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Research paper

From spears to automatic rifles: The shift in hunting techniques as a mammal depletion driver during the Angolan civil war

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ABSTRACT

Access to sophisticated hunting strategies increases in some political and economic contexts, such as during civil war episodes in Angola (Central Africa) in which there was a widespread distribution of automatic rifles to citizens. This facility favours the local people to slaughter larger animals, mainly during conflict gaps and in the post-war period. Herein, we conducted interviews with hunters to identify the hunting techniques used before, during and after the Angolan civil war in two different landscapes - savannah and forest. We collected information on techniques used by the hunter to approach, pursue and capture game species. Through a network approach and regression models we found that rifles introduced by the Angolan civil war magnify the spectrum of species caught from small-bodied to large-bodied species, and might induce a mammalian population abundance erosion. We also found a clear species-specific conjunct of hunting techniques, valuing the cost-benefit of each approach. The usage frequency of rifles was also higher in the savannah than in the forest. We reveal that changes over time for prey approximation and persecution techniques, which are possibly guided to attend the animal trade chain. Finally, these hunting technique changes has resulted in the predominance of individual hunting events with relatively low bushmeat shared between hunters, indicating a hunting pattern that contrasts with the historical hunting strategy based on collective expeditions. We can conclude that the shift in hunting techniques arising from the Angolan civil war induced a body-mediated decline in mammal diversity, causing their overwhelming annihilation.

1. Introduction

The development of sophisticated hunting strategies has enabled humans to be the most efficient hunters among all animals worldwide (Alves et al., 2018). Ancient and modern humans developed strategies and tools throughout history for capturing different animals living in virtually all environments, from small-bodied birds to mammoths and whales (Alves et al., 2009; Surovell et al., 2016). This behavior led to an overwhelming decline in many vertebrate populations and has been causing non-anecdotal extinctions of species, with overkills being documented since pre-history to modern times (Levi et al., 2011; Surovell et al., 2016).The use of technologies such as motorcycles and cars has also optimized the time for approach and pursuit of the prey, and its transportation to the hunting trade center (Souto, 2014). Moreover, in the last decades, occurred an increase in access to remote areas due to the improvement of the roads, leading to unsustainable hunting practices even in the most distant and inaccessible places worldwide (Benítez-López et al., 2017; Duda, 2017).

The adoption of gun hunting, which is much more efficient than traditional methods, has specifically been promoting greater success to catch the wildlife (Alves et al., 2009). Hunting trips in Cameroon using shotguns result in an average of 2.6 captures per trip, whereas hunting trips with snares and traditional techniques (smoke and others) seem less successful, presenting an average of less than 1.0 catch per trip. Shotgun hunting displays the largest catching efficiency (CPUE: 1.8 kg/h) compared to all other techniques (0.6 kg/h for trapping and 0.4 for smoking out) and enable capturing of larger prey (7.96 kg in average) than by traditional methods (2.2 kg average for smoking hunt technique and 5.9 kg average for snaring) (Duda, 2017). Empirical evidence indicates that switching from bow- to gun-hunting changes the hunting catch efficiency by approximately one order of magnitude. This is mathematically the same as having 10 times the human bow-hunting

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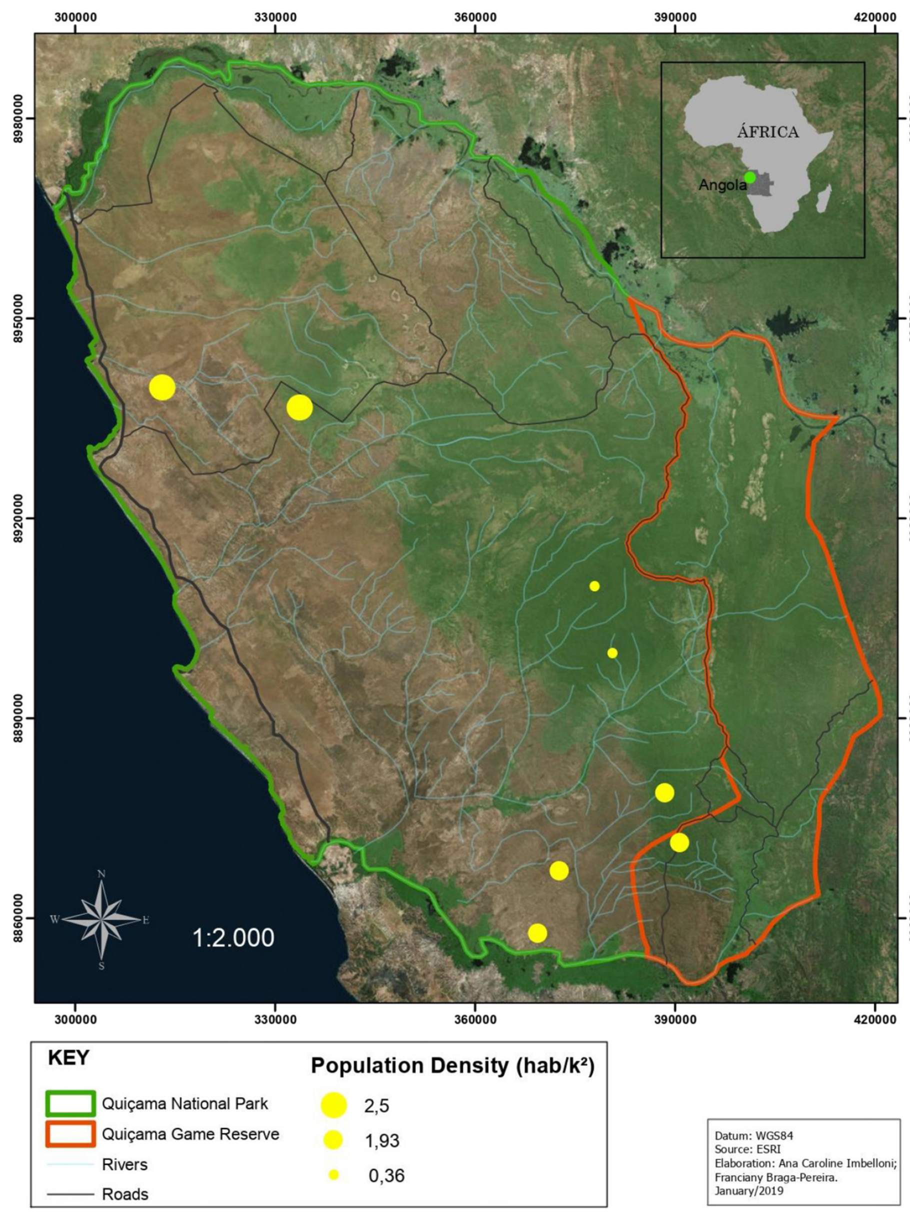

Fig. 1. Quiçama National Park (demarcated by the green line) and Quiçama Game Reserve (demarcated by the orange line). The yellow points represent the visited townships, which represent more than one human settlement. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

population or each hunter hunting 10 times as often. It shows that weapons technology is more important than the human population size per se in determining the spatial pattern of game depletion and capture per unit effort (Levi et al., 2011).

Access to automatic weapons becomes easier in some political and economic contexts. For example, during civil war episodes in which there is widespread distribution of rifles (such as AK-47) to the military and citizens (Craigie et al., 2010; Daskin and Pringle, 2018; Di Marco et al., 2014). Despite being carried out by local militias, automatic weapon distribution is usually fostered by foreign powers with secondary interests in the conflicts. Furthermore, the foreign role would not only be limited to support the execution of the war, but also in its origin (Guimaraes, 1992). Thus, the collapse of many populations of vertebrates during war conflicts should be treated as an international co-responsibility.

Accordingly, the Angolan civil war is considered one of the most destructive and longest civil wars in Africa, along with an important foreign role. Portuguese colonizers arrived in the West and Central African region at the end of the 15th century. The criterion for the territorial division of what today is Angola had only considered Portugal's interests, disregarding the territorial limits based on ethnicity and the cultural differences of the local Angolan population. As a consequence, Angolan guerrilla groups started a civil armed conflict for the leadership of the Republic of Angola after the Angolan conquest for independence from Portugal (on November 11th, 1975). During 27 years this conflict was divided into three periods of great fighting: 1975–1991, 1992–1994 and 1998–2002, and interspersed with fragile periods of peace (Guimaraes, 1992). However, the violent internal dynamics of the Angolan militias also had an international co-responsibility due to the massive foreign intervention during the conflict years. In this context, the once extinct Soviet Union and the United States of America respectively supported the MPLA (*Movimento Popular de Libertação de Angola*) and UNITA (*União Nacional para a Independência Total de Angola*), considered the two main parties that disputed leadership of Angola. These external relationships did not just foment the conflicts during the war period, but also modified the nature of the internal political dispute, and they became an intricate part of the initial encouragement of the Angolan war (Guimaraes, 1992; Saunders, 2008).

At its end, the Angolan civil war displaced over four million people, cost the lives of thousands more civilians, and also decimated wildlife populations (Breytenbach, 2001). For example, Angola elephants drew international alarm during the 1980s with reports of up to 100,000 elephants being exterminated in rebel-controlled territories (Breytenbach, 2001; Chase and Griffin, 2011). The elephants killed in the area had their ivory taken to the natural resources sector of each political party responsible for the capture, probably to be exchanged for war material (Dudley et al., 2002; Reeve and Ellis, 1995).

Although mammalian declines during the Angolan civil war have been shown for some sites, a chronological-scale analysis would strengthen our understanding of the effects on mammal declines due to the shift in hunting techniques boosted by this historical conflict. Thus, herein we identify the hunting techniques used before, during and after the Angolan civil war and the species targeted for each technique in two different types of landscapes of savannah and forest. We also discuss the impact of different techniques on the wildlife trade chain. Through a network approach using metrics and regression models, we expect to show that modern or non-usual hunting techniques introduced by the Angolan civil war promoted a sequence of mammalian erasure, from large-bodied animals to the persistent small-bodied species during a long-lasting event of human conflict.

2. Methods

2.1. Study area: landscape and social context

This study was carried out in the Quiçama National Park and neighboring Quiçama Game Reserve, which together have an extension of 960,000 ha (9°09′ to 10°23′ S, and 13°09′ to 14°08′ E) representing the main conservation area in Angola. We selected sites in forest (n = 4) and savannah (n = 4) landscapes (Fig. 1). The human population in the sampled areas are not legally authorized to live and hunt there (Braga et al., 2017). Most of the population is native to the study area, belonging to the Ambundo ethnicity. However, the area further north of the park also contains residents from eastern Angola (Chokwes and Ganguelas ethnicity) where armed conflicts were more intense resulting in emigration (Redinha, 2009). In these human communities, the main access to knowledge is oral exchange of information, since they do not have access to the internet and television programs.

2.2. Ethics statement

This study was registered in the Plataforma Brasil, which is a Brazilian national and unified database of research records involving human beings and obtained approval by the Research Ethics Committee of the Health Sciences Center of the Federal University of Paraiba (CEP/CCS/UFPB; CAAE 59846816.3.0000.5188). This study was also authorized by the Environmental Ministry of Angola (*Ministério do Ambiente de Angola*) based on license number 148INBAC.MINAMB/2016. We confirm that the field studies did not involve handling of any specimens, but only records via interviews (non-invasive sampling). This work was not submitted to an Institutional Animal Care and Use Committee (IACUC) or equivalent animal ethics committee because the data were all based on interviews. We also received a municipal authorization from the mayor of Quiçama via license number 017/GAB.ADM.M.Q/2017.

2.3. Data gathering: Interviews, compilation and species body size

We collected the data via semi-structured interviews to obtain information about hunting techniques and target mammal species (Bernard, 2006). The entire area was visited from January 2014 to January 2015 to carry out a prior survey of the species richness and distribution. Next, data were collected in specific communities from January to April 2017 selected to attend: i) areas in savannah and forest; ii) areas which received war refugees from Eastern Angola and areas which did not receive refugees.

Interviews were conducted with experienced local hunters to acquire information, as chosen by the snowball sampling technique (Bailey, 1994). This approach consists of one hunter indicating another, who in turn indicates one more, and so forth. There was previous personal contact with key informants and the first author to establish a trust relationship between them in order to reduce potential problems of testimonial redundancy and other problems caused by the snowball method. This was important because the quality of the referring process is naturally related to the quality of the interaction (Noy, 2009). This confidence generated good interviews and ensured that all experienced hunters in the areas were selected, and not just those who think similarly and relate more with the previously interviewed hunters.

A total of 115 informants (113 men and 2 women) were selected ranging from 20 to 80 years-old. During the interviews we asked the hunters to: i) list the technique used to capture each specimen pre, during (when the rifles were distributed to the citizen) and post-war (when rifle use was prohibited); from this we could calculate the number of times (frequency) each technique was mentioned in the study. (ii) indicate which set of target species were more selected during the war.

The data of relative abundance estimate of prior to (before 1975), during (from 1975 to 2002) and after the Angolan civil war (after 2003) in Quiçama were obtained from (Braga-Pereira et al., 2020). Thus, we compered the abundance values (Supplementary material, Fig. A1) and calculated the Delta Abundance (Δab), defined as the species-specific difference in abundance between the pre- and post-war periods. We sourced the information on the body mass and trophic level of each species from Jones et al. (2009). Thus, all mammal species were classified into seven functional groups based on Wilman et al. (2014) being ranked in an energetic stratum of modal dietary patterns as follows: (1) folivore < (2) frugivore < (3) granivore < (4) insectivore < (5) myrmecophage < (6) mesocarnivore < (7) hypercarnivore. We then weighted the proportion of each major dietary mode of any given species by these energetic levels based on Bogoni et al. (2018) (e.g., if the Tragelaphus oryx population consumes 30% fruit and 70% grass, its trophic level would be 2.7 (i.e. $(0.3 \times 2) + (0.7 \times 3)$).

According to Alves et al. (2018) and Ferreira-Fernandes (2014) each of the techniques mentioned by local peoples were described and categorized as: (i) the purpose (approach, pursuit or capture); (ii) capture autonomy (active and passive); (iii) lethality (lethal and non-lethal); (iv) species selectivity; and (v) abundance of captured specimens (individual and collective). Regarding autonomy, it is possible to distinguish active techniques when the presence of the hunter is required at the captured moment (firearms or harpoons). The passive technique is defined as when capture is performed through traps, without necessarily requiring the hunter's presence at the captured moment, as they may seek their prey after a predetermined period.

2.4. Data analysis

2.4.1. Network topology

We first utilized descriptive statistics to depict the hunting techniques used in the Quiçama meta-region in the pre, during and post period of the Angolan civil war. Next, we analysed the topology of the weighted two-mode technique per species networks and for each evaluated period in which a set of nodes representing hunting techniques is connected to another set of nodes representing the hunted species. In doing so, we show the interactions of techniques-frequency per species topologically for each temporal milestone period (i.e. pre-, during-, and post-war). Furthermore, we also calculated one quantitative metric for each historic period of Angolan civil war: (a) modularity,

Table 1
Usage frequency (UF) and categorization of all techniques registered as being used in the Quiçama National Park and the Quiçama Game Reserve pre, during and post-war regarding Purpose APP: approach; PUR: pursuit; CAP: capture. Capture autonomy - AC: active; PA: passive. Lethality LE: lethal; NL: non-lethal. Selectivity S: specific; R: random. Amount of captured specimens I: individual; C: collective.

Technique	UF pre-war (before 1975)	UF during-war (from 1975 to 2002)	UF post-war (after 2002)	Purpose	Lethality	Autonomy	Selectivity	Amount
Follow prey tracks	286	625	625	APP	NL	AT	S	I/C
Dogs	163	418	418	APP	NL/LE	AT	S	I/C
Waiting	74	338	338	APP	NL	AT	S	C
Net	264	132	107	APP	NL	AT	S	C
Bait	114	128	128	APP	NL	PA	S/R	I/C
Simulacrum	25	25	25	APP	NL	AT	S	C
Fire to make pasture	14	14	14	APP	NL	AT	R	C
Fire to drive animals away	14	9	6	APP	NL/LE	AT	S	I/C
Shoot the leader	0	3	0	APP	LE	AT	S	C
blocks with pointed irons	2	2	0	APP	NL	PA	S	I
Obfuscate	1	1	5	APP	NL	AT	S	C
Car	0	20	0	PUR	NL	AT	S	C
Helicopter	0	10	0	PUR	NL	AT	S	C
Motorbike	0	0	40	PUR	NL	AT	S	I
Automatic rifle	5	746	2	CAP	LE	AT	S	I/C
Spear	739	122	285	CAP	LE	AT	S	I
Stick	280	240	245	CAP	LE	AT	S	C
Run over	0	22	27	CAP	LE	AT	S	I/C
Bow and arrow	150	5	0	CAP	LE	AT	S	I
Throw objects	177	322	327	CAP	LE	AT	S	I
Shotgun	0	0	96	CAP	LE	AT	S	I/C
Snare trap	667	552	405	CAP	NL/LE	PA	R	I
West snare trap	0	156	232	CAP	NL	PA	R	I
Poison	35	50	55	CAP	NL/LE	PA	R	C
Metal snap trap	0	0	119	CAP	NL	PA	R	I
Squirrel trap	23	15	30	CAP	LE	PA	S	I
Monkey snare trap	179	160	171	CAP	NL/LE	PA	R	I
trap with rifles	0	41	0	CAP	LE	PA	R	C
Monkey cover trap	10	5	5	CAP	NL	PA	S	C
Hole	5	3	0	CAP	NL/LE	PA	R	I/C
Stone trap	10	3	0	CAP	LE	PA	R	I/C

and three qualitative (binary) metrics: (b) average degree; (c) connectance; and (d) nestedness (Boccaletti et al., 2006).

We tested the Modularity (M) to verify the species-specific use of hunting techniques which quantifies the inclination of the nodes to cluster into cohesive groups which are more connected among themselves than with other parts of the network. We analysed the Connectance (C) to check when there was a greater number of techniques being used to capture a greater number of species, which represents the relativized number of interactions observed by all possible interactions (Boccaletti et al., 2006). Lastly, we analysed the Nestedness (N) to check if certain species are only captured by some specific techniques, and which measures the degree by which the nested network shows a possible hierarchical pattern (Almeida-Neto et al., 2008).

We used Newman's metric (Newman, 2004) for modularity, comparing its empirical value with a benchmark distribution of modularity values based on an ensemble of 1000 theoretical matrices created by a null model in which species-hunting technique degrees (links) range between zero and the mean of the degree of the empirical network. Significance ($p \leq .05$) was based on the location of the observed M concerning a 95% confidence interval derived from the null model (Bascompte et al., 2003). We used the NODF metric for nestedness, which ranges from zero (when the matrix is perfectly non-nested) to 100 (when the matrix is perfectly nested) (Almeida-Neto et al., 2008). We also compared the NODF value of the empirical network with a benchmark distribution generated by 1000 theoretical matrices generated by a null model based on a probability matrix (null model 2 of Bascompte et al., 2003) and adopted the same aforementioned criterion for M significance. Network analyses were performed in R ver. 3.5.3 (R Core Team, 2019) based on the *bipartite* (Dormann et al., 2008) package.

2.4.2. Generalized linear models

We used generalized linear models (GLM) to disentangle the influence of predictors on the rifle use frequency and abundance depletion. In doing so, we considered an additive model to understand the rifle use frequency containing the predictive variable as follows: (i) habitat type (savannah or forest); (ii) species body mass; (iii) species energetic level; and (iv) game target species. Thus, the model formula was: rifle use frequency ~ factor(habitat) + species body mass + energetic level + target specie. We used Poisson distribution given that the rifle use frequency consists of count data. We considered a model with the follow predictive variables to understand the abundance depletion: (i) rifle use frequency; (ii) species body mass; and (iii) species energetic level. Thus, the model formula was: abundance depletion ~ rifle use frequency + species body mass + species energetic level. We observed overdispersion of abundance decline data via plot diagnostic and therefore we used quasi-Poisson distribution. We also used body mass data re-scaled via a $\log_{10}$- transformation due to the variation in numerical magnitudes.

We analysed the models quality based on the R^2 only considering models with variance-inflation factor (VIF $<$ 2). We used a Spearman correlation coefficient which measures a linear dependence between two variables (x and y) to understand the relationship between predictive variables of each model, with a significance level of 5%. The magnitude of the correlation effect is represented by correlation coefficients which take values from -1 to $+1$, in which values from 0.1 to 0.3 are weak; those from 0.31 to 0.7 are moderate; from 0.71 to 0.9 are strong; and correlations > 0.9 are considered very strong (Spearman, 1904). The models were also plotted based on their respective best continuous predictive variable. All analyses were performed in R ver. 3.5.3 (R Core Team, 2019) based on the *vegan* (Oksanen et al., 2013) and *rms* (Harrel Jr, 2018) packages.

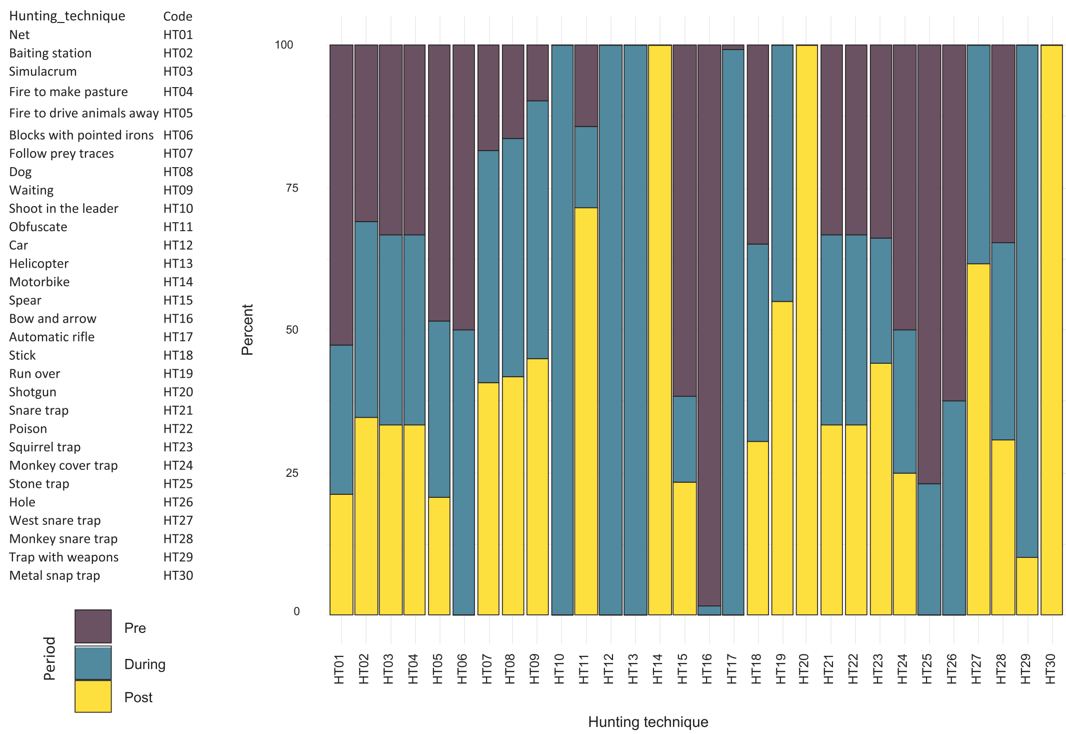

Fig. 2. Percent of techniques used before, during and after the Angolan civil war.

3. Results

3.1. *Frequency of hunting techniques used pre, during and after the Angolan civil war*

We recorded 30 hunting techniques of human-prey approximation and pursuit, and prey captures (Table 1), changing largely across the pre- and post-civil war event. Some techniques were used with similar frequency across all periods considered (e.g., snare trap and stick). However, other techniques were more frequently used in certain periods. We can highlight the spear, bow-and-arrow, poison, squirrel trap and net among the techniques with higher species capture in the pre-war period (Table 1; Fig. 2).

The war period counted 99.3% and 90% of the cases in which rifle and trap-with-rifles had been used, respectively. The practice of shoot-the-leader, and also the use of a car and helicopter were mentioned only for the war period. On the other hand, some techniques have their use restrict to the post-war period, namely pursuit via motorbike, and capture via shotgun and metal-snap-trap (Table 1; Fig. 2). The automatic rifle was widely displaced during the civil war and used to capture the greater richness of specimens in this period. There was an increase in the use of the wire rope trap during the war, which is a technique brought by migrant peoples from eastern Angola to the Midwest of the country, and were responsible for capturing medium- to small-bodied mammals which use shrub fragments in the savannah as a refuge (Fig. 3). There was a rifle collection from the citizens at the end of the conflicts, and introduction of two new techniques of using metal snap traps and shotguns. All hunting techniques are further described in the Supplementary material.

3.2. *Network topology and metrics*

Our network approach showed that the modularity (M) in pre- and during-war was numerically lesser than the post-war period [$M_{pre} = 0.43$; $M_{dur} = 0.42$; $M_{pos} = 0.45$] (Fig. 4A). However, we found a significant difference between empirical modularity and the respective null models for all analysed periods [$M_{pre\_null} = 0.12$; $p < .001$; $M_{dur\_null} = 0.12$; $p < .001$; $M_{pos\_null} = 0.12$; $p < .001$] (Fig. 4A). Moreover, modularity showed that there were three groups of mammal species depleted by seven hunting capture techniques in the pre-war period; for example, spotted hyena and african wild dog were quasi-exclusively slaughtered by poison (Fig. 4B). The network modularity induced by the more pervasive hunting techniques during the war period showed three mammal groups, mainly depleted via rifle and snare trap (Fig. 4B). The post-war period modularity was characterized by five groups of hunting techniques without the presence of rifles (Fig. 4B).

We found small connectance (C) for all periods, increasing numerically during the war period [$C_{pre} = 0.22$; $C_{dur} = 0.30$; $C_{pos} = 0.25$] due to the increase in the number of techniques used, as well as the number of species which were captured by the informants. Network nestedness (N) was increased during the civil war [$N_{pre} = 32.2$; $N_{dur} = 46.2$; $N_{pos} = 24.1$] as the rifles and snare traps are overwhelmingly responsible for mammal capture, irrespective of body size. However, nestedness did not presented statistical significance when compared with expected at random [$N_{pre\_null} = 29.5$; $p = .21$; $N_{dur\_null} = 38.44$; $p = .02$; $N_{pos\_null} = 29.6$; $p = .97$] (Fig. 4A).

3.3. *Regression model*

The model explained 25% of data variation regarding the rifle use frequency ($R^2 = 0.25$, $p < .001$, VIF = 0.25), revealing that species energetic level (i.e. penalizing the species with low energetic level more, such as grazers and granivores), and game target species are responsible for determining the intensity of rifle use during the Angolan civil war. Moreover, the intensity of rifle use is conditioned by the habitat type, being higher in the savannah when compared to the forest (Fig. 5A; Supplementary material, Fig. A2). We found the largest z-value in magnitude (considering the rule of thumb is to use a cut-off value of 2, either positive or negative) for habitat, target species and energetic level variables (in this order of importance), which indicates that these χ-variables are significant and presented a p-value less than 0.01 (Supplementary material, Table A1). The spearman analysis showed a negligible correlation between all the predictive variables of

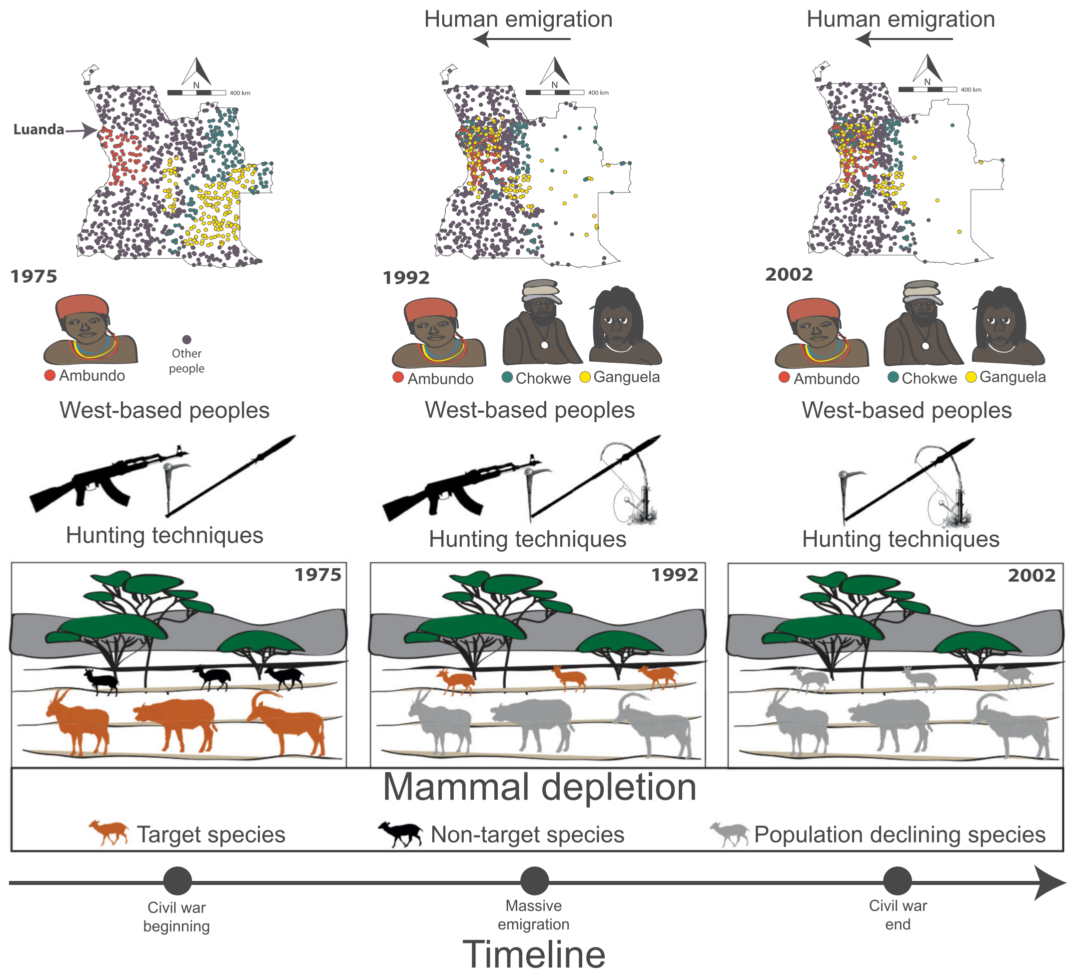

Fig. 3. At the beginning of the war in 1975, large-bodied species (in orange) were hunted, mainly slaughtered by rifles, and so began to suffer population decline. People from eastern Angola (Chokwes and Ganguelas) started to migrate more intensely to Quiçama in 1992. They used wire traps to slaughter medium-sized species which took refuge in the bushes. Large and medium-sized species had their populations depleted by the end of the war in 2002. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the model, except for the correlation between body mass and target species ($R = 0.79$), indicating that larger species are perhaps the main hunting targets of the informants (Supplementary material, Fig. A3).

The abundance decline model was 55% explained by our prior model ($R^2 = 0.55$), showing a positive relationship between body mass and abundance decline (Supplementary material, Fig. A4), which indicates that the largest species suffered a greater decline in their abundance. In addition, species with higher energetic levels (carnivores) showed a higher decline in their abundance. Finally, we found a relationship between the use frequency of the rifle and the abundance depletion (Fig. 5B). We found the largest z-value in magnitude (considering the rule of thumb is to use a cut-off value of 2, either positive or negative) for all predictive variables, which indicates that these χ-variables are significant and presented a *p*-value less than 0.01 (Supplementary material, Table A1). The spearman analysis showed a moderate correlation between body mass and rifle use (0.35), indicating a possible tendency for the rifle to have been used more for larger species, and a negligible correlation between the other predictor variables (Supplementary material, Fig. A5).

4. Discussion

4.1. Implications of the shift in hunting techniques during the Angolan civil war

Our main results showed that there was a replacement of the traditional hunting techniques to a prevalence of firearms being used along the Angolan civil war in Quiçama, and this correlate to the depletion of mammal fauna, notably large mammals. Modularity increased in the post-war period because large-bodied mammal populations became a pale shadow of their former populations once depleted; thus, some post-war techniques were employed for less specific mammal groups, increasing the modular behavior of our hunting technique-species network. Moreover, the observed modularity for all temporal periods was approximately four times higher than expected at random. This issue denotes a clear species-specific conjunction of hunting techniques, valuing the cost-benefit of each approach. However, specific techniques were more applied in the pre-war period than during the war to capture small mammals (i.e. with a stick and monkey cover trap), and Spotted hyenas and African wild dogs by poison. Thus, the modularity increases in the post-war period can be explained by capturing the target species (usually traded animals) with a shotgun, metal snap or snare traps, rifles to capture elephants, poison to kill carnivores, and simpler and cheaper techniques for non-traded species. The rifle use to catch elephants in the post-war period was registered for a few hunters who illegally kept the automatic weapon due to the greater difficulty in obtaining ammunition and the concern of being seen hunting with a prohibited weapon.

The connectance increased during the war because there was an increase and easier access to automatic weapons and the eastern wire trap; therefore, the range of slaughtered species was enlarged irrespective of body size. On the other hand, once rifles were collected post-

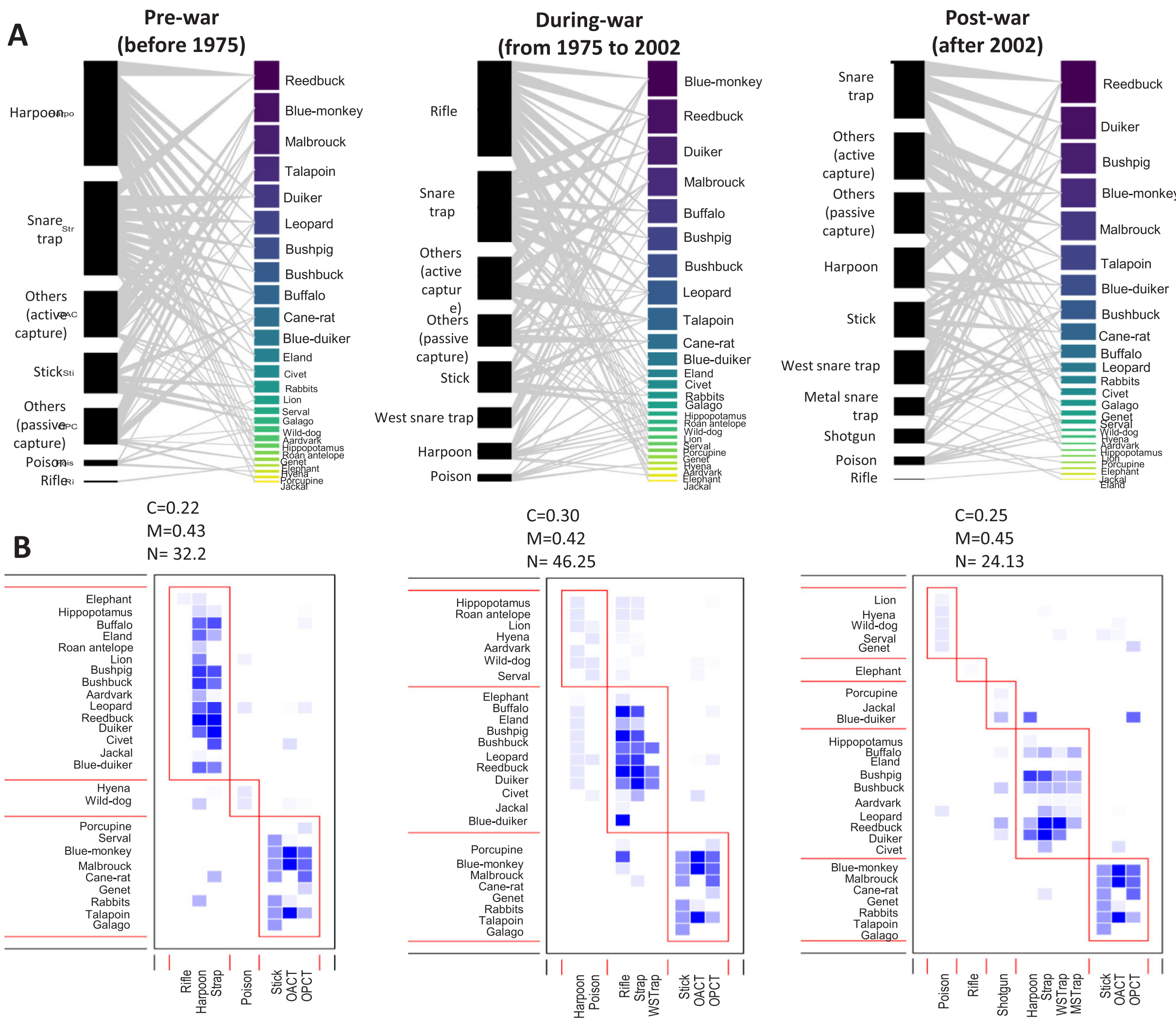

Fig. 4. (A) Topology of the total network by technique for pre-, during- and post-war years to evaluate the usage diversity of each technique per species in Quiçama, Angola; and (B) Modularity pattern for pre-, during- and post-war years.

war from the citizens by the Angolan government, the available hunting techniques to catch larger mammals (e.g., antelopes and bushpigs) became shotguns, metal snap and snare traps, and smaller specimens (which are not the main target) are captured by simpler and lower-cost techniques. The fact that fewer specimens are captured with a shotgun during the post-war period than with a rifle during the war years could be associated also due to higher shotgun prices and its ammunition when compared to the prices of the rifles and its ammunition during the war period.

The nestedness increases with network complexity expressed in terms of species richness and connectivity (Allesina and Tang, 2012). Thus, the network nestedness also increased during the war. More specifically, this increase is because the rifle and snare trap are overwhelmingly responsible for mammal capture, irrespective of body size, including large species such as elephants (only with rifles), eland, and red buffalo, which would be difficult to capture through other hunting techniques. The stability of the network would be negatively affected by nesting of the matrices (Allesina and Tang, 2012), which in the case of this study means that some species would no longer be captured in the absence of the automatic rifle and snare trap, at least by some hunters. Regarding this, some seminal studies showed that medium-sized mammals are significantly more vulnerable to snaring than to other techniques, including shotguns (Fa and Garcia Yuste, 2011; Noss, 1995).

Our regression models showed that the use of rifles could be associated to mammalian population abundance erosion, affecting species of larger and smaller body masses. However, although all species were shot with rifles, we observed that larger species were more captured with this technique by the Spearman analysis. For this reasons, we believe that the result obtained by the GLM in which the body mass did not have an effect on the frequency of the rifle use may have been skewed. This may happened because first, the rifle was associated to elephant hunting (the largest species among all game species) by few informants, which in turn may happen because: i) elephant slaughter is considered dangerous and only few fearless hunters can kill the animal; ii) maybe some hunters did not want to say in the interview that they slaughtered an elephant, worried about future criminalization. Secondly and contrastingly, because medium-sized antelopes had a high rifle use frequency. Therefore, the higher frequency of rifle usage could also partly explains the major decline in the larger species abundance. However added to this we should also consider that large species generally exhibit lower fecundity rates, larger home ranges and lower population densities (Cardillo et al., 2005). Therefore, they are more affected by external influences to their population. The fact that carnivores have shown a major decline in their abundance may directly be a result of the poaching action due to the capture of the own carnivore individuals, and indirectly because of the capture and consequent reduction of their prey.

Rifles were used more frequently in the savannah when compared to the forest in this study. Rifle use could be more efficient in open areas

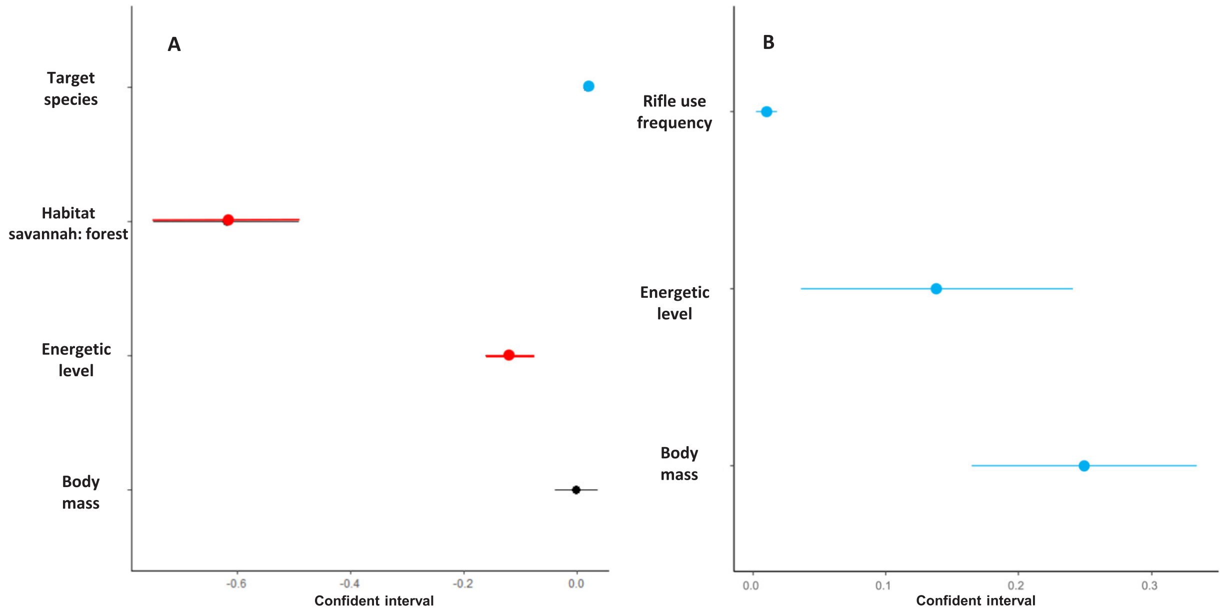

Fig. 5. Coefficient estimates (confidence intervals of ± 95%) showing the magnitude and direction of the relation of different variables on (A) automatic rifle frequency and (B) mammal abundance depletion. The blue and red symbols respectively represent positive and negative significant effects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

such as savannah as there are no physical barriers like trees and the hunter can see for a distance and reach the target animal more efficiently (Braga-Pereira et al., 2020). Therefore, the hunting impact in savannahs could potentially be higher. Furthermore, there was an increase in the use of the wire rope trap in this landscape during and post-civil war conflicts; a technique brought by migrant peoples from eastern Angola to the Midwest of the country where the research was conducted. Rifles were also mainly used in the savannah during the first years of the civil war (1975–1992) for slaughtering large animals because these animals could not penetrate the bush patches of the landscape, and so they were more exposed and hit by rifle shot. In contrast, medium- and small-bodied animals generally use the bush patches to hide from the hunters. As large animals were first depleted and shooting an animal which is in the bush is more difficult, the snare-trapping technique brought from the East was frequently used and responsible for capturing medium- to small-bodied mammals which were hiding in shrub fragments.

In addition, the traps brought by emigrants were responsible for reducing wildlife in the area not only by the capture per se, but also because once this snare holds the animal by its locomotor members, the trapped animal would make noise, signalling threats to other animals. This causes other individuals to perceive the danger and flee from the area. However, the snare trap captures the prey by haging, killing it quickly, and making it impossible for the captured animal to signal the threat to others. Some hunters did not kill the animal immediately when finding it alive in the metal snap or snare trap, waiting for it to die from bleeding (when caught by metal snap trap) or by hanging (when caught by snare trap). This is because the hunter does not want to waste ammunition on a trapped animal that will die later. In the case of felines, which will have their fur traded, it prevents their fur from being damaged by shooting or from harpoon perforation, and so, aggregated a good price to the four- it is also why the poison technique is often applied to kill carnivores. Another important aspect is that many weapons used in warfare, such as the AK-47, are not suitable to shoot game animals. This fact, coupled with the poor hunter skill in weapons handling, implies that many animals are injured but do not die instantly, and so are able to flee and are therefore not captured.

4.2. Techniques for approximation and persecution employed in Angolan civil war

According to our results, following prey tracks (e.g., tracking, faeces or smell) is the most used technique for approximation in the study region, and it is mainly easier to catch those species which usually pass through the same pathway (*Philantomba monticola*) or use the same latrine (*Civettictis civetta*) by this technique. The practice of following prey tracks is adopted by hunters to actively pursue prey or to choose the site for the installing a trap. It is in accordance with previous studies (Alves et al., 2009; Fitzgibbon et al., 1995) which recorded that species that make trails through vegetation or use burrows, particularly simple and single-exit ones, are more vulnerable to snaring than those species that have less-defined movement patterns. Also, evidence from our interviews showed that passive capture techniques are often placed to capture target specimens which make trails through vegetation frequently captured other animals accidentally which access the trails. This occurs when traps are placed in trails opened by large species and these traps are activated by other animals, such as medium-bodied omnivores like *C. civetta*. We also found fortuitous capture of carnivores in traps placed on prey trails in the moment that a carnivore was using the path to locate possible prey or going to eat a prey caught by the traps on the trail (in the case of trails where more than one trap was installed). Servals and leopards (mentioned by 60% and 31% of respondents, respectively) were the most accidentally caught animals.

Several animals are nocturnal, and therefore flashlights might be used for hunting. Strong flashlights are used by hunters in Kenya to temporarily blind duikers (Fitzgibbon, 1998), while in Brazil they are used to obfuscate the vision of birds on branches (Alves et al., 2009; Bezerra et al., 2012). Similarly, we registered the use of flashlights in Quiçama, Angola to obfuscate duikers and primates. Another practice which facilitates prey persecution identified in this study was derived from dog-based hunting. As shown by a study conducted in Nicaragua, this is a conservation problem because the use of dogs can increase prey capture efficiency by nine times and expand the range of captured prey (some prey are exclusively captured with this technique) (Koster, 2008). Another problem identified by some studies is that hunting with dogs is responsible for the local extinction of several species because even though a given species may be sought, other types of animals are often captured or killed by the dogs (Alves et al., 2009; Redford and Robinson, 1987).

Moreover, we found that the net is the only technique used for approximation exclusively in savannah. This technique consists of one of the most important traditional hunting tools in this landscape, requiring the participation of many people (adults and children), who encircle a delimitated area with their nets and so obtain a plenty of games. However, just as other collectively techniques, net use is going into disuse. The main reason associated with the increasing commercial focus of hunting will be better addressed in the next section. Finally, the frequent use of equipment such as motorcycles, helicopters, and cars registered in this study could also optimize the time to reach hunting sites, pursue prey, as well as the transport of the hunting products up to the trade centres.

4.3. Socioecological changes derived from human conflicts

Socioecological changes have recently been pushing hunters to use more efficient hunting techniques, such as steel cable snares, shotguns, and motorcycles (Duda, 2017; Kümpel et al., 2009; Yasuoka, 2014). However, hunters from different communities are not equally affected by these socioecological changes, as we can find strong disparities between hunting revenue, wealth and bushmeat dependence (Rickenbach, 2015). Our results showed that hunters located in northern Quiçama are closer to Luanda (the capital city of Angola and which received most of the civil war refugees) and so have monetary incentives to engage in hunting. These facts allied to easier hunting in the open savannah, which is the northern Quiçama landscape, make the area potentially more sensitive to defaunation.

Shotgun hunting expansion has occurred through different external incentives of the local hunter settlements. For example, the contemporary use of the shotgun in some traditional communities in Cameroon seems to be related to the emergence of a specialized and highly efficient type of hunter with clear market orientation (Duda, 2017). We reveal that this orientation has also resulted in a predominance of individual hunting events with a relatively low share of large game between hunters or local dwellers, and just relatively abundant and small species such as small duikers, porcupines and rats are usually shared. Evidence thus far indicates that the individual hunting pattern contrasts with the historical importance of a hunting strategy based on collective expeditions targeting large mammals in human local communities worldwide, thereby generating cultural loss since collective activity enables greater knowledge sharing (Bennett and Robinson, 2000).

One conservation problem we highlight here is based on the tragedy of the common hypothesis (Hardin, 1968), in which individuals acting independently and rationally according to their own interests behave contrary to the best interests of a community, depleting some common resource. In this case, a change from collective to individual hunting has a greater impact on biodiversity, because if a group of hunters initially captured (for example) five individuals and were content with catching 5, each hunter in the current individual hunting scenario will possibly tend to capture the same five individuals. This issue arises under the perspective that the hunter assumes that he/she is able to capture the same amount of animals obtained from collective hunting, and is motivated by the profit that will be obtained by marketing a certain amount of wild products alone. Finally, as much as collective hunting optimizes animal search and capture, individual hunting generates greater competition among hunters, which in itself is a motivator. After all, hunting in foraging societies often confers a special social status (Duda, 2017; von Rueden et al., 2011) and “the best hunters” are perceived as more efficient, being able to kill larger and more culturally significant species (Duda, 2017; Reyes-García et al., 2016). Consequently, prestigious hunters clearly exercise a powerful fascination over young people.

5. Conclusion

Human and wildlife blood inevitably mingles on the ground during armed conflicts, and the socioecological impact of wars on native biota usually remains underestimated along with deep scars on native peoples. We have presented a comprehensive overview of the chronology of war-induced changes in hunting techniques in the Quiçama meta-region of Angola. Based on our main results we can conclude that the shifts in hunting techniques arising from the Angolan civil war induced a body-mediated decline in mammal diversity. It is understandable that the animal protein remnant in this situation comes from native fauna which was overwhelmingly annihilated. Thus, future conservation strategies should consider an intensive automatic rifle collection program, continuous control of illegal hunting and selling in trade centers, and rewilding programs to repair a parcel of the damage to mammalian fauna which occurred from this long-term conflict. In doing so, failures in mammal-mediated ecosystem functioning can be recovered, thus bringing back the past ecological complexity. For countries which are experiencing armed conflict, we highlight that the external countries involved should assume their responsibility for the impact on wildlife. Furthermore, we warn that the impact of widespread distribution of firearms and the introduction of hunting techniques by refugees can lead to wildlife collapse, especially larger wildlife.

CRediT authorship contribution statement

Franciany Braga-Pereira: Conceptualization, Methodology, Data collection, Formal analysis, Elaboration of figures; Funding acquisition, Research authorization, Project administration, Supervision, Write of original draft, and Review of final manuscript. **Juliano André Bogoni:** Formal analysis, Elaboration of figures, Edition of the manuscript; Review of final manuscript. **Rômulo Romeu Nóbrega Alves**: Conceptualization, Methodology structuration; Edition of the manuscript; Review of final manuscript.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

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