29e−03	−2.19e−03	2.89e−03	0.10
V.SDW.sup30	−1.14e−03	4.27e−03	−9.56e−03	7.28e−03	0.09
V.FDW.inf7.5	4.39e−03	0.02	−0.03	0.04	0.09
Reproduction site subset					
(Intercept)	4.12	0.21	3.70	4.54	
S.FDW.inf30	1.96e−04	3.05e−04	−4.08e−04	7.99e−04	0.37
S.FDW.inf7.5	2.20e−04	4.02e−04	−5.75e−04	1.02e−03	0.31
V.FDW.inf30	2.10e−03	5.27e−03	−8.34e−03	0.01	0.19
V.FDW.inf7.5	6.07e−03	0.02	−0.03	0.04	0.14

SE standard error associated with the model, *CI* 95 % confidence interval. Relative weight quantifies the evidence for each parameter across all of the models. See text for abbreviation meanings

a positive effect but shows a weight of only 0.10. There were slightly more individuals in Rambouillet (site: weight = 0.12). The abundance of *Hypoxylon* fungi tended to have a negative effect. The volume of dead wood had no more effect than the null model (weight = 0.09).

For the reproduction site subset, the surface area per hectare of medium and small fallen dead wood had a positive effect with weights of 0.37 and 0.31, respectively. The volumes of medium and small fallen dead wood also tended to have a positive effect (weight = 0.19 and 0.14).

Discussion

Habitat characteristics of Aradidae species

Scientific literature on the ecology of saproxylic insects is abundant but is focused on specific groups: Coleoptera (e.g. Okland et al. 1996; Grove 2002; Similä et al. 2003; Bouget et al. 2009; Vodka et al. 2009), or Coleoptera and Diptera (e.g. Irmler et al. 1996; Schiegg 2000, 2001; Fayt et al. 2006), their hymenopteran parasitoids (Vanderwel et al. 2006), and sometimes Lepidoptera (Jonsell and Nordlander 2002). Ecological data on other groups remain scarce. Our study on Aradidae species in French deciduous forests showed that *A. avenius* and *A. laevis* are apparently very common in such forests. These two species have been reported to have similar habitat preferences, i.e. small branches lying on the forest floor (Heiss and Péricart 2007). This could explain their high abundance as fine woody debris are generally the most abundant (Gibb et al. 2005). This was partly confirmed by our results as those two species responded to the same environmental factors, particularly at the piece-of-wood scale. However, we showed that their abundance also depends on other previously unstudied factors and that slight differences in their habitat preferences do exist.

Aneurus avenius was mostly found on fresh wood characterized by dehiscent bark and is more abundant on oak and hornbeam than on other tree species. The size of dead wood generally seems to be an important factor for saproxylic insects (Schiegg 2000, 2001; Siitonen 2001; Grove 2002; Fayt et al. 2006) including *A. avenius* (Gossner et al. 2007). However, we showed that at least at piece-of-wood scale, the size is not the best explanatory factor for Aradidae abundance. As for mycetophagous beetles (Lassauce et al. 2012), tree species and bark dehiscence play an even more important role. Indeed, dehiscent bark apparently provides a suitable habitat for these species (in terms of foraging, nesting and protection from predators). At the plot scale, in line with Gossner et al. (2007), the abundance of *A. avenius* tended to be positively correlated with the surface area of small snags and negatively correlated with the surface area of large logs, but none of these factors had a significant effect in our study. In addition, the abundance of *A. avenius* on a plot was related to the presence of Ascomycetes rather than to tree species. This was especially true for larvae for which, though not mentioned by Heiss and Péricart (2007), *Fomes* species could be particularly important. Similarly, fungi like *Trametes* or *Stereum* which are known to host *Aneurus* species (Gossner et al. 2007; Heiss and Péricart 2007), tended to increase the abundance of *A. avenius*. Despite the fact that we could not test the effect of fungi at the piece-of-wood scale because fungi are often invisible or difficult to identify based solely on mycelium, the presence of fungi has probably more influence than the tree effect detected here, especially for the reproduction and the feeding of larvae.

Aneurus laevis was mainly found on decayed wood with dehiscent bark. The dehiscence reflects bark decomposition, which is strongly related to the degree of wood decay. We can therefore conclude that global decomposition was the most important factor for *A. laevis*. Contrarily to *A. avenius*, the abundance of *A. laevis* at the plot scale did not tend to be affected by a particular fungal species, which may mean that it has a less specialized diet than *A. avenius.* This could also explain the larger number of *A. laevis* specimens encountered in both study forests. At the plot scale, *A. laevis* seemed to be also sensitive to the surface area of deadwood, which confirmed the trends previously observed (Heiss and Péricart 2007). However, more generally, the effects at the plot scale were non-significant. Maybe these two species are too generalist to allow us bringing to light a specific factor to explain their abundance at the plot scale.

Aradus species were totally absent from Rambouillet and quite rare in Fontainebleau. Consequently, correlative analyses for these species were impossible to carry out and conclusions concerning the ecology of these species cannot be reached. However, several points can be mentioned.

First of all, despite the low abundance of *Aradus* species in Fontainebleau, they were reported mainly on *Fagus*, which was much more abundant in Fontainebleau than in Rambouillet. This difference could explain the absence of these species in Rambouillet.

According to Heiss and Péricart (2007), *A. conspicuus* is known to live under the bark of *Fagus* infested with fungi like *Polyporus*, *Trametes*, or *Fomes*. This species has also been reported on *Quercus, Populus, Tilia*, but less frequently, and even on *Pinus, Picea and Abies* (Heiss and Péricart 2007). In our study, we found it only on *Fagus*, especially on fresh snags or stumps. Gossner et al. (2007) found that *A. conspicuus* prefers larger dead wood structures, but in managed areas it can occur on smaller pieces of wood. In our study it was found only on pieces of wood from 5 to 30 cm in diameter.

Aradus versicolor was also found only on fresh dead beech, and mostly on standing trees or stumps of small to medium diameter. This species is known to live on *Fagus*, and also on *Betula*, *Quercus*, *Populus*, *Salix*, and *Platanus*, associated with fungi like *Coriolus, Trametes, Polyporus* or *Funalia* (Heiss and Péricart 2007).

Aradus brenskei seems to have different habitat requirements: we encountered it more often on large diameter (20–50 cm) senescent beeches infested by fungi. The species is associated with *Fagus* and *Populus* tree species that can be attacked by *Schizophyllum* or *Trametes* (Heiss and Péricart 2007).

According to our results and the previous litterature, *Aradus* species seem to depend on larger dead branches than *Aneurus* species, and that could explain their lower abundance in our study.

Implications for forest management and conservation

As reported by Siitonen (2001), most of the studies on the relation between deadwood attributes and biodiversity conclude that large dead trees at intermediate stages of decay are much more important than smaller, less decayed pieces. Our results on *Aneurus* species do not confirm this statement. These species seem to depend more on small diameter deadwood with different degrees of bark dehiscence rather than on larger pieces. This has also been confirmed by other authors for other organisms (e.g. Coleoptera and Diptera, Schiegg 2001). We also detected a strong effect of tree species on the abundance of *A. avenius*, with more individuals on oaks and hornbeam than on beech. This is in line with the results obtained for saproxylic beetles (Lassauce et al. 2012). In addition, in accordance with Gossner et al. (2007), we show that, at both the individual piece-of-wood and stand scales, deadwood volume is not the best descriptor for the abundance of Aradidae species though deadwood volume is generally thought to be a better predictor of species richness and abundance, even for cortical species (Väisänen et al. 1993; Schiegg 2001). However, these results are mostly restricted to boreal forests, whereas in temperate forests the relation is less clear (Lassauce et al. 2011). Furthermore, at the plot scale, Aradidae abundance is mainly correlated with the surface area of deadwood in our study. This seems logical since the small pieces of wood on which they depend present a higher surface/volume ratio than larger pieces of wood. As a consequence, for Aradidae, the surface area of small deadwood seems to be a better indicator of resource availability than does volume, at least at the plot scale.

Based on their habitat preferences, current forest management does not seem to be a threat for Aradidae abundance, in particular for the *Aneurus* species we studied. Indeed, whether in managed or unmanaged forests, fine woody debris are generally the most abundant (Gibb et al. 2005), and their quantity can sometimes be increased by forest management (Schiegg 2001). For example, *A. betulae* and *A. corticalis* are more often encountered in clearcut forest stands (Johansson et al. 2010) and are probably favored by woody residues left after clearcutting.

Furthermore, we found *A. conspicuus* and *A. versicolor* mainly on stumps. This result indicates that harvesting artifacts may efficiently serve as surrogate habitats for those species (Gossner et al. 2007).

However, in the context of an increasing demand for woodfuel, the absence of effect of forest harvesting on Aradidae biodiversity may seriously be questioned. Woodfuel harvesting is known to have a negative impact on biodiversity for different groups (Nordén et al. 2004; Jonsell 2007; Robertson et al. 2008), in particular when whole tree harvesting is applied. Indeed, woodfuel harvesting considerably reduces the amount of small dead wood in managed forests (Rudolphi and Gustafsson 2005) and may therefore be detrimental to populations of Aradidae (in our case for *Aneurus* species). This impact may be even more serious if woodfuel harvesting preferentially targets tree species that host the most Aradidae individuals (i.e. oak and hornbeam rather than beech for *Aneurus* species in our case). In addition, different species have different habitat requirements (for example *A. brenskei* seems to depend on larger pieces of wood) and may be affected differently by forest management.

Conservation of species demands knowledge on threshold values for different habitat parameters that are demanded for long term survival (Müller and Bütler 2010). *Aneurus* species are not or poorly found on deadwood with a diameter superior to 30 cm. However at the plot scale, the explanatory variables weakly explained abundance of species, and our results tend to show a linear relationship between abundance and explanatory variables as the surface area of dead wood. This is in contradiction with results from previous authors who found non linear biodiversity-volume relationships (see Müller and Bütler 2010 for a review). Then, thresholds values cannot be estimate from our dataset. Further studies are needed to determine variables which can explain abundance of Aradidae species. Estimate a threshold values for these variables would provide more precise management recommendations.

Our study has enhanced knowledge on Aradidae species, yet it is only a first step towards the comprehension of the mechanisms involved in their ecology. However, many parameters did not show significant effect. The sampling strategy considers the piece of wood of the plot rather than the whole community of Aradidae in the plot. Sampling strategies have to be modified and adapted to models with low abundances such as Aradidae. For Aradidae as for other saproxylic species, such knowledge is crucial to be able to adapt forest management to the species' requirements. Further research is needed to specify these requirements and to define conservation measures.

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