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Modelling functional response of reptiles to fire in two Mediterranean forest types

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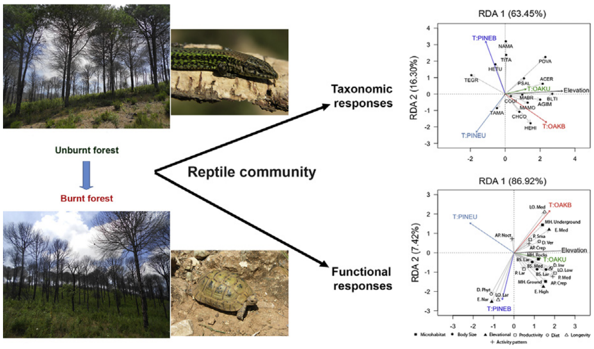
HIGHLIGHTS

- Reptile functional responses to fire have been examined in north-western Africa.
- Functional richness was higher in native cork oak forests than in pine plantations.
- Functional resilience of reptiles to fire was also higher in cork oak forest.
- Pine plantations give few functional opportunities to reptiles.
- Burning improves the functional richness of the reptile community in pine plantations

GRAPHICAL ABSTRACT



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ABSTRACT

Fire is one of the main disturbances to terrestrial environments, transforming habitat structure and affecting community composition. Coupled with fire, forest type and vegetation structure modulate the taxonomic response to fire by ectotherm organisms such as reptiles. The response of each reptile species to fire is based on their functional attributes, which make some species resilient to fire and others vulnerable to that disturbance and only adapted to long-unburnt landscapes. We studied the functional response of a reptile community at 13 burnt sites within the African rim of the Western Mediterranean, and in two contrasting forest types, i.e. native cork oak forests (five sites) and pine plantations (eight sites). We compiled seven functional traits for the reptile species in the study areas, and quantified reptile functional diversity at each sampled plot. Variation in this index was examined from burnt to nearby unburnt plots, both in cork oak and pine forests, with generalized linear mixed models. Redundancy analysis was used to identify which functional traits were associated with particular plot types. We found 2149 individual reptiles from 15 species. The functional response of reptiles to fire was forest-type dependent: functional richness did not change with fire in cork oak forest plots, but increased with fire in the pine plantation ones. High reptile functional richness in cork oak plots was due to high species richness in this forest type. The functional-redundancy analysis showed that cork oak forest hosts a reptile community functionally composed of small Mediterranean ground- and rock-dwelling lizards. In pine plantation plots, however, saxicolous geckos and phytophagous tortoises indicate the availability of other microhabitat and food resources to be exploited by reptile species with different functional traits.

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1. Introduction

Fire is a recurrent disturbance in many terrestrial ecosystems that shapes landscape structure (Bond and Van Wilgen, 1996; Keeley et al., 2012), strongly influencing the composition of biotic communities (Bond et al., 2005). Fire is also an essential ecosystem process in many biomes (Bond and Van Wilgen, 1996) and has been so over long geological time scales (Pausas and Keeley, 2009). In fire-prone ecosystems, natural fire regimes are conducive to the resilience of their natural communities by the acquisition of particular life-history traits by organisms (Keeley and Pausas, 2019).

In Mediterranean landscapes, the response of plants to fire has been extensively examined (Keeley et al., 2012; García et al., 2016). Several adaptive traits have been described to exemplify how plant species are able to persist in burnt landscapes, namely seeder and resprouter strategies (Keeley et al., 2011). Seeder species respond to fire by storing seeds in seed banks (tree canopy or in the soil; Pausas and Keeley, 2014). Most pine tree species are seeders, for which post-fire responses are based on seeds stored in serotinous cones (Daskalakou and Thanos, 1996; Habrouk et al., 1999; Thanos and Doussi, 2000). By contrast, most Mediterranean native oaks resprout immediately after fire from aerial or underground buds (Habrouk et al., 1999; Pausas, 1997; Retana et al., 2002).

According to McGill et al. (2006), functional traits are measurable properties of organisms that strongly influence their performance. In fire-prone ecosystems, functional-trait approaches can offer a valuable framework for understanding post-fire changes in community structure caused by abiotic and biotic shifts. Thus, the response of organisms to fire can be influenced by their functional traits, which make some species resilient to fire and others vulnerable and thus better adapted to long-unburnt landscapes (Westgate et al., 2012). Vagility and lack of modularity make it difficult to identify the functional responses of animals to fire (Pausas and Parr, 2018). However, some studies have already reported that animal species occurrence in post-fire scenarios depends primarily on their adaptation to changes in habitat structure (Swan et al., 2015), food and refuge availability (Sousa, 1984), reproductive success (Le Galliard et al., 2005), predation rates (Hawlena et al., 2010), and thermal environments (Hossack et al., 2009). In short, species occurrence in fire-prone ecosystems depends on their functional response.

Identifying functional traits that shape species vulnerability and resilience to fire can help us to predict the response of organisms to this disturbance. This approach has been widely examined in plants (Pausas et al., 2004; Clarke et al., 2013; Casals et al., 2018) and to a lesser extent in some animal taxa such as ants (Arnan et al., 2013), bees (Moretti et al., 2006; Moretti and Legg, 2009), beetles (Driscoll et al., 2019), and spiders (Langlands et al., 2011), but remains lacking in many taxonomic groups such as reptiles.

Reptiles are ectothermic organisms highly dependent on the habitat structure (Solan et al., 2018). Reptile individuals can escape from flames by hiding under ground objects, climbing trees, entering refuges such as burrows, or leaving burning areas (Russell et al., 1999; Smith et al., 2012). Moreover, reptile species display different environmental requirements (e.g. forest and open species), and consequently they are expected to exhibit different short-term responses to fire (Abom and Schwarzkopf, 2016; C. Ferreira et al., 2016; D. Ferreira et al., 2016; Smith et al., 2013). For this reason, detailed ecological (functional) information of species (e.g. body size, habitat selection, dietary habits, reproduction, longevity) can help to build a functional model to explain the response of reptiles to fire (Smith, 2018). Previous studies have partially described particular functional traits of reptiles that drive responses to fire at different levels: the community (e.g. species composition [Abom and Schwarzkopf, 2016]), the population (e.g. abundance [Santos and Poquet, 2010]), genetics and phenotype (Schrey et al., 2011), and the individual (e.g. by changing thermoregulatory opportunities [Webb and Shine, 2008]).

Modelling the functional responses of reptile species to fire has proved to be only weakly predictive (Driscoll et al., 2012; Nimmo et al., 2012). However, several functional traits are expected to confer reptile species with resistance and resilience to fire. For example, nocturnal reptiles tend to be early post-fire colonizers with respect to species with diurnal activity (Smith et al., 2013; Pausas, 2018). The decline in diurnal skinks and dragons rather than nocturnal geckoes in tropical savannas of Australia, suggests that the lack of cover is critical either by causing either increased diurnal predation or overheating risks (Legge et al., 2008). Burrowing species that forage in open areas are favoured in post-fire landscapes (Driscoll and Henderson, 2008) and undergo less mortality during fire than non-burrowing species (Smith et al., 2012), while saxicolous species tend to be resistant to fire events (Santos et al., 2016). These examples suggest that some microhabitat preferences and activity patterns can confer reptile species with resilience to fire.

Reptile distribution is strongly aligned with habitat complexity, which is important for thermoregulation, foraging, nesting, and refuge (McElhinny et al., 2006). Thus, postfire changes in the composition and abundance of available prey can affect the range and abundance of reptiles (Pastro et al., 2013; Santos and Cheylan, 2013; Hu et al., 2016). Burning delivers a pulse of nutrients to soil and plants (Bond and Van Wilgen, 1996) that can be used by consumers through an increase in food availability. For example, insectivore reptiles can benefice from an increase in arthropods (Smith, 2018), and immature Hermann's tortoises *Testudo hermanni* take advantage of the sudden increase in food availability brought by the fire, growing faster and accelerating the onset of sexual maturity (Stubbs et al., 1985). The tolerance to changes in thermal and hydric conditions can also shape the response of reptile species to fire (Hu et al., 2016). Unfortunately, physiological tolerance (e.g. lethal and preferred temperatures and hydric stress) is available for only few species (C. Ferreira et al., 2016; D. Ferreira et al., 2016), although elevational range of species distribution can be a surrogate of physiological tolerance of species (Adolph, 1990; Sears and Angilletta, 2003). Some reproductive parameters can also be indirectly affected by food availability along the postfire succession (Smith, 2018). Species that have long life spans and delayed maturity are prone to slow population recovery in scenarios of high mortality rates of reproductive individuals in fire events (Couturier et al., 2014). All these examples suggest that dietary, physiological, and reproductive traits can also be useful to model the functional response of reptile species to fire.

Body mass shows allometric relationships to a number of life-history traits (e.g. mobility, home-range size, resistance to variation, reproductive frequency, and productivity), and it can be used as a proxy for life-history traits that are favourable or unfavourable under different disturbance regimes (e.g. Stearns, 1992; Shine et al., 1998), for example, for modelling the response of reptiles to fire.

We selected a set of functional traits in order to model the response to forest fire among reptiles along the African rim of the Western Mediterranean. In this region, the reptile community is rather diverse (Mediani et al., 2015) and has a high endemicity rate (Pleguezuelos et al., 2010; Martínez-Freiría et al., 2013). It is composed by a suite of species with quite different biogeographic origin (Schleich et al., 1996), including Mediterranean species, relict elements of Palaearctic fauna, and Ethiopic species along the northern border of their range (Bons and Geniez, 1996). The region is undergoing a continual process of degradation due to overgrazing and the conversion of natural ecosystems to agricultural land (Taïqui et al., 2008; Gatchui et al., 2014). For example, degraded natural *Quercus suber* forests are being replaced by coniferous plantations, mostly of maritime pine *Pinus pinaster* (Pastor-López et al., 1997). The maritime pine was considered by the Framework Reforestation Plan of the Moroccan government as a basic species for the reforestation of the Rif Mountains, in northern Morocco (Belghazi and Romane, 1994). These plantations were originally planned to retain soil and regain plant cover, and, to a lesser extent, for timber (Wahid et al., 2009). Pine plantations are often unproductive for timber because of high tree density together with climate and soil limitations. Moreover, these plantations now generate many ecological challenges, such as increasing the risk of fire and hindering the development of native vegetation (Pausas and Fernández-Muñoz, 2012).

Our study is aimed at comparing the functional response to fire of reptile species in cork oak woodlands and pine plantations. In the Rif mountains, both forest types are frequently affected by fire (Chergui et al., 2018a). Our previous studies have identified cork oak forests as being structurally more fire resilient than pine plantations (Pausas et al., 2008; Chergui et al., 2018b), and the reptile community living in cork oak forests is taxonomically more resilient to fire than is the community living in pine plantations (Chergui et al., 2019a). Based on these previous conclusions, here we examine three predictions: 1) Reptile species richness is higher in cork oak forests compared to pine plantations (Chergui et al., 2019a); accordingly, we expect similar differences at the functional level of the reptile community, with higher functional richness in cork oak forests. 2) Pre- and post-fire reptile communities are taxonomically similar in cork oak plots (Chergui et al., 2019a); thus, we expect a similar response at the functional level, with similar functional richness between pre- and post-fire cork oak plots. 3) Fire will increase the reptile species richness and abundance in pine plantations as a consequence of increased openness (Chergui et al., 2019a); accordingly, we expect greater reptile functional richness in burnt than in unburnt pine plantation.

2. Materials and methods

2.1. Study area and sampling design

The study area covers 12,650 km^2 in north-western Africa (Rif region; Fig. 1a). The climate is typically Mediterranean, with mean annual temperatures ranging between 15 and 19 °C, and average annual rainfall between 600 and 2000 mm (Cheddadi et al., 2016). Further descriptions of the study area are available in Chergui et al. (2019a,b). In this region, fires occur mainly in the dry season (summer; Mharzi Alaoui et al., 2015; Chergui et al., 2018a), and fire mapping is characterized by relatively small fires (usually <1000 ha burnt) due to socioeconomic causes (i. e. dense rural human population and high fuel use; Chergui et al., 2018a).

We sampled reptile species at 13 sites affected by recent fires (from 2006 to 2015; Table S1), ranging from 97 to 1261 m elevation. For each site, the information of the fire history was taken from the Department of Water and Forests of Morocco. At each site, 2 or 3 burnt and 2 or 3 unburnt transects were selected (see an example in Fig. 1b). In total, we sampled reptiles in 70 transects averaging 726 m long (± 10.6 SE). The starting point of all transects was set at >100 m from the fire edge to avoid ecotone effects on reptile counts (C. Ferreira et al., 2016; D. Ferreira et al., 2016).

Each transect was sampled six times (hereafter surveys: two in spring 2015, one in autumn 2015, and three in spring 2016) by one researcher (mainly BCH). For uniform sampling effort among and within transects, surveys were limited to 45 min, during periods of maximum reptile diel activity and detectability (sunny days at environmental temperatures of 20–30 °C). During the surveys, the researcher visually searched for reptiles investigating rocks, logs, and other potential refuges, each item disturbed being thereafter returned to its original state. Animals were only visually surveyed and not caught (see a similar sampling methodology in Santos et al., 2016).

2.2. Species traits

For all reptile species in the sampling sites, we considered a set of functional traits of potential importance in determining fire response (see references in the Introduction). Some traits are qualitative classes and others quantitative values. In the latter case, values were assigned to three classes per trait. Relative abundance of the three classes per trait and transect were used to calculate functional diversity indices (see below). For each reptile species, trait values were collected from those available in the scientific literature for populations from the study area (northern Morocco), and in a few cases from the closest conspecific or congeneric populations (references in Table S2). Some relevant traits for reptiles such as the thermal physiology were not included because of the scant information available for this trait in the literature. The list of traits and classes per trait was as follows:

(1) Body mass, represented by the mean value of female body mass. Classes: small <10 g, medium 10–50 g, and large >50 g.
(2) Microhabitat preference, as a small specialized area within a larger habitat where a species develop a significant part of its activity. Classes: rocks, aboveground, and underground.
(3) Activity pattern. Classes: diurnal, nocturnal, and crepuscular.
(4) Elevation range, based on the difference between the maximum and minimum elevations for each species in the study area. Classes: small range 0–900 m, medium range 900–1400 m, and large range 1400–1800 m.
(5) Dietary preferences. Classes: predominantly phytophagous, invertebrate consumers, and vertebrate consumers.
(6) Annual productivity, as the mean yearly output of an adult female, considering the clutch or litter size and their reproductive frequency. Classes: 0–4, 4–8, and >8 eggs/offspring per year.
(7) Age of females at sexual maturity. Classes: 0–1, 1–3, and >3 years.
(8) Longevity for the species in the wild, generally calculated from skeletochronology. Classes: 0–5, 5–10, and >10 years.

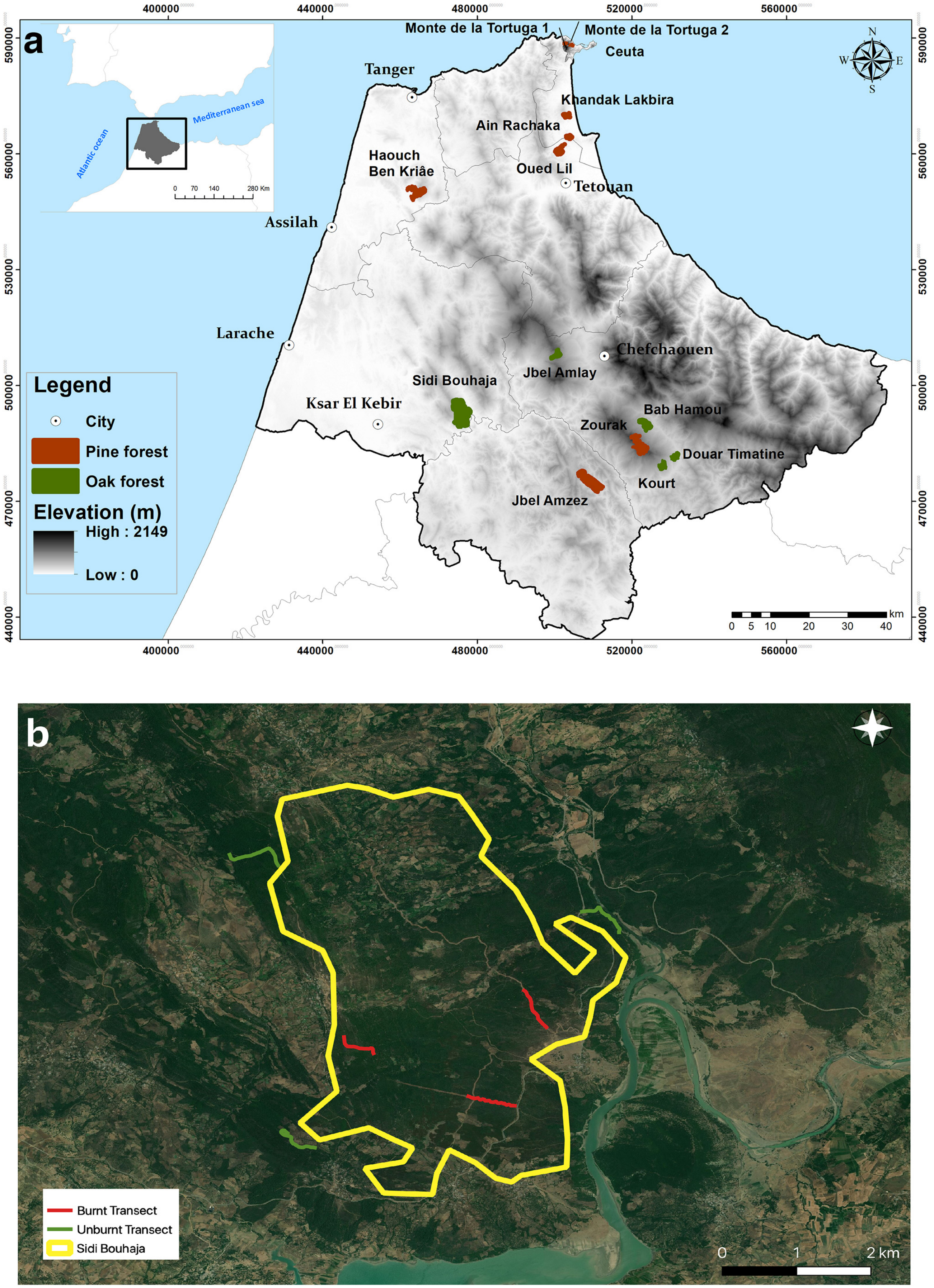
2.3. Data analysis

We performed two types of analyses according to the data sets. First, a taxonomic analysis to identify differences in community composition between transect types and to associate each reptile species within a type of transect according to forest type and fire condition (unburnt or burnt). Second, a functional analysis aimed to identify and compare functional diversity of the reptile species among transects, and to associate each functional trait with transects according to forest type and fire condition.

2.3.1. Taxonomic analysis

Firstly, we compared the similarity of the reptile community among the four transect types: burnt pine, unburnt pine, burnt cork oak, and unburnt cork oak. Based on the matrix of reptile counts for each species at each transect, the four transect types were compared by permutational multivariate analysis of variance (PERMANOVA), using the Bray-Curtis distance between pairs of transects (Anderson, 2001). The advantage of the permutation approach is that the resulting test is “distribution free” and not constrained by many of the typical assumptions of parametric statistics (Walters and Coen, 2006). This test was conducted with the package *vegan* (Oksanen et al., 2018), with 9999 permutations. A non-metric multidimensional scaling (NMDS) analysis was performed to visualize how transects were similar in terms of species composition. Similarity between pairs of transects was calculated with the Bray-Curtis indices for a presence-absence and abundance species matrix. NMDS was performed using the metaMDS function in the package *vegan* (Oksanen et al., 2018).

Secondly, we used a redundancy analysis (RDA) to identify the association between each reptile species and the four transect types (unburnt cork oak, burnt cork oak, unburnt pine and burnt pine), and elevation (this factor was included given the complex orography and the importance of elevation for the distribution of reptiles on the study area; Pleguezuelos et al., 2010). RDA is an extension of multiple regression methods to modelling multivariate response data (Legendre and Legendre, 2012). The data were separated into two sets, i.e. a response matrix with species abundance per transect, and


a
400000
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Mediterranean sea
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Monte de la Tortuga 2
Ceuta
Tanger
Khandak Lakbira
Ain Rachaka
Haouch Ben Kriâe
Oued Lil
Tetouan
Assilah
Larache
Chefchaouen
Jbel Amlay
Sidi Bouhaja
Ksar El Kebir
Bab Hamou
Zourak
Douar Timatine
Kourt
Jbel Amzez
N
S
W
E
Legend
City
Pine forest
Oak forest
Elevation (m)
High : 2149
Low : 0
km
0 5 10 20 30 40
b
Burnt Transect
Unburnt Transect
Sidi Bouhaja
0 1 2 km

an explanatory matrix with transect types. We calculated the significance of the explained variance in the RDA by performing ANOVA-like permutation tests (9999 permutations), using the RDA function in the *vegan* package (Oksanen et al., 2018).

In a preliminary analysis, we used as explanatory variables elevation, forest type (cork oak and pine), fire condition (unburnt and burnt), and time since the last fire (TSF). The collinearity among the selected explanatory variables was tested by calculating the variable inflation factor (VIF) using the vif.cca function in the *vegan* package. VIF > 10 indicates that a variable is strongly dependent on others and therefore does not have independent information (Oksanen et al., 2018). Time since the last fire (TSF) proved to be strongly correlated with fire condition (vif.cca > 10 for both variables). When TSF was excluded, fire condition shifted to a VIF < 2. The two variables were strongly correlated because all the unburnt transects had been long unburnt (TSF $=$ 50 years according to the Moroccan government data set, Chergui et al., 2019a) whereas the burnt transects ranged from 1 to 9 years since fire. These pronounced TSF differences between burnt and unburnt transects resulted in a high correlation of this variable with the variable fire condition.

2.3.2. Functional analysis

We first classified each reptile species within a functional class for each functional trait (Table 1). Based on this classification, we performed a matrix of trait abundance values within each transect and calculated four functional diversity (FD) indices as primary components of functional diversity (Mason et al., 2005): functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis). Functional richness can be measured by the convex hull volume of the functional space occupied by the community (Villéger et al., 2008). Functional evenness measures the regularity of abundance distribution in the functional trait space (Mason et al., 2005). Functional divergence measures the abundance distribution within the volume of functional trait space occupied by the species, in which the value increases when the most abundant species have extreme functional trait values (Mason et al., 2005; Villéger et al., 2008). Functional dispersion is defined as the mean distance in the multidimensional trait space of individual species to the centroid of all species (Laliberté and Legendre, 2010).

We made an exploratory data analysis to detect possible multicollinearity among functional traits, by evaluating Spearman's bivariate correlations among all traits. The r coefficient > 0.7 was used as the criteria for identifying pairs of correlated variables, and the trait Age at Maturity was removed from subsequent analyses, because of collinearity with Body mass. The definitive traits used in the analyses are shown in Table 1.

Functional diversity calculations were implemented with the dbFD function in the FD package for R (Laliberté et al., 2015). We evaluated differences in FD indices between transects, considering forest type (cork oak and pine plantation) and fire condition (burnt and unburnt), and using GLMMs with data adjusted to a Poisson distribution, plus site as a random effect. We performed a generalized linear mixed model (GLMMs) using the lmer function in the lme4 package (Bates et al., 2015).

Statistical significance was set at p level < 0.05.

As in the taxonomic analysis, we conducted a functional RDA analysis to identify which functional classes are associated to particular forest types (unburnt and burnt cork oak, and unburnt and burnt pine). All the analyses were performed using the R software packages (R Development Core Team, 2017).

In field-based studies, species abundance may have been biased by differences in detectability of reptile individuals between burnt and unburnt transects. This is because recently burnt sites are less vegetated than unburnt ones, and this could result in higher reptile detectability in the former sites. However, previous experience of the authors using the same methodology showed no differences in the distance of detection of reptiles in burnt and unburnt transects (Santos and Cheylan, 2013). For this reason, distance sampling models were not used in this study.

3. Results

Overall, considering the 70 surveys, we found 2149 individual reptiles from 15 species (52% of the terrestrial reptile species in the region; Table S3), four endemic to north-western Africa. The number of species recorded within each transect ranged from 1 to 9. The six most commonly detected species were: three lacertid lizards, *Psammodromus algirus*, *Podarcis vaucheri*, and *Acanthodactylus erythrurus*; an agamid lizard, *Agama impalearis*; a gecko lizard, *Tarentola mauritanica*; and a tortoise, *Testudo graeca*. Each of these species occurred in at least 50% of the surveyed plots, with *P. algirus* and *P. vaucheri* being recorded at all 13 sites (Table S3).

3.1. Taxonomic results

The PERMANOVA analysis showed significant differences in reptile species composition between forest types i.e. cork oak and pine plantations ($F = 9.637$, $R^2 = 0.1223$, $p = 0.001$); no differences were found in the community composition with respect to fire condition (unburnt and burnt transects) or forest type $*$ fire condition interaction. The NMDS ordination plots suggested differences in species composition between transect types (Fig. S1); species composition was highly variable between burnt and unburnt pine transects, whereas burnt and unburnt oak transects had more similar species composition and abundance.

The taxonomic RDA confirmed that the values for the reptile community composition and specific abundance varied among transect categories ($F = 1.568$, $p = 0.012$), the effect of elevation also being statistically significant ($F = 2.768$, $p = 0.009$). The first axis of the RDA explained 63.45% of the variation, whereas the second axis explained 16.30%, for a total of 79.75%. The first axis of the RDA was significant ($F = 4.822$, $p = 0.001$) and separated cork oak transects (positive values) from pine transect (negative values). Notably, most reptile species showed a stronger association with cork oak transects, except *T. graeca* and *T. mauritanica,* which were associated with pine transects (Fig. 2).

3.2. Functional results

Based on the functional indices calculated for reptile abundances recorded at each transect, the GLMMs detected significant variation of functional richness for the fire condition and for the interaction fire condition $*$ forest type (Table 2). Functional richness remained similar between burnt and unburnt cork oak transects but strongly increased from unburnt to burnt pine transects (Fig. 3). Functional richness also increased with species richness (all transects pooled; $F = 46.800$, $p < 0.0001$; Fig. S2). Other functional indices did not change with fire condition or forest type (Table 2).

The functional RDA showed a significant association between particular functional traits and transect categories ($F = 2.177$, $p = 0.007$). The variable elevation also contributed significantly to these effects ($F = 4.087$, $p = 0.005$; Fig. 4). The first axis of the RDA explained 86.92% of the variation, whereas the second axis only explained 7.42% of the variation. The first axis ($F = 9.230$, $p = 0.001$) discriminated between functional groups associated with forest type. All classes of three functional traits, namely body mass, microhabitat, and annual productivity, were related to cork oak transects. By contrast, narrow elevation range,

Fig. 1. Location of the 13 study sites in the Rif region; the inset corresponds to the location of the study region within the Western Mediterranean Basin (a); location of three burnt and three unburnt transects in the site Sidi Bouhaja (b).

Table 1
Functional traits of reptile species recorded in the 13 forested study sites from north-western Africa (Rif region). Each functional trait was divided in three classes. See more details on these variables in the Material and methods section.

Species	Code	Microhabitat	Body size		Elevational range		Annual productivity		Diet	Activity pattern	Longevity	
			Grams	Class	Meters	Class	Eggs/newborns	Class			Years	Class
Testudo graeca	TEGR	Ground	628	3	490	1	8.7	3	Phytophagous	Diurnal	18	3
Acanthodactylus erythrurus	ACER	Ground	5.5	1	1378	2	4.4	2	Invertebrates	Diurnal	2.1	1
Timon tangitanus	TITA	Ground	31.6	2	1260	2	16	3	Invertebrates	Diurnal	11	3
Podarcis vaucheri	POVA	Rock	3.6	1	2370	3	6	2	Invertebrates	Diurnal	3	1
Psammodromus algirus	PSAL	Ground	8.3	1	2275	3	9.8	3	Invertebrates	Diurnal	5	1
Agama impalearis	AGIM	Rock	51.8	3	1314	2	24	3	Invertebrates	Diurnal	5	2
Chalcides colosii	CHCO	Underground	11.20	2	1430	2	2.1	1	Invertebrates	Diurnal	6	2
Hemidactylus turcicus	HETU	Rock	3.7	1	410	1	4	1	Invertebrates	Nocturnal	4	1
Tarentola mauritanica	TAMA	Rock	8.7	1	1390	2	4	1	Invertebrates	Nocturnal	4	1
Blanus tingitanus	BLTI	Underground	7.8	1	1470	3	0.5	1	Invertebrates	Diurnal	7	2
Coronella girondica	COGI	Ground	24.3	2	1735	3	4.8	2	Vertebrates	Crepuscular	9	2
Hemorrhois hippocrepis	HEHI	Ground	116.3	3	1780	3	6.1	2	Vertebrates	Diurnal	20	3
Macroprotodon brevis	MABR	Underground	18.3	2	1270	2	2.1	1	Vertebrates	Crepuscular	10	2
Malpolon monspessulanus	MAMO	Ground	168	3	1545	3	6.7	2	Vertebrates	Diurnal	14	3
Natrix maura	NAMA	Ground	37.1	2	1500	3	11.2	3	Vertebrates	Diurnal	20	3

great longevity, and phytophagous diet (Fig. 4), all of these being functional traits characteristic of *T. graeca*, were related to pine transects. Finally, the nocturnal activity pattern correlated to unburnt pine plantation (Fig. 4).

4. Discussion

4.1. Taxonomic responses of reptiles to fire and forest type

Our field-based study in north-western Africa has demonstrated that the response of the reptile community to fire is forest-type dependent. This result supports previous findings along the European rim of the Mediterranean Basin (Santos et al., 2016; Pinto et al., 2018). Reptile diversity was higher in cork oak forest, both burnt and unburnt, than in pine plantations. This is related to the low impact of fire on its habitat structure (Pausas, 1997; Chergui et al., 2018b), and to the high quality of this habitat for reptiles; e.g. large numbers of plant species and structurally complex vegetation that generate high food and microhabitat diversity (Ioannidis et al., 2008; Santana et al., 2011; Chergui et al., 2018b). Cork oak forest is characteristic of siliceous soils of Mediterranean regions in north-western Africa (Aronson et al., 2009), and the reptile community that occupy this forest appear to be adapted to the fire regime in this habitat (recurrent small fires, <1000 ha in area; Chergui et al., 2018a).

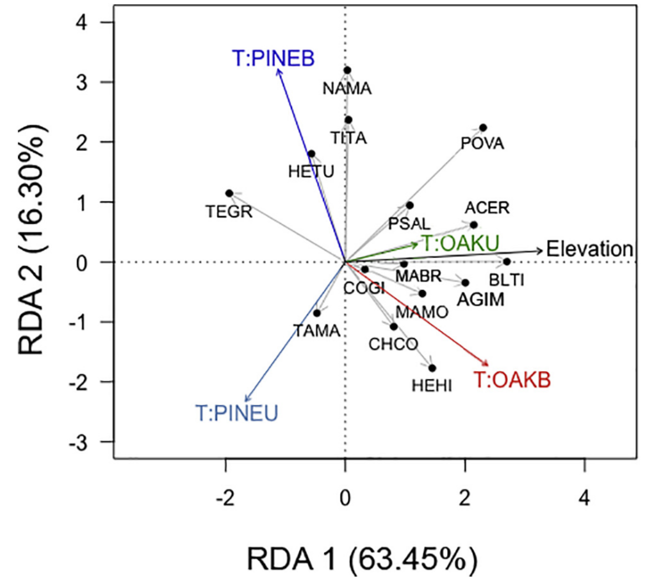

Fig. 2. Redundancy analysis plot with reptile species abundance and four transect category on forests from the north-western Africa (Rif region). Burnt oak transect (T: OAKB), unburnt oak transect (T: OAKU), burnt pine transect (T: PINEB), and unburnt pine transect (T: PINEU). See reptile abbreviations in Table 1.

By contrast, the low numbers of reptile species and individuals from the unburnt pine plantation suggest that this forest may constitute a low-quality habitat for reptiles (Mott et al., 2010; Reading and Jofré, 2018; Chergui et al., 2019a), as demonstrated elsewhere when compared to open areas and oak forests (e.g. Amo et al., 2007; Ioannidis et al., 2008; Azor et al., 2015). Pine plantations have more simplified understories and receive less radiant energy at the ground level than do native forests (Mott et al., 2010). Among the species of this community only *T. graeca*, a typical colonizer of recent pine plantations (Rodriguez-Caro et al., 2017), was associated with burnt pine transects, and just one lizard was associated with unburnt pine plantations, the gecko *Tarentola mauritanica*. Despite the negative impact of fire on *T. graeca* populations (Couturier et al., 2014; Chergui et al., 2019b) rather high numbers of tortoises were found in burnt pine transects. We speculate that tortoises migrate to burnt pine patches as these areas lead to better habitat quality for the thermoregulation of tortoises (see also Wright et al., 1988; Anadón et al., 2006; Cunnington et al., 2008), and its understorey produce plant assemblages (grass) suitable for tortoise grazing (Means, 2007; Mott et al., 2010). In any case, the high number of tortoises recorded in part could have been due to the high detection probability of *T. graeca* in burnt areas compared to unburnt ones (Chergui et al., 2019b).

4.2. Functional responses to fire and forest type

In accord with our first prediction, we detected higher reptile functional richness in unburnt cork oak transects compared to unburnt pine transects. This forest-type effect was caused by differences in the reptile community composition and ultimately by the habitat quality of both forest types (Amo et al., 2007). In our study area, canopy, shrub cover, rock cover, and bare ground differs between cork oak forests and pine plantation, and between burnt and unburnt plots of both forest types (Chergui et al., 2018b). Habitat complexity is higher in the cork oak forests than in pine plantations, and also higher in burnt compared to unburnt pine plantations (Chergui et al., 2018b). This variation in habitat complexity could increase ecological opportunities for a larger number of reptile species and may explain the differences found in reptile functional richness. The lack of differences in other functional metrics may be caused by their low discriminative power to identify

Table 2
Results of the analysis using GLMMs for four measures of the functional diversity of the reptile community at 13 sites of north-western Africa (Rif region), according to fire condition (unburnt, burnt), two forest types (native cork oak, pine plantation), and their interaction: (FRic) Functional richness, (FEve) Functional evenness, (FDiv) Functional divergence, and (FDis) functional dispersion in relation to fire and forest type. Z values are provided for data modelled with Poisson distribution. Significant *p* values in bold. ns, not significant.

Functional index	Fire			Forest type			Fire ∗ Forest type		
	Estimate	z value	*P*	Estimate	z value	*p*	Estimate	z value	*p*
FRic	−0.5280	−2.507	**0.012**	−0.2486	−0.740	ns	0.6231	2.164	**0.0304**
FEve	−0.0342	−0.073	ns	0.0220	0.035	ns	−0.0315	−0.046	ns
FDiv	−0.1848	−0.449	ns	−0.0147	−0.025	ns	0.2422	0.402	ns
FDis	0.0852	0.308	ns	0.0645	0.138	ns	−0.1452	−0.344	ns

functional changes in the reptile community related to fire (e.g. Body mass and Activity pattern; see similar results in Hu et al., 2016).

Our second prediction was also fulfilled, as we found that the interaction of fire and forest type influences the reptile functional richness. The reptile taxonomic (Chergui et al., 2019a) and functional richness (this study) did not vary between burnt and unburnt cork oak transects. Unburnt cork oak forests were dominated by small Mediterranean lizards, and we detected a notable functional resilience to fire in the reptile community from this forest type. This functional resilience can be caused by the fast resprouter response to fire of the cork oak tree (Pausas, 1997), and also by the fire regime in the Rif region, characterized by small burnt areas (<350 ha except one fire; Chergui et al., 2019a), and its low frequency (i.e. most of the burnt sites underwent a single fire over the last 50 years or more; Chergui et al., 2018a). This contrasts with areas along the northern rim of the Mediterranean Basin, where recurrent fires in cork oak forest have caused taxonomic and functional differences in the reptile community between burnt and unburnt areas (e.g. in the Massif des Maures, southern France; Santos and Cheylan, 2013). There, the recurrent-fire regime has heavily altered the habitat structure and plant composition (Delitti et al., 2005; Malkisnon et al., 2011), and this is expected to stress other components of the biota through bottom-up effects that can disturb species interactions and constrain ecosystem functioning (Pausas, 2018). In these recurrent-fire cork oak forests, the reptile community is depauperate compared to unburnt patches (Santos and Cheylan, 2013).

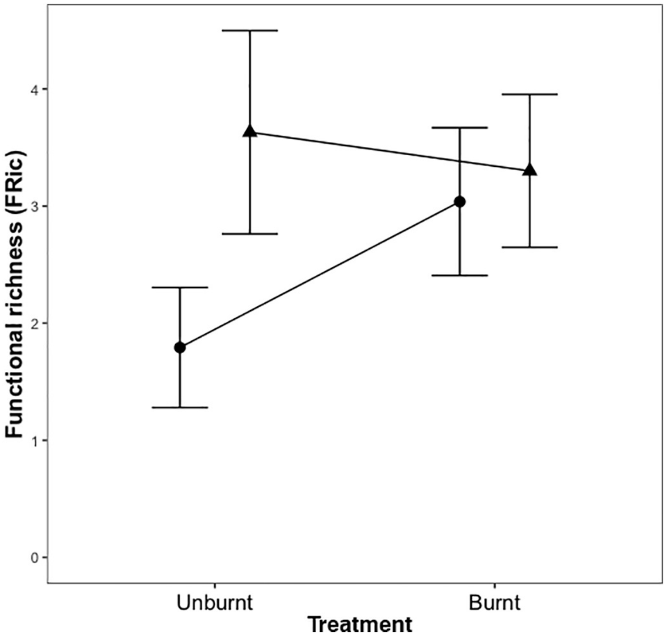

Fig. 3. Significant Generalized Linear Mixed Models association between indices of functional richness of the forest reptile communities and interaction forest type x fire in the Rif region, north-western Africa. Symbols (circles for pine forest and triangles for cork oak forest) refer to mean values and whiskers are ± one standard error.

Our third prediction was also supported, as functional richness increased from the unburnt to burnt pine plantations. This result was again due to greater reptile species richness and abundance from unburnt to burnt pine patches (Chergui et al., 2019a), due to greater microhabitat quality of the burnt pine transects (Berriozabal-Islas et al., 2017; Chergui et al., 2018b). Also, some species may even move into recently burnt areas because of greater food abundance (Griffiths and Christian, 1996; Costa et al., 2013). In fact, high values of functional richness are caused by the availability of large numbers of functional spaces (niches) occupied by species within a community (Kosickia and Hromada, 2018). For instance, fallen logs after a fire can create large functional spaces (and potential refuges; Houston, 2017), consistent with the positive response of reptile communities to more heterogeneous and open habitats (Todd and Andrews, 2008), such as those generated by forest thinning (Azor et al., 2015). Thus, a patchy landscape of forested and open areas generated by a fire can provide shelter as well as favourable spots for the thermoregulation of ectotherms (Webb et al., 2005; Greenberg et al., 2010; Wild and Gienger, 2018).

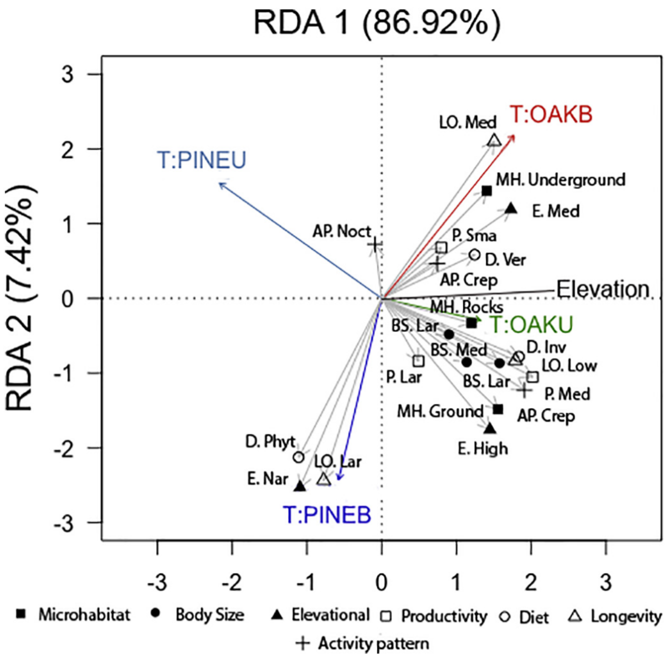

Fig. 4. Redundancy analysis plot with functional traits of the reptile species in forest of the north-western Africa (Rif region) and four transect categories. Acronyms are as follows. For the transects according to forest type and fire condition: unburnt cork oak transect (T: OAKU), burnt cork oak transect (T: OAKB), unburnt pine transect (T: PINEU), and burnt pine transect (T: PINEB). For the functional traits of the reptile species: Microhabitat (MH): rocks, ground, and underground; Body Size (BS): small (Sma), medium (Med), and large (Lar); Elevational Range (ER): narrow (Nar), medium (Med) and high (AR High); Productivity (P): small (Sma), medium (Med), and large (Lar); Diet (D): phytophagous (Phyt), invertebrate consumers (Inv) and vertebrate consumers (Ver); Longevity (LO): low (Low), medium (Med) and high (Lar); Activity Pattern (AP): crepuscular (Crep), diurnal (Diur), nocturnal (Noct).

Elevation proved to be an important variable to explain reptile taxonomic and functional richness among the 13 sites studied. This is related to the elevation of cork oak forests and pine plantations studied (cork oak at higher elevations than pine sites). This distribution was limited by the location of the burnt sites. Since cork oak forests have higher taxonomic and functional richness than pine plantations have (the former appearing at higher elevations), we detected an elevation effect on the RDAs performed.

Our functional analysis indicated that the reptile community in burnt pine plantation was composed of species characterized by a phytophagous diet, great longevity, and a distribution in narrow elevational ranges. Over the short term, fire may create landscapes which attract species that specialize in early successional habitats (Valentine et al., 2012; Smith, 2018). In burnt habitats for example, increased grass biomass (Means, 2007) can be exploited by tortoises due to their herbivory (Costa et al., 2013; Drake et al., 2015). Following aestival fires, the rapid growth of grass vegetation after rain in early autumn may well provide sufficient food for tortoise survival (Lecq et al., 2014). These findings suggest that tortoises can adjust well to burnt habitats (in non recurrent-fire landscapes; Santos and Cheylan, 2013). By contrast, reptiles specializing in invertebrate or vertebrate prey were associated with cork oak transects. An exception was *T. mauritanica*, which prefers unburnt pine patches where this lizard can find adequate microhabitats such as refuges in the pine trunk bark and rocky walls, a result also observed in some areas of the northern rim of the Mediterranean basin (Santos et al., 2016, 2018).

Several functional traits were scarcely predictive. This may have resulted from the low functional diversity exhibited by the most common Mediterranean reptiles (i.e. most being small insectivorous lizards) and the small weight of rarest species (i.e. snakes) in the statistical analyses, despite of our rather large sample size. The climate features that make the Mediterranean Basin a fire-prone region (dry and hot summers) and its crown fire type (fire spreads through tree crowns; Keeley et al., 2012) could be strong evolutionary drivers that have removed particular functional traits among reptiles, such as arborealism, phytophagy, and longevity. This argument is based on the fact that the reptile community studied here includes only one arboreal, one phytophagous, and one long-lived species (Pleguezuelos et al., 2010). These functional traits are more abundant among reptiles in other biomes such as tropical forests and deserts (Berriozabal-Islas et al., 2017; Grimm-Seyfarth et al., 2019). By contrast, other reptile traits such as insectivorous diet, low body mass, rock (rupicolous) and ground-dwelling specialization, are abundant in fire-prone Mediterranean landscapes, as occurred with serotinous or resprouting traits from some Mediterranean trees (Keeley et al., 2011).

The fire regime is currently changing in the Mediterranean Basin (Chergui et al., 2018a), and some of our study sites are suffering from arson with increasing numbers of fires, which, over the long term, could reduce the survival capacity of the cork oak (Santos and Cheylan, 2013). Moreover, other types of impact, such as overgrazing and indiscriminate felling of trees, burnt or not, or expanding the area of land dedicated to cultivating cannabis, an increasing activity in the region (Gatchui et al., 2014), can exacerbate the effects of fire. Such impacts can reduce both the taxonomic and functional resilience of Mediterranean reptile communities to fire.

5. Conclusions

Our study demonstrates that forest fires affecting cork oak forest exert a low impact on the Mediterranean reptile community, both in terms of taxonomic and functional traits. In contrast, burning can (functionally) improve the quality of the depauperate communities of reptiles in pine plantations, apparently due to changes in the habitat structure (Mott et al., 2010; Chergui et al., 2018b). The high resilience of Mediterranean reptiles in cork oak forests may result from the adaptation of these forests to resist small fires. We conclude from this study that fire can also be a beneficial disturbance for biodiversity when homogeneous pine plantations supporting little functional biodiversity are burnt. Given the large extent of pine plantations in the Mediterranean Basin, our results and proposal can be projected to a larger geographic scope for the maintenance of the animal taxonomical and functional biodiversity within a scenario of recurrent and increasing forest fire.

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CRediT authorship contribution statement

Brahim Chergui: Conceptualization, Investigation, Writing - original draft.**Juan M. Pleguezuelos:**Investigation, Writing - original draft. **Soumia Fahd:**Conceptualization, Writing - original draft.**Xavier Santos:**Conceptualization, Writing - original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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