

Soil factors affecting density of three giant land snail species in different habitats of Dassa-Zoumè district (Central Benin)

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ABSTRACT

This study examines the environmental factors affecting the density of the exploited giant land snail species, *Archachatina marginata*, *Achatina fulica* and *Limicolaria flammea* in the Dassa-Zoumè district of Benin. Thirty plots of 30 m × 30 m were laid out, within four vegetation types (fallows, forest, woodlands and wood savannah). Inside each plot the numbers of each giant land snail species were counted, and soil characteristics were measured. ANOVA and generalized linear models (GLMs) with Poisson distribution were used to examine the influence of soil factors on the giant land snails. *A. fulica* has the highest mean density (507 snails/ha) while *A. marginata* has the lowest density (110 snails/ha). ANOVA showed no significant difference in density between habitat types for any species. The most parsimonious GLM model showed that the abundance of *A. fulica* was positively associated to the fine sands, fine silts and pH, while the interactions were negatively associated with the abundance of the species. The abundance of *L. flammea* was negatively associated with the fine sands, fine silts and pH, while the interactions were positively associated with the abundance of the species. As for *A. marginata*, the abundance was negatively associated with the fine silts, pH and litter, while the interactions were positively associated with the abundance of the species. The abundance pattern of forest molluscs is likely to be affected by different processes. Exploitation of these giant snails will affect their density, and further research is needed to establish appropriate levels of harvesting and habitat management.

Keywords: Benin, habitat, land snail, soil parameters

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INTRODUCTION

Land snails represent one of the most important groups of invertebrates in terrestrial ecosystems. In forest ecosystems, they contribute, as well as the other species, to soil production and calcium concentration of the soil, and are targeted to be very useful indicators of environmental conditions (structure and texture of the soil, safety and healthy environment).¹ Land snails are also involved in the plant litter decomposition process, as most species are considered to be consumers of decaying plant materials, including microbial decomposers such as fungi and bacteria.^{2,3} In West Africa, a majority of the regional snails are forest dwellers,⁴ and most regional forests are rapidly declining as result of human exploitation.⁵ This is particularly true for southern Benin, where forest habitats are patchily distributed into small, forested islands and have been continuously logged for agricultural development.⁶ Giant land snails face additional threats, as they are an important part of the local diet in Benin (*Archachatina marginata* and *Achatina fulica*). This occurs particularly in central Benin, where some people are full-time snail gatherers for human consumption. *Limicolaria flammea* are also ingested by the local population. This situation may explain the recent decline in availability of giant snails in the region (*Archachatina marginata* and *Achatina fulica*), due to over-collection and habitat destruction.^{7,8}

Despite the conservation challenge facing the terrestrial malacofauna, information on their biodiversity patterns from many parts of the world remain poorly understood. While there is good data from parts of East Africa,^{9,10} these are lacking for West African forests, other than in hard to access, grey literature. The high biological significance of these forests, the escalating human exploitation and the negative impact that human disturbance has on the snails in Benin suggests that there is the need for a detailed malacological investigation, especially of species subject to direct exploitation as food. Such information is vital for formulation of malacofauna conservation strategies and policy. As far as we are aware, this study represents the first detailed examination of relationships between giant land snail density and soil factors in Benin. The objectives were to determine the preferences of giant land snails in analyzing the combined effects of soil properties (pH, humidity of the soil, vegetation cover, clays, silts and sands), on total density and species abundance in different forest ecosystems of the Dassa-Zoumè district.

2. MATERIAL AND METHODS

2.1 Study area

Data was collected in the Dassa-Zoumè district, located at the centre of the Republic of Benin, at approximately latitude 7° 25' 49" and 7° 41' 21" N, and longitude 2° 6' 58" and 2° 25' 10" E (Figure 1). The study area belongs to the Soudano-Guinean transition zone defined by White,¹¹ and characterized by Soudano-Guinean climate with two seasons: a dry season occurring from March to October, and a rainy season from November to March. Mean annual precipitation is 1100 mm, with most rain falling between May and July. The mean annual temperature is 32°C. The landscape is dominated by outcrop vegetation (small forests and savannah), while the peneplain is covered by woodland and wood savannah dominated by *Sarcocephalus latifolius*, *Newbouldia laevis*, *Azelia africana*, etc. Fallows are less represented in the district. The fauna present in the outcrop vegetation consists of small mammals, including small carnivores such as the mongoose, genet and civet species and some reptile species, all of which prey on snails.¹²

2.2 Data collection

The abundance of giant land snails were investigated within 30 plots of 900 m², randomly installed at the vicinity of the Tangbe, Okemere and Tchachegou villages in the Dassa-Zoumè district. An exploratory survey was made and helped to identify the importance of the vegetation types in the prospected areas: woodlands, wood savannah, forest and fallows. As the snails were randomly distributed in the villages of study, care was taken to cover all of the four vegetation types identified in the study area (woodlands, wood savannah, forest, and fallows).¹³ The nearest habitat was 3 km from any house. Each plot of 900 m² was marked with pegs, delineated with a rope and GPS coordinates taken at the centre. The snails were collected from September to November 2010, within the plots using a direct search. This involved examining all potential microhabitats that could be accessed by eye within each plot, such as tree trunks, logs, deep litter, rock faces, etc.¹⁴ For the three species, the counts were made on adults and sub adults, as juveniles cannot be identified accurately. Alive specimens

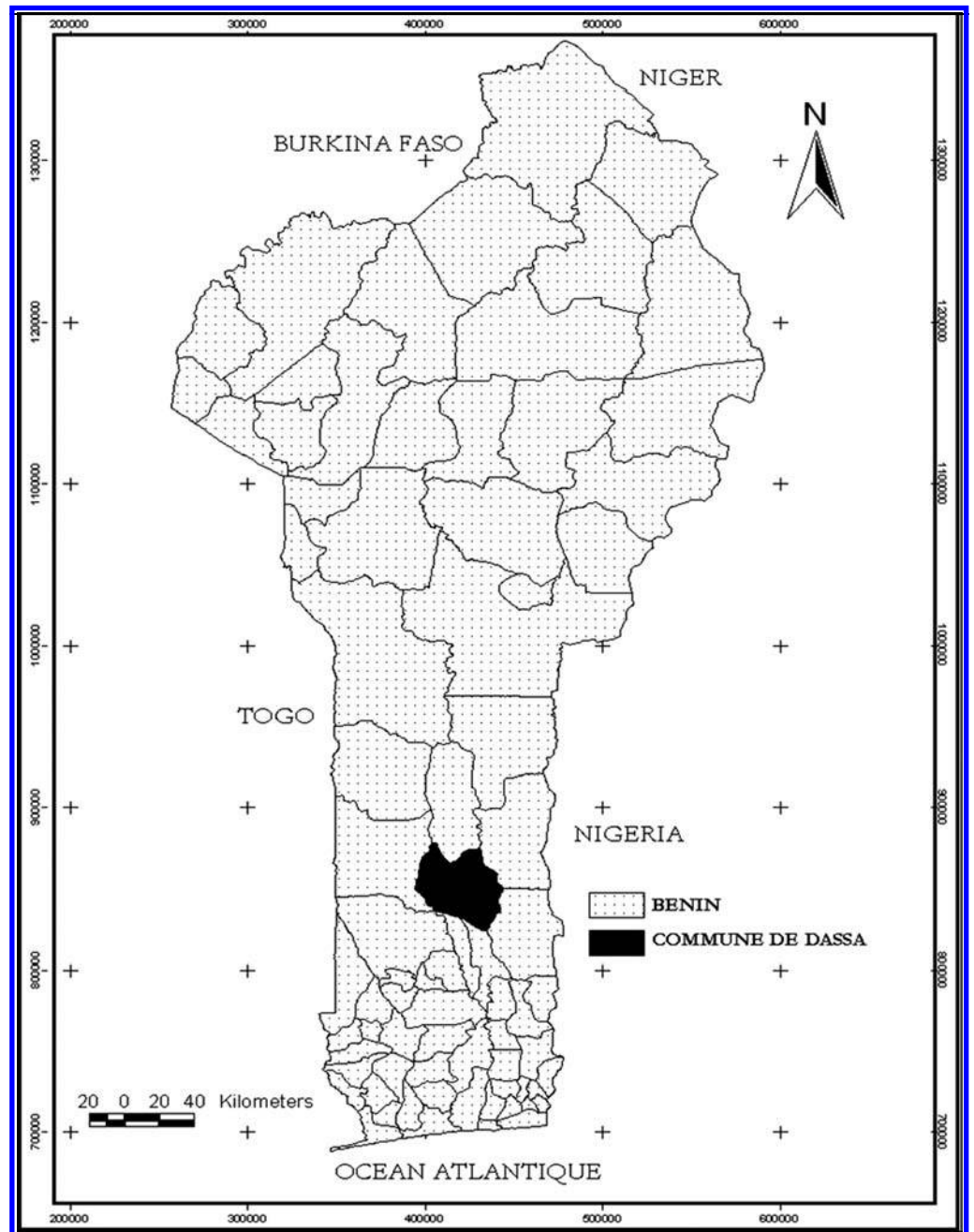


Figure 1. Benin map showing the Dassa-Zoumè district.

counted in the field and samples of dead specimens were carried to the laboratory for identification. Due to the importance of each vegetation type in the prospected areas, the numbers of plots differ. First, a vegetation map of the township has been used to identify the importance of each vegetation type in the study area. The map showed that the vegetation types do not have the same importance in the prospected areas. Thus, the random distribution of the plots was as follow: Tangbe (2 in forest, 2 in woodlands, 3 in wood savannah and 3 in the fallows), Okemere (3 in forest, 3 in woodlands, 3 in wood savannah and 1 in the fallows) and Tchatchegou (2 in forest, 2 in woodlands, 3 in wood savannah and 3 in the fallows). Within each plot, three randomly placed quadrats of 1 m² were installed from which litter was collected, sieved to remove any soil components, and weighed with a balance (0.05 g sensitivity). A sample of soil, 0 to 300 mm, was taken within each plot with an auger, transported in plastic bags to the laboratory at Faculty of Agronomic Sciences, University of Abomey-Calavi, to determine soil

properties, including texture, pH and moisture content. The granulometry of the soil was determined in four steps: soil attack with hydrogen peroxide at 10% (used to remove organic matter from the collected samples), upheaval of the mixture, successive withdrawal with a Robinson pipette (first the drawing of clay + fine silts + coarse silts 40 s after upheaval, then clays + fine silts 3 min 45 s after upheaval, then clay 6 h after upheaval). The washing of coarse particles (coarse and fine sands) using wet sieving. To calculate the humidity of the soil, the empty weight of the caps was determined, and the weight of the soil + cap (P₁), were kept in a steam room, at 105°C for 24 h. After weighting, the dry weight (P₂) was determined to calculate the humidity. The pH of each soil sample was determined by taking 20 g of soil and sieved. Then, 50 mL of distilled water was added and left for 2 h. A pH meter was used to measure the pH until a stable value of pH could be ascertained.

While our sampling method and design gave a quick and cheap way of assessing abundance, some caution should be applied to its use as a tool of conservation management. Data collection was carried out only during the wet season, so we cannot rule out the possibility that some density differences could be caused by the animals' seasonal movements between habitats.

2.3 Data analysis

The total number of individuals recovered per plot, is used as an estimate of abundance of each species and help to determine the density of the species.¹⁵ ANOVAs were applied to the abundance data (as individuals per plot) on each giant land snail species to determine vegetation type effects, using R for Microsoft Windows version 2.3.1.¹⁶ A log-transformation of abundance data was used to reach normality and variance homogeneity. To examine the influence of soil factors affecting habitat selection of giant land snails, generalized linear models (GLMs) with Poisson distribution for the count data¹⁷ were used. The response variable was snail abundance, while the predictors were the various measured soil attributes (% coarse sands; % fine sands; % fine silts; pH; % moisture content) and litter mass. The factors were considered as well as the interactions between the most significant factors. The estimate is the coefficient of each possible parameter to include in the model. The parameter clay and coarse silt were not included in the model due to the high correlations noticed with other parameters, such as humidity and pH (see Table 1). Thus, the models were established with the lasting parameters taking into account the experimental design and the random distribution of the plots across villages and habitat types. The connection of each species with the soil parameters, depend on its preferences. Model selection was conducted using a backward stepwise procedure, where we used Akaike's Information Criterion¹⁸ to remove parameters stepwise (factors were excluded if this improved the model fit by > 2 AIC units), and select the most parsimonious model with the best fit to the data.^{19,20} Colinearity among the predictor variables was investigated by examining the Pearson correlation coefficients (with their signs) between the measured variables (with the associated probabilities) (see Table 1). We performed most of our analysis using R for Microsoft Windows version 2.14.0.¹⁴

Table 1. Correlation between the measured variables. Pearson's correlation probabilities are shown, with associated significance levels.

	Clay	Coarse_sands	Fine_sands	Coarse_silts	Fine_silts	pH	Humidity
Clay							
Coarse_sands	-0.214 0.256						
Fine_sands	-0.661 0.000***	-0.056 0.77					
Coarse_silts	0.319 0.086	-0.279 0.135	-0.116 0.541				
Fine_silts	0.225 0.231	-0.168 0.374	-0.319 0.086	0.254 0.176			
pH	0.076 0.69	0.108 0.569	-0.077 0.686	-0.487 0.006**	-0.183 0.334		
Humidity	-0.403 0.027*	-0.204 0.281	0.120 0.529	0.411 0.024*	-0.084 0.657	0.077 0.686	
Litter	0.054 0.778	-0.054 0.776	0.131 0.491	0.003 0.989	0.329 0.076	0.047 0.807	-0.242 0.786

***: very highly significant **: highly significant *: significant.

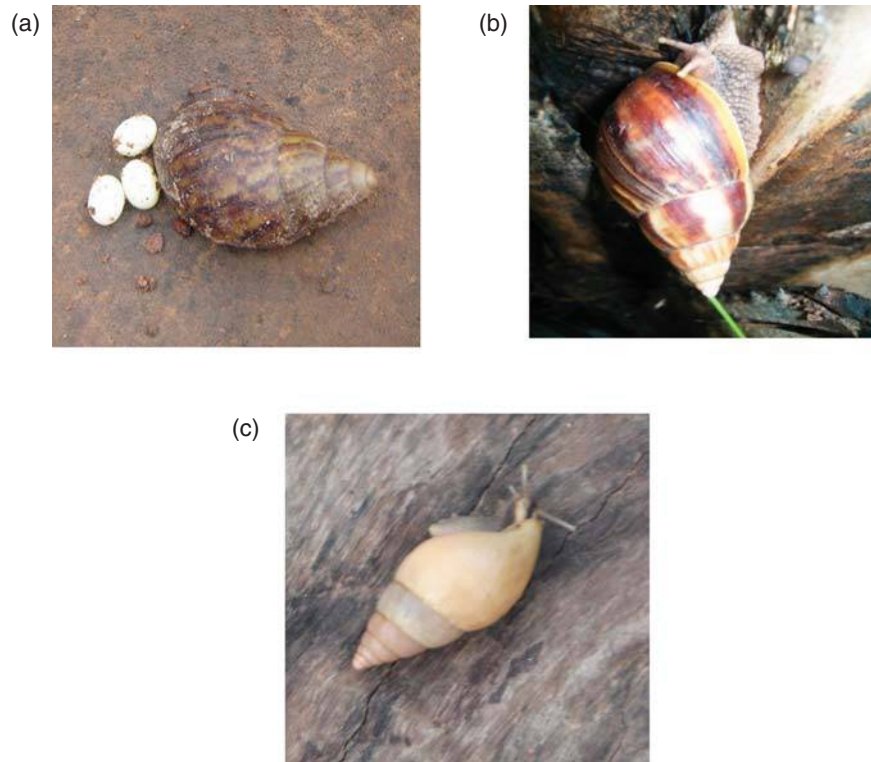


Figure 2. Land snail species (a) *Archachatina marginata* (b) *Achatina fulica* (c) *Limicolaria flammea*.

3. RESULTS

3.1 Giant land snail abundance

Three species of giant land snails were identified in the plots (Figure 2a, b and c). These species are: *Archachatina marginata* (Swainson, 1821), *Achatina fulica* (Bowdich, 1822) and *Limicolaria flammea* (Muller, 1774). *Archachatina marginata* is a snail species that presents many vertical scratches. The scratches on the shell have the appearance of a woven texture. This giant snail is primarily vegetarian. *Achatina fulica* is a snail species that presents a shell more lengthened than that of *Archachatina marginata*. It is a polyphagia herbivorous snail, i.e. it is not very demanding in consuming vegetables. *Limicolaria flammea* is a snail species smaller than the previously described species, but also presenting a lengthened shell. It is more herbivorous than the former two species. All three species are more active at night and reproduce better during wet seasons. Among the three species, *A. fulica* had the highest density, 507 snails/ha (Table 2, appendix 1), followed by *L. flammea* with a density of 490 snails/ha, while *A. marginata* had the lowest density with 110 snails/ha. The abundance of giant land snail species was recorded across different habitat types. We recorded no significant difference of the giant snail abundance across the different habitat types for *A. fulica* ($F = 0.01$; $df = 3, 29$; $p = 0.999$), *A. marginata* ($F = 0.17$; $df = 3, 29$; $p = 0.917$) and *L. flammea* ($F = 0.47$; $df = 3, 29$; $p = 0.703$). These results show that the extent of forest cover has no effect on these species.

Table 2. Estimate of the mean and standard errors of density in each habitat.

Species	HABITAT							
	Fallow		Forest		Woodland		Wood savannah	
	m	SE	m	SE	m	SE	m	SE
<i>Achatina fulica</i>	506.67	94.19	507.41	79.18	515.87	42.81	593.06	17.68
<i>Limicolaria flammea</i>	520	84.70	518.52	84.70	484.92	25.75	469.44	52.69
<i>Archachatina marginata</i>	92.55	27.80	77.78	27.96	116.67	11.22	119.44	12.19

m = mean. SE = Standard Error.

The results of soil analysis in the laboratory are as follows: pH ranges between 4.8 and 7.37, while humidity ranges between 8.72 % and 29.04%. For the granulometry, the coarse sands range between 2 % and 45%; the fine sands range between 17.25 % and 57 %; the coarse silts range between 1.5 % et 24.75 %; the fine silts ranges between 1.5 % and 25.25 %. Finally, the clay ranges between 11.75 % and 33.5 %.

3.2 *A. fulica* abundance as a function of soil characteristics

The relationship between the abundance of *A. fulica* per plot, and some soil characteristics were modeled (Tables 3 and 4). Comparison among 10 candidate generalized linear models (GLM) indicated the importance of coarse sands, fine sands, fine silts, pH, humidity and litter in affecting the variability of *A. fulica* abundance (Table 3). However, fine sands, fine silts and pH contributed to explaining such variability, as shown by the top ranked selected models ($\Delta\text{AICc} < 2$; Table 4, top panel). The most parsimonious model averaging (Table 3, bottom panel), clearly shows how the abundance of *A. fulica* was strongly affected by fine sands, fine silts and pH, accounting for the lowest value of ΔAICc . So, from this model the abundance of *A. fulica* was positively associated with the fine sands (0.188 ± 0.073), fine silts (0.247 ± 0.112) and pH (1.500 ± 0.588), while the interactions were negatively associated with the abundance of *A. fulica* (Table 3).

Table 3. Estimates for the most parsimonious model of ecological characterization for *A. fulica*.

Coefficients	Estimate	SE	Pr(> z)
(Intercept)	-7.156	3.755	0.056
E	0.188	0.073	0.010*
F	0.247	0.112	0.027*
G	1.500	0.588	0.010*
E × F	-0.002	0.000	0.000***
E × G	-0.028	0.011	0.014*
F × G	-0.025	0.017	0.151

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05. E: fine sands. F: fine silts. G: pH.

Table 4. Ten of the most parsimonious and global model for *A. fulica*.

Model	AICc	ΔAICc
E + F + G + E × F + E × G + F × G	258.84	0
F + G + I + F × G + F × I + G × I	266.30	7.46
D + E + G + D × E + D × G + E × G	269.15	10.31
D + E + I + D × E + D × I + E × I	269.44	10.60
D + E + F + D × E + D × F + E × F	270.86	12.02
F + G + H + F × G + F × H + G × H	272.96	14.12
G + H + I + G × H + G × I + H × I	273.62	14.78
E + F + I + E × F + E × I + F × I	274.34	15.50
E + F + H + E × F + E × H + F × H	274.60	15.76
D + E + H + D × E + D × H + E × H	275.10	16.26

D: coarse sands. E: fine sands. F: fine silts. G: pH. H: humidity. I: litter; The models were ranked by the corrected Akaike Information Criterion corrected for small samples (AICc). (ΔAICc = difference in AICc between the best and the actual model; the most parsimonious model is first).

3.3 *L. flammea* abundance as a function of soil characteristics

The abundance of *L. flammea* was modeled with soil characteristics as predictor variables (Tables 5 and 6). The 10 candidate generalized linear models (GLM), best models in predicting habitat use of *L. flammea* pointed out the importance of coarse sands, fine sands, fine silts, pH, humidity and litter (Table 5). Nevertheless, fine sands, fine silts, pH contributed to explaining such variability, as shown by the top ranked selected models ($\Delta\text{AICc} < 2$; Table 5, top panel). The most parsimonious model averaging (Table 5, bottom panel) clearly showed how the abundance of *L. flammea* was strongly affected by fine sands, fine silts and pH, accounting for the lowest value of ΔAICc . So, from this model the abundance of *L. flammea* was negatively associated with the fine sands (-0.041 ± 0.074), fine silts (-0.313 ± 0.118) and pH (-0.309 ± 0.618), while the interactions were positively associated with the *L. flammea* abundance (Table 5).

Table 5. Estimates for the most parsimonious model of ecological characterization for *L. flammea*.

Coefficients	Estimate	SE	Pr(> z)
(Intercept)	4.816	3.925	0.220
E	-0.041	0.074	0.578
F	-0.313	0.118	0.009**
G	-0.309	0.618	0.617
E × F	0.003	0.001	0.004**
E × G	0.005	0.012	0.645
F × G	0.037	0.019	0.046*

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05. E: fine sands. F: fine silts. G: pH.

Table 6. Ten of the most parsimonious and global model for *L. flammea*.

Model	AICc	ΔAICc
E + F + G + E × F + E × G + F × G	246.54	0
E + F + I + E × F + E × I + F × I	249.07	2.53
F + G + I + F × G + F × I + G × I	251.60	7.86
D + E + F + D × E + D × F + E × F	256.93	16.19
D + E + I + D × E + D × I + E × I	265.26	19.56
F + G + H + F × G + F × H + G × H	268.63	22.53
G + H + I + G × H + G × I + H × I	271.60	24.37
E + F + H + E × F + E × H + F × H	273.44	26.16
D + E + G + D × E + D × G + E × G	275.23	29.17
D + E + H + D × E + D × H + E × H	278.24	56.48

D: coarse sands. E: fine sands. F: fine silts. G: pH. H: humidity. I: litter; The models were ranked by the corrected Akaike Information Criterion corrected for small samples (AICc). (ΔAICc = difference in AICc between the best and the actual model; the most parsimonious model is first).

3.4 A. *marginata* abundance as a function of soil characteristics

The relationship between the abundance of *A. marginata* per plot, and some soil characteristics were modeled (see Tables 7 and 8). Comparison among 10 candidate generalized linear models (GLM) indicated the importance of coarse sands, fine sands, fine silts, pH, humidity and litter in affecting variability of the *A. marginata* abundance (Table 7). The soil parameters (fine silts, pH and litter) contribute to explaining such variability, as shown by the top ranked selected models (ΔAICc < 2; Table 8, top panel). The most parsimonious model averaging (Table 7, bottom panel) showed how the abundance of *A. marginata* was strongly affected by fine silts, pH and litter accounting for the lowest value of ΔAICc. Thus, the abundance of *A. marginata* was negatively associated with the fine silts (-0.342 ± 0.118), pH (-1.183 ± 0.461) and litter (-0.016 ± 0.013), while the interactions were positively associated with the *A. marginata* abundance (Table 7).

Table 7. Estimates for the most parsimonious model of ecological characterization for *A. marginata*.

Coefficients	Estimate	SE	Z value	Pr(> z)
(Intercept)	10.342	2.960	3.494	0.000***
F	-0.342	0.190	-1.795	0.073
G	-1.183	0.461	-2.569	0.010*
I	-0.016	0.013	-1.193	0.233
F × G	0.030	0.033	0.900	0.368
F × I	0.001	0.001	4.307	0.002***
G × I	0.001	0.002	0.750	0.453

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05. F: fine silts. G: pH. I: litter.

4. DISCUSSION

Forest destruction for agricultural purposes is a major source of biodiversity loss in Africa and many other species are on the verge of disappearing. In Benin, and especially in the Dassa-Zoumè district, the vegetation is cleared each year for the needs of agriculture.²¹ The local populations generally use fire to clean the vegetation before planting crops, which is likely to eliminate the forest-dwelling

Table 8. The ten most parsimonious and global model for *A. marginata*.

Model	AICc	Δ AICc
F + G + I + F × G + F × I + G × I	187.93	0
E + F + I + E × F + E × I + F × I	190.65	2.72
E + F + H + E × F + E × H + F × H	193.98	6.05
D + E + I + D × E + D × I + E × I	196.77	8.84
E + F + G + E × F + E × G + F × G	197.21	9.28
F + G + H + F × G + F × H + G × H	201.70	13.77
D + E + F + D × E + D × F + E × F	208.43	20.50
D + E + H + D × E + D × H + E × H	212.41	24.48
G + H + I + G × H + G × I + H × I	212.96	25.03
D + E + G + D × E + D × G + E × G	213.37	25.44

D: coarse sands. E: fine sands. F: fine silts. G: pH. H: humidity. I: litter; The models were ranked by the corrected Akaike Information Criterion corrected for small samples (AICc). (Δ AICc = difference in AICc between the best and the actual model; the most parsimonious model is first).

mollusc fauna. This could impact on the abundance of giant land snail species in their natural habitat. This study is the first documented data on these land snail species in Benin, specifically in the Dassa-Zoumè township. As there is no available data on the density of the same species in the country, the results have been compared to those of a study in Nigeria,²² where more species were encountered with higher densities. This comparison is relevant as Benin and Nigeria are bordering countries and share climatic conditions and species living in the different habitats.

The inventory is more critical with *A. marginata*, which has the lowest density of individuals found. This situation could be explained by the impact local inhabitants have on the habitat of the snails.²³ In comparison, studies in an oil palm agroforest in Egbeta,²⁰ together with studies elsewhere at the coastal forest of Tanzania documented from Nanganga forest,¹ recorded higher densities of these three giant land snails. These differences could be explained by culinary habits, which may differ between Beninese (especially people from the Dassa-Zoumè township) and East African people. Furthermore, the urbanization of the area we have investigated can explain the significant difference noted by comparing our data with other African regions. While increased disturbance levels might have indirect effects on survival,²⁴ these land snails are an important part of the local diet in parts of West Africa,²⁵ where some people are full-time snail gatherers.²⁶ The flesh of *A. marginata* and *A. fulica* is a very important source of nutrients. These species of snail are often harvested, both opportunistically when people are in the forest and during systematic collection, for personal consumption and commercial sale.²⁷ The flesh of *A. marginata* is particularly appreciated by the local inhabitants of many parts of Benin,⁸ especially in the Dassa-Zoumè district. This may account for its low abundance in the region.

An interesting finding of this study is that while various soil properties affect the density of these giant species, the different habitats, from wooded to very open do not. This may be due to the period of census (wet season) during which every habitat is wet and the snails may not have a preference. Moreover, given the status of *A. fulica* in particular as a pest in many parts of the tropical world, it appears that these species are pre-adapted to, at least partially, open habitats and can even survive in areas subjected to heavy human disturbance. While variation in density may depend partly on collecting pressure, the different associations with soil characteristics shown by each species show that there are ecological differences among them. According to our findings, disturbances at the soil surface may account for this, as was the case at the geomorphologically active sites. The need to preserve appropriate conditions for the estivation of these commercially valuable species would greatly strengthen the case for land use that protected other fauna and flora. The conservation of the fauna in the township is necessary and requires the concerted effort of all, including government officials, local communities and scientists. As no previous modeling studies of snail species have taken place, our data provides a baseline for future monitoring of the populations of the snail species and their relationships with the environment. Furthermore, this is an ongoing study and the further investigations will help to discover more about other soils characteristics that affect the abundance of these land snails.

CONCLUSION

Results from this study show *A. fulica* to be the giant land snail with the highest mean density in the prospected areas. In addition, ANOVA showed no significant difference in density among habitat types for any of these species. The most parsimonious GLM model showed that the abundance of *A. fulica*

was positively associated with the fine sands, fine silts and pH, while the abundance of *L. flammea* was negatively associated with these parameters. As for *A. marginata*, the abundance was positively associated with the abundance of the species. This could be very useful in the setting of conservation management for these species. Further studies are needed to widen our knowledge on the correlation of other soil parameters with giant snails occurrence and abundance.

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Authors' contributions:

IR designed and performed the fieldwork, analyzed and drafted the manuscript.

CAMSG gave conceptual advice, read and corrected the drafted manuscript.

BK gave conceptual advice and improved the drafted manuscript.

AEA gave conceptual advice, read, corrected the language and improved the drafted manuscript.

JTC gave conceptual advice and improved the drafted manuscript.

REFERENCES

- [1] Tattersfield P. Patterns of diversity and endemism in East African land snails, and the implications for conservation. *J Conchol.* 1998;2:77–86.
- [2] Bishop MJ. The Mollusca of acid woodland in West Cork and Kerry. *Proc R Irish Acad.* 1977;77:227–244.
- [3] Corsmann M. Die Schneckengemeinschaft (Gastropoda) eines Laubwaldes: Populations dynamik, Verteilungsmuster und Nahrungsbiologie. *Berichte des forschungszentrums Waldökosysteme, Reihe.* 1990;58:1–208.
- [4] Verdcourt B. The zoogeography of the non-marine Mollusca of East Africa. *J Conchol.* 1972;27:291–348.
- [5] Burgess ND, Clarke GP, Rodgers WA. Coastal forests of eastern Africa: status, endemism patterns and their potential causes. *Biol J Linn Soc.* 1998;64(3):337–367.
- [6] Sayer JA, Green AA. The distribution and status of large mammals in Benin. *Mammal Rev.* 1984;14(1):37–50.
- [7] Codjia JTC, Noumonvi R. Les escargots géants. Guide technique d'élevage. *J Hardouin.* 2002; B.E.D.I.M, FUSAGx. 2002; 5030 Gembloux.
- [8] Sodjinou E, Biaou G, Codjia JTC. Commercialisation des escargots géants africains (Achatines) dans les départements de l'Atlantique et du Littoral au sud-Bénin. *Ann Sci Agronomiques FSA/UAC, Benin.* 2003;12.
- [9] Martin K, Sommer M. Relationships between land snail assemblage patterns and soil properties in temperate-humid forest ecosystems. *J Biogeogr.* 2004;31(4):531–545.
- [10] Fontaine B, Gargominy O, Neubert E. Land snail diversity of the savanna/forest mosaic in Lope National Park, Gabon. *Malacologia.* 2007;49(2):313–338.
- [11] White F. *La végétation de l'Afrique. Adaptation française P. Bamps.* Paris: ORSTOM et UNESCO; 1986.
- [12] Kingdon J. *East African mammals: An atlas of evolution in Africa.* 3(C). New York: Academic Press; 1982:p.300.
- [13] White F. *La végétation de l'Afrique. Adaptation française P. Bamps.* Paris: ORSTOM et UNESCO; 1986. Coll. Recherches sur les ressources naturelles;20:384.
- [14] Tatterseld P. Local patterns of land snail diversity in a Kenyan rain forest. *Malacologia.* 1996;38(1–2):161–180.
- [15] Dajoz R. *Précis d'écologie.* Paris: Bordas; 1985;p.100.
- [16] R Development Core Team. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. Version: 2.12/2006.
- [17] Crawley MJ. *Statistics: An Introduction Using R.* UK: Wiley and Sons, eBook; 2011:125–154.
- [18] Akaike H. Information theory as an extension of the maximum likelihood principle. In: Petrov BN, Csaki F, eds. *Second International Symposium on Information Theory.* Budapest, Hungary: Akademiai Kiado; 1973:267–281.
- [19] Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol.* 2009;24(3):127–135.
- [20] Johnson JB, Omland KS. Model selection in ecology and evolution. *Trends Ecol Evol.* 2004;19(2):101–108.
- [21] Capo-Chichi Y. Monographie de la commune de Dassa-Zoumè. Programme d'appui au démarrage des communes au Benin. 2006. http://www.ancb-benin.org/pdc-sdac-monographies/monographies_communales/Monographie%20de%20DASSA.pdf. Accessed 22/08/2013.
- [22] Oke OC, Alohan FI, Uzibor MO, Chokor JU. Land snail diversity and species richness in an oil palm agroforest in Egbeta, Edo State, Nigeria. *Biosci Res Commun.* 2008;20(5):249–256.
- [23] Cobinnah JC, Vink A, Owunka B. *L'élevage d'escargots: production, transformation et commercialisation.* Wageningen: Fondation Agromisa; 2008:p.85.
- [24] Setsaas TH, Holmern T, Mwakalebe G, Stokke S, Røskoft E. How does human exploitation affect impala populations in protected and partially protected areas? – A case study from the Serengeti Ecosystem, Tanzania. *Biol Conserv.* 2007;136(4):563–570.
- [25] Memel JD, Otchoumou A, Kouassi DK, Dosso H. Inventaire, potentiel et répartition des escargots terrestres d'une forêt tropicale humide de Côte d'Ivoire: le Parc National du Banco (PNB). *Novapex.* 2008;9:119–127.
- [26] Agbelusi EA, Ejidke BN. Utilization of the African giant land snail *Archachatina marginata* in the humid area of Nigeria. *Trop Agric.* 1992;69(1):88–92.
- [27] Kouassi K, Otchoumou DA, Gnakri D. Le commerce des escargots (*Achatina achatina*), une activité lucrative en Côte d'Ivoire. *Livest Res Rural Dev.* 2008;20(4):1–16.

Appendix 1. Number of species of snails per plot and soil characteristics.

Plots	Species abundance			Habitat_type	pH	Humidity	Soil Characteristics (%)				
	<i>Achatina fulica</i>	<i>Limicolaria flammea</i>	<i>Archachatina marginata</i>				Coarse silts	Fine silts	Clays	Coarse sands	Fine sands
P1	44	36	9	woodlands	7.37	21.45	12.75	15.75	33.50	25.75	12.25
P2	5	42	3	fallow	6.63	22.12	11.75	13.50	19.50	42.90	12.35
P3	48	25	14	woodlands	6.33	23.16	15.75	19.25	20.50	36.00	8.50
P4	56	35	4	forest	6.08	12.80	10.00	9.75	17.00	34.00	29.25
P5	47	44	7	woodlands	6.48	13.13	6.75	9.75	17.25	34.50	31.75
P6	44	42	8	woodlands	5.78	22.81	19.75	20.50	19.00	38.75	2.00
P7	32	61	5	forest	6.03	16.67	9.50	11.50	15.00	38.25	25.75
P8	54	52	7	fallow	6.95	20.02	9.25	10.75	16.25	37.75	26.00
P9	12	56	7	fallow	7.12	12.44	1.50	4.25	13.50	35.75	45.00
P10	46	49	13	wood savannah	7.31	21.04	11.25	16.50	22.25	22.00	28.00
P11	49	44	12	forest	7.18	20.76	7.50	1.75	14.50	37.50	38.75
P12	60	40	8	wood savannah	5.28	24.48	24.75	17.00	18.00	36.75	32.50
P13	52	30	11	wood savannah	6.10	12.85	7.25	6.50	15.75	43.00	27.50
P14	50	65	10	wood savannah	6.12	24.21	9.50	12.25	25.50	25.75	27.00
P15	34	50	4	woodlands	4.80	19.43	12.75	25.25	28.00	17.25	16.75
P16	54	40	8	woodlands	7.22	29.04	9.25	5.75	20.50	52.00	12.50
P17	64	36	18	woodlands	5.26	12.52	20.75	20.00	20.25	27.75	11.25
P18	53	25	5	wood savannah	5.70	22.26	11.75	4.25	13.00	52.50	18.50
P19	52	54	15	wood savannah	6.45	8.72	6.50	6.75	15.50	40.00	31.25
P20	12	55	11	woodlands	6.40	11.52	5.25	6.50	18.50	28.50	41.25
P21	25	54	12	woodlands	6.33	11.01	9.00	3.25	14.75	35.25	37.75
P22	56	32	12	wood savannah	6.25	23.39	9.00	3.00	20.75	38.75	28.50
P23	56	43	10	woodlands	5.80	20.39	9.50	1.50	14.00	57.00	18.00
P24	55	35	8	fallow	6.84	16.81	11.50	8.75	18.25	28.50	33.00
P25	64	40	10	woodlands	5.61	19.13	9.75	5.00	14.50	51.75	19.00
P26	57	49	18	fallow	6.80	21.76	4.50	7.75	19.50	29.25	39.00
P27	58	43	12	wood savannah	6.30	19.66	12.50	4.75	13.25	48.75	20.75
P28	54	56	9	woodlands	6.18	15.93	6.75	1.75	11.75	52.35	26.40
P29	53	50	17	woodlands	6.25	10.06	4.25	1.50	12.75	42.00	40.50
P30	51	40	10	woodlands	6.15	19.22	12.75	4.75	19.75	42.50	20.25