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Adaptations of tenebrionid beetles to Mediterranean sand dune environments and the impact of climate change (Coleoptera: Tenebrionidae)

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Abstract
Tenebrionids represent a conspicuous component of the fauna of Mediterranean coastal dunes showing particular adaptations to the extreme climatic conditions of these environments (high temperature and aridity). These adaptations involve, for example, distinct morphological traits (such as long legs and subelytral cavity), finely tuned life cycles, ecological specialization, and diel and seasonal activity patterns that vary in response to temperature changes. Although these species are able to cope with high temperature and water scarcity, the ongoing climatic change may represent a serious threat. Increases in average temperatures and in frequency and severity of extreme events may affect profoundly species that already live close to their upper climatic tolerance limits. Tenebrionids in Mediterranean sand dunes are also flightless: although flightlessness is advantageous in this type of environment, it reduces substantially dispersal capabilities, and hence the possibility of tracking suitable climatic conditions. In fact, because of their adaptations to sand substrates and the limited extension of sandy shores, these animals are strictly confined to environments that are experiencing a dramatically fast increase in average temperature with no possibility to escape.

Keywords: activity patterns, aridity, climate change, coast, darkling beetles, desert, thermoregulation, insects.

Introduction

The family Tenebrionidae is one of the largest of Coleoptera, comprising more than 30,000 known species worldwide (Bouchard et al. 2021). Adult tenebrionids exhibit an extraordinary diversity of forms, whereas larvae are more uniform (Lawrence & Spilman 1996; Matthews et al. 2010). Tenebrionids (both adults and larvae) are primarily saprophagous, feeding on a variety of dead plant and animal matter, although a number of species feed on living plants and a few are predators or semipredators; termitophiles and myrmnecophiles are also known (Aalbu et al. 2002; Matthews & Bouchard 2008; Matthews et al. 2010). The majority of adult tenebrionids are more or less heavily sclerotized, dark in color, and active on the ground or on the surfaces of logs or tree trunks. Brachyptery and aptery are common, and characterize almost all members of certain large groups like the subfamily Pimeliinae. Tenebrionids can be divided into two groups according to their major habitats: (i) xylophilous species, which occur in rotten wood and associated cambium and subcortical spaces, and (ii) geophilous species, which occur in the soil and leaf litter (Lawrence & Spilman 1991).

Tenebrionids are strongly represented in tropical and subtropical regions and in both hot and cold deserts, being less numerous in damp, cool-temperate climates (Matthews et al., 2010). Many geophilous tenebrionids occur in the steppes and deserts, where larvae mature in the soil, mostly feeding on plants or decaying materials, as well as in costal sand dunes. Tenebrionids are a conspicuous element of most arid and semiarid environments (Nicolson 1990; Guodong & Youzhi 1999; de los Santos 1994; de los Santos et al. 1988, 2000; Dajoz 2002; Matthews & Bouchard 2008; Matthews et al. 2010; Lamb & Bond 2013; Carrara et al. 2021), and many species inhabiting these habitats exhibit a number of morphological, physiological and behavioral adaptations for thermoregulation and water balance (e. g. Nicolson 1990; de los Santos 1994; Zachariassen 1996; Flores 1998; Cloudsley-Thompson 2001). It is possible that these adaptations have promoted tenebrionid diversity in arid environments by reducing extinction rates and increasing speciation rates (Cloudsley-Thompson 2001). For example, morphological and ethological adaptations might have reduced extinction rates by allowing tenebrionids to exploit a variety of niches, which in turn reduces extinction for competition (Carrara & Flores 2015). At the same time flightlessness (a common feature of tenebrionids of arid environments) might have contributed to increase speciation rates by increasing population isolation (Kergoat et al. 2014).

Although the tenebrionid faunas of arid environments are rich, their communities are usually composed of few species (Dajoz 2002; Fattorini et al. 2020) and strongly dominated by locally very abundant species (Thomas 1983; Aldryhim et al. 1992; Ayal & Merkl 1994; Niu et al. 2019). These communities exhibit species-abundance distribution patterns that conform to the "niche pre-emption" model, which is indicative of simple communities of harsh environments (Fattorini et al. 2016, 2017, 2020). Both desert and beach-dune systems are strongly influenced by scarce resources (mostly represented by debris) and challenging climatic and edaphic factors. Thus, these environments can be best colonized by a small number of sand-specialized *r*-selected tenebrionid species that can use decaying organic matter (Fattorini 2008; Fattorini et al. 2012, 2016, 2017).

Tenebrionids are among the most diversified and abundant arthropods in sand dune ecosystems of the Mediterranean basin (Fattorini 2008; Audisio & Vigna Taglianti 2010; Fattorini et al. 2012, 2015, 2016, 2017). However, their conservation is strongly threatened by the profound human impacts that affect these environments. Most of the Mediterranean sand dunes have disappeared or have been severely damaged, and most of the few that are still in relatively good conditions are in danger of being altered or destroyed by coastal erosion, farming practices, urban development, and pressure from tourism (Fattorini 2022). Additionally, since the Mediterranean costal dunes are frequently interrupted by rocky shores, the insects associated with sandy shores have naturally fragmented populations, and this isolation is further exacerbated by anthropogenic impacts. As a result, many tenebrionids in Mediterranean coastal areas are in strong decline and some formerly common species have now disappeared from various areas (Fattorini 2008, 2022).

An important source of concern about the conservation of insects inhabiting the Mediterranean dunes is the possible impact of the ongoing climate change. The Mediterranean region is warming 20% faster than the global average and precipitations are expected to drop dramatically (a 2 °C global warming will reduce precipitation by ~10 to 30%) (Cramer et al. 2020). With 2 °C global warming, maximum daytime temperatures will likely increase by 3 °C, and for 4 °C of global warming nearly all nights will be tropical, with almost no cold days (Cramer et al. 2020). Additionally, even a small increase in mean temperature can dramatically increase the frequency and magnitude of extreme high temperature events. In the Mediterranean Basin, the occurrence and the duration of extreme temperature events have already increased by 200%–500% over the past 70 years (Diffenbaugh et al. 2007; Vargas-Yáñez et al. 2008, 2010). In the future, warm temperature extremes will further increase, and heat waves will intensify in duration and peak temperatures (Cramer et al. 2020). These changes will have deleterious effects on the coastal biotas, which already experience very high temperatures and water scarcity.

Increasing temperatures may severely threaten species living close to their upper climatic tolerance limits, and the rapidity of climate change may make difficult for many species to track suitable climatic conditions, particularly if they have low dispersal abilities (Garcia et al. 2014). Thus, despite their adaptations to extreme temperatures, species living in arid environments may be particularly vulnerable to increasing temperature, due to physiological limits constraining the evolution of species' tolerances to high temperatures. Diurnal ectotherms of hot environments are especially vulnerable to temperature changes, as they regulate body temperature directly from external sources (Barrows 2011).

Changes in precipitations patterns are also expected to severely affect species of arid environments (Vale & Brito 2015). In arid environments, rain has a pivotal role in promoting germination and hence food and water supply for animal communities (Beatley 1969; Brown & Ernest 2002), and increasing aridity has already documented negative impacts on arid adapted animals (Vale & Brito 2015).

Specifically, this review will: 1) illustrate how high temperatures may represent challenging conditions even for thermophilous tenebrionids of Mediterranean dunes; and 2) discuss how the ongoing climate change, with increasing average temperatures and extreme events, is likely to negative influence these insects because of the constraints represented by their adaptations to the dune environment.

Morphological and physiological adaptations

Tenebrionids of arid environments show several morphological and physiological adaptations to cope with high temperatures and water scarcity (e.g., Marcuzzi 1960a,b; Edney 1971; Fiori 1977; McClain & Gerneke 1990; Nicolson 1990; Cloudsley-Thompson 1991, 2001; Heinrich 1993; Dajoz 2002; Matthews et al. 2010). Tenebrionids found in Mediterranean sand dunes resemble in many aspects those living in desert environments (with many genera being in common), because desert and coastal sand dunes have many similarities, being characterized by high temperatures, pervading aridity, and sand substrates. Thus, although research on the morpho-physiological adaptations of tenebrionids living on Mediterranean sand dunes are virtually lacking, some considerations can be made on the basis of their resemblance with allied groups living in desert environments whose adaptations have been well investigated.

One of the most striking features exhibited by diurnal tenebrionids of Mediterranean dunes is their dark coloring, a situation also common in many desert species (Cloudsley-Thompson 1999, 2001; Matthews et al. 2010). The possible role of a black coloration in sunny environments has been long debated and no satisfactory explanation has been proposed (Marcuzzi 1960b; Edney 1971; Heinrich 1993; Cloudsley-Thompson 2001; Matthews et al. 2010). Even the hypothesis that a black color may help diurnal species to maximize the mean time of potential activity at elevated body temperatures (Hamilton 1973, 1975) seems to be not supported experimentally (Ward 1991). Interestingly, while coloration of diurnal tenebrionids of desert environments varies from black to white, that of diurnal species inhabiting the Mediterranean dunes is invariably dark (Marcuzzi 1960b; Cloudsley-Thompson 2001). A possible explanation of dark colors in diurnal species among Mediterranean tenebrionids might lie in their phylogenetic history. Mediterranean species belong to clades that likely evolved in desert areas (see below), and which might require high body temperatures to maximize their metabolic activities. Although the ambient temperatures in the Mediterranean might easily exceed these thresholds (and even the lethal ones) during the hottest hours, a black coloration might provide an advantage in heat absorption for most of the day (e.g., during the morning), when temperatures are relatively low. On the other hand, especially in summer, temperatures on Mediterranean dunes can be very high even for thermophilous species. Sand temperatures in Mediterranean dunes can reach very high values in summer (exceeding, for example, 55 °C in Central Italy; Chelazzi et al. 1990), which may expose tenebrionids to intolerable heat. Thus, most of morpho-physiological and ethological adaptations of Mediterranean tenebrionids are clearly associated with the need to cope with high temperatures.

Elongated legs may represent an important adaptation in diurnal species which are active on hot sand of both desert and Mediterranean dunes. The adaptations of the legs of desert tenebrionids have been reviewed by Dajoz (1984), whereas there are no reviews for Mediterranean species. In desert tenebrionids, elongated legs allow these beetles to run swiftly across the hot sand from the shade of one plant to another (Cloudsley-Thompson 2001), and the same behavior can be observed in the tenebrionids living on the Mediterranean dunes (e.g., *Pimelia*, *Erodius*, *Tentyria*), although there are no precise measures of their speed. Clinal variations in the relative length of legs also support their adaptive value in Mediterranean ecosystems. In *Adesmia*, the relative length of legs increases gradually from the Mediterranean zone to the eremic region of Palestine, at both intra- and interspecific level (Broza et al. 1983). Notably, populations of the same subspecies that live in different places show larger differences than those between distinct taxa living in the same habitat, which suggests a decisive importance of leg length to the survival of these beetles in arid environments (Broza et al. 1983). The increase in the relative leg length with increasing environmental harshness also supports a possible role of stilting (that is, elevating the body as high as possible above the hot substrate) as an adaptation to hot substrates (Krasnov et al. 1996). The importance of silting in thermoregulation is however debated, being likely limited to particular environmental circumstances, and generally less relevant than that of other behavioral strategies, like finding shelter into the sand or in shaded places (Ward & Seely, 1996; Cloudsley-Thompson 2001). Clinal variations in length legs and other morphological traits have been interpreted as adaptive trends also in the genus *Hegeter* along an elevational gradient in Tenerife (Canary Islands) (de los Santos et al. 2000). Here, beetles from lowland, xeric environments show a lengthening of the legs and an increase in the body volume (which allows for a large subelytral cavity, see below), as adaptations to hot and arid climates and alluvial soils; by contrast, beetles from the highest altitudes have smaller and more cylindrical bodies and comparatively shorter legs, which might be an adaptation to hypogeic life (in turn associated with the presence of stony soils and hydric and thermic contrasts). In general, tenebrionid living in ultraxeric habitats with sandy soils tend to have large, robust, and ambulatory forms, whereas those that are associated with stony substrates or that burrow into the substrate tend to have flattened and oval forms, with shorter and strengthened legs and antennae (Fattorini 2009). Although soil temperature may play an important role in selecting leg length, the structure of the substrate is also obviously crucial. In fact, soil characteristics may be the leading factor in selecting species morphologies in Mediterranean tenebrionids. In sites with similar climatic conditions, but very different soil types, species characterized by elongated and/or fossorial legs are mainly associated with sandy soils, whereas species with broad bodies and short legs tend to prevail in stony soils (Fattorini 2009).

It is well known that desert tenebrionids (including diurnal species with very high lethal temperature levels) take shelter rhythmically during the day in burrows, hide beneath stones and rocks, or tunnel into loose sand to avoid excessively heat (Cloudsley-Thompson 2001). This behavior is also common in diurnal tenebrionids inhabiting the Mediterranean dunes whose forelegs are more or less markedly adapted for digging, which may be essential for these animals to find shelter from too high diurnal or to low nocturnal temperatures. Their fossorial adaptations, however, are not limited to the shape of the fore legs, but involve also the use of all legs to burrow, as observed in *Pimelia grossa* Fabricius, 1792 (Alicata et al. 1979). Since this species cannot dig vertically, burrowing is done against a dune relief (as also observed in the congeneric *P. bipunctata* Fabricius, 1781; Fattorini & Di Stefano 2004). Also, elongated legs might have an anti-predatory role, which may be important for animals that do not produce obnoxious substances. If burrowed individuals of *P. bipunctata* are extracted, they appear torpid and limit their movements to stretching the legs, thus appearing much bigger and more difficult to manipulate (Fattorini & Di Stefano 2004).

A common feature of tenebrionids living in arid environment is the loss of metathoracic wings, which leads to a preponderance of flightless species in both desert and Mediterranean faunas (Carpaneto & Fattorini 2002; Dajos 2002). Several aspects of dune environments may advantage flightless beetles. In general, it is assumed that environmental stability tends to favor flightlessness, since energy can be channeled into reproduction instead of being used for dispersal (Roff 1986). Since coastal dunes are relatively stable environments (McLachlan 1991), this might have favored flightless beetles. While Mediterranean rocky coasts have typically experienced a complex geological history with profound effects on the species associated with marine rockpools (e.g., Sabatelli et al. 2021), coastal dunes are geologically young environments, which continuously changed their extension and geographical location, but which maintained a substantial contiguity and similar conditions for long times (Fattorini 2008). Another environmental characteristic of Mediterranean dunes that might favor flightless species is habitat uniformity, since insects do not need to cover large distances to find suitable habitats. Coastal dunes are uniformly long, narrow strips, with physical, chemical and vegetational gradients only occurring perpendicularly to the shore (McLachlan 1991). Therefore, a ground dwelling insect can largely exploit the system by walking and burrowing, with no need of flying. Since resources in these environments are very limited, and the high winds occurring along seashore would make flying very costly, flight is disadvantageous. Also, the sea- and landward limits of aeolian sand transport represent clear boundaries that make coastal dunes substantially isolated environments (McLachlan 1991), which advantages flightless species, since flying individuals that disperse faraway may fail to locate favorable habitats (Darwin, 1872; Roff 1986; Wagner & Liebherr 1992). Specifically, in coastal environments, flyers could reach non-hospitable inland biotopes, or can be blown over the sea. The preponderance of flightless species in coastal dune environments can be also a consequence of the fossorial life and detritivorous feeding habits of many tenebrionids, because fossorial life combines well with flightlessness, and the spatial distribution of detritus deposits probably reduces the need to fly (Holm & Scholtz 1980). Finally, loss of wings allows the presence of a subelytral cavity hermetically sealed by connected elytra, which may represent an important adaptation to warm and arid conditions.

The subelytral cavity is a common feature of desert tenebrionids (Marcuzzi 1960b; Fiori 1977; Heinrich 1993; Draney 1993) and is also particularly evident in large-sized diurnal species commonly found on Mediterranean dunes (e.g., *Erodius*, *Pimelia*, *Tentyria*). The subelytral cavity is an important adaptation in dry and hot environments because it helps beetles to retard heat flow from the elytra to the abdomen. Actually, there is evidence that the temperature of the subelytral cavity is lower than that of the body itself (Heinrich 1993). The subelytral cavity has been long considered also an important adaptation to reduce water loss. Beetles living in arid environments have reduced their cuticular transpiration to such an extent that respiratory water loss has become the major component (Cloudsley-Thompson 2021). Since the abdominal spiracles open into the subelytral cavity, it has been postulated that the presence of a subelytral cavity may have an important function in preventing water loss by spiracular transpiration (Cloudsley-Thompson 2001). However, experiments conducted in the tenebrionid *Onymacris multistriata* (Haag-Rutenberg, 1875), a desert species with a large subelytral cavity, showed that ventilation is virtually limited to the mesothoracic spiracles, thus indicating that the function of the subelytral cavity in respiration needs to be re-evaluated (Duncan 2003). It has been also suggested that the subelytral cavity may allow the abdomen to expand for the storage of water, food, and eggs (Fiori 1977), and these functions might be the most important ones. In desert beetles, gas exchanges occur through a discontinuous ventilation pattern characterized by three periods: (1) a first period, in which the spiracles are closed; (2) a flutter period, in which discrete bursts of carbon dioxide are emitted through miniature openings; and (3) a burst period, in which a rapid unloading of carbon dioxide minimizes the time the spiracles are widely open and therefore reduces the loss of water vapor (Duncan 2003). Although in insects that use discontinuous gas exchange cycles only a relatively small fraction of the overall water loss is due to respiration, even this small reduction would increase their survival chances, and restricting gas exchange to only the mesothoracic spiracles will help to further minimize potential water loss (Duncan 2003). In *Pimelia grandis* Klug, 1830, dehydrated beetles use discontinuous gas exchange cycles, whereas beetles given access to food and water show a form of continuous carbon dioxide release, which supports the hypothesis that the discontinuous gas exchange cycle is an adaptation to reduce respiratory water loss (Duncan et al. 2002).

The lack of experimental research on the physiology of Mediterranean tenebrionids represents a relevant gap of knowledge. Most of the scarce information available for Mediterranean species seems so far restricted to pioneering research by Marcuzzi (1960a), who found a rapid decrease in the water content in *P. bipunctata* with decreasing levels of environmental humidity, and a relatively high value of water loss due to transpiration in *Scaurus striatus* Fabricius, 1792, and *Tentyria grossa* Besser, 1832. Further research on the physiology of tenebrionids of Mediterranean coastal environments might open very promising perspectives, especially for comparative analyses with desert species.

Although some fossorial tenebrionid beetles living on Mediterranean dunes are very small (like *Ammobius rufus* (Lucas, 1846) and *Trachyscelis aphodioides* Latreille 1809, which have a total body length smaller than 4 mm), surface active tenebrionids tend to have large body size (for example, *Erodius*, *Pimelia* and *Tentyria* have body lengths approximatively ranging between 10 and 20 mm). It has been suggested that this might have an adaptative value: since larger species should have lower transpiration rates in proportion to smaller species, they might use transpiration to reduce body temperature without losing excessive amounts of water (Marcuzzi 1960b). However, this hypothesis contrasts with the very low transpiration rates observed in desert beetles (Cloudsley-Thompson 2021) and in at least one Mediterranean species (*Tentyria cypria* Kraatz, 1865; Constantinou 1988)

In contrast with diurnal tenebrionids, nocturnal tenebrionids of Mediterranean dunes (e.g., *Halammobia* spp., *Phaleria* spp., *Xanthomus* spp.) tend to have pale-colored, less convex, and smaller bodies (typically between 4 and 8 mm), because they are less exposed to high temperatures and dehydration (Colombini et al. 1994; Ferrer & Whithead 2002; Fattorini 2008). However, in these nocturnal species there is a subelytral cavity, particularly well developed in *Halammobia* and *Xanthomus*, which supports the idea that it might have a secondary role in thermoregulation and respiration, being possibly more important for storage of water, food, and eggs. Melanistic individuals are common in the genus *Phaleria*, possibly as an adaptation to black (volcanic) sand (Aliquò 1993), although this contrasts with the co-occurrence of yellow individuals and the habitats they occupy (they find shelter under debris, where they cannot be found by predators that search for insects by eye) (Marcuzzi 1996). Legs in nocturnal species tend to be less elongated compared to those of diurnal ones. However, differences in leg length can be observed in species with different ecology. *Phaleria* spp., which live under detritus stranded on the beaches, have relatively short legs (with the fore legs showing apically enlarged tibias to assist digging). By contrast, *Xanthomus* spp., which are associated with plants growing on the dunes, have elongated legs, more adapted to climbing than to digging (Ponel 1983).

All the aforementioned morphological adaptations to arid and hot conditions shown by tenebrionids living in Mediterranean coastal areas are not the result of adapting to the coastal sand dune environment, but may be regarded as pre-adaptations already present in the desert lineages from which the Mediterranean species likely derived. Since the Mediterranean dunes are geologically recent, the tenebrionids living there are probably derived from stocks of desert species already adapted to colonize hot and sand environments (Fattorini et al. 2017). For example, based on molecular data, Mas-Peinato et al. (2018) suggest North Africa as the most likely origin area of the genus *Pimelia*, which then colonized the Mediterranean. Unfortunately, however, there are no sufficiently detailed phylogenetic reconstructions to assess how and where the adaptive traits of these lineages evolved, and this lack of information represents an important gap for our understanding of the evolution of adaptations of tenebrionids to harsh climatic conditions.

However, the low mobility due to being flightless may have promoted speciation rates in coastal tenebrionids, which, coupled to reduced extinction rates due to adaptations that allow them to exploit efficiently a great number of niches, may explain the high diversity of certain tenebrionid groups (*Erodius*, *Pimelia* and *Tentyria*) in Mediterranean ecosystems.

Despite the increasing interest in the use of detailed analyses of larval characters in beetle taxonomy and systematics (Sabatelli et al. 2013; Mahlerová et al. 2021), tenebrionid larvae are still very poorly known (Kamiński et al. 2019) and the possible adaptive value of morphological traits of tenebrionid larvae living in arid environments has been explored only very recently (Raś et al. 2022). Larvae of Mediterranean tenebrionids are almost completely unknown, with few and generally outdated descriptions (Marcuzzi & Rampazzo 1960; Marcuzzi et al. 1980). However, a very low ratio between the size of spiracles and body surface observed in certain coastal species has been interpreted as an adaptation to reduce dehydration (Marcuzzi 1960a), suggesting that more research on this field would lead to important results for understating the ability of larvae to cope with the harsh conditions of Mediterranean dunes.

Species life cycles

Species life cycles of tenebrionids inhabiting the Mediterranean dunes show peculiar adaptations to cope with the unfavorable conditions of these environments. For example, a high abundance of *Phaleria provincialis* Fauvel, 1901 in summer might be due to the need of producing a high number of individuals to compensate the high mortality occurring in autumn (Fallaci et al. 2002). Additionally, autumn and summer populations of this species show differences in the size of larvae and adults as a result of the influence of temperature on larval development, with higher temperatures inducing higher metabolic rates, and hence a more rapid development, which turns into smaller larvae in summer; these smaller larvae produce smaller autumn adults; by contrast, larvae developing at the lower temperatures of autumn months develop slowly, which means longer feeding periods and hence bigger adults (Fallaci et al. 2002). In this species, activity rhythms differ between sexes, with females being more active than males in autumn, possibly because of their need of finding food for future egg production (Fallaci et al. 2002). *Ammobius rufus*, a fossorial species widely distributed on the Mediterranean dunes, is ovoviviparous (De Marzo 2004). Ovoviviparity or viviparity are rare among beetles, where they are limited to one Micromalthidae, some myrmecophilous and termitophilous Staphylinidae, some Chrysomelidae, a myrmecophilous Carabidae, and some Tenebrionidae from Madagascar and Southern Africa (Iwan 2000). Ovoviviparity in tenebrionids has been interpreted as a possible adaptation to extremely adverse habitat conditions (Iwan 2000), and it can be speculated that ovoviviparity in *A. rufus* also has an adaptative role, allowing females to oviposit at some depth, after they have incubated eggs in the superficial sand layer (De Marzo 2004).

Temperature is an important driver of the life cycle of Mediterranean tenebrionids, as exemplified by *Pimelia bipunctata*. Observations conducted in France (Brun 1970) indicate that the species has a winter diapause with two periods. If in the first period (November to February, when sand temperature is between 0 and 10 °C), corresponding to the true diapause, individuals are exposed at higher temperatures, they became shortly active, and then return into diapause; by contrast, in the second period (i.e., after February), individuals placed at higher temperatures became permanently active. Egg viability, embryonic development, and larval development are positively conditioned by temperature. Embryonic development has an upper thermal threshold of 36 °C, egg viability is maximum at 26.5 °C, and maximum growth rate occurs at temperatures above 30 °C. The importance of temperature variations in regulating tenebrionid life cycles has been also investigated in some species of Mediterranean grasslands and pinewoods, showing the presence of two types of life cycles: a "one-year life cycle, overwintering as larvae" (in which adults emerge in spring), and "two-year life cycle, larvae and adults overwintering" (in which adults emerge in midsummer), whereas the aforementioned cycle of *P. bipunctata* would be classified as "three-year life cycle, adult and two generations of larvae overwintering" (de los Santos et al. 1988).

For desert tenebrionids, maximum tolerated temperatures have been measured in numerous species and they are usually between 43 °C and 53 °C (Draney 1993; Cloudsley-Thompson 2001). Unfortunately, evidence for Mediterranean tenebrionids is very limited, since there is virtually no available data, apart those reported for a few species studied by Bodenheimer (1934; Figure 1). However, these are consistent with the effects of increased temperatures reported for allied taxa from similar environments. For example, Heatwole & Harrington (1989) reported that *Blaps gigas* (Linné, 1767) survived 40 minutes at 45 °C, whereas *Pimelia obsoleta* Solier, 1836 survived for only 8 minutes. These two species are not typical inhabitants of dunes, yet they are Mediterranean species associated with arid environments (notably, *P. obsoleta* is common in very arid and hot places in North Africa). Thus, these data are indicative of how high temperatures (which can be easily reached on Mediterranean sand dunes) might be lethal even for short exposures.

In general, low nocturnal temperatures usually experienced by the tenebrionids living in Mediterranean coastal areas during their activity periods seem to be not challenging for these animals, yet they are exposed to intolerably low temperatures in the winter as overwintering adults or larvae. Although there is no specific information on the lethal lower temperatures for tenebrionids inhabiting the Mediterranean dunes, it is known that in *P. bipunctata* mortality rates are high at temperatures lower than 10 °C (Brun 1970), and it has been observed that the adults of *Blaps mucronata* Latreille, 1804, a species associated with humid and cool places in Central and Southern Europe, can survive only few hours when exposed to temperature below 0 °C (Belcari et al. 1980). Thus, it can be expected that more thermophilous species such as those that live on Mediterranean dunes will be even more sensitive to low temperatures.

Zonation

Tenebrionids of coastal sand dunes show distinct zonations perpendicularly to the shoreline that reflect temperature and humidity gradients (Fattorini 2008). In general, zonal preferences appear related to the nocturnal/diurnal habits of the species. Nocturnally active species (*Phaleria provincialis* and *P. bimaculata* (Linnaeus, 1767), *Halammobia pellucida* (Herbst, 1799) and *Xanthomus pallidus* (Curtis, 1830)) are generally found further seawards and have larger zonations than those active by day (like *Erodius siculus* (Solier, 1834) and *Pimelia bipunctata*), which are more strictly associated with the base of the dune (Colombini et al. 1994) possibly because of their overall preferences for drier substrates (Fallaci et al. 1997).

Experiments conducted in nocturnal species such as *Phaleria acuminata* Küster, 1852, *P. provincialis* and *P. bimaculata*, *H. pellucida*, *X. pallidus,* and *X. pellucidus* (Mulsant & Rey, 1856) indicated that they can maintain or change their foraging and resting zonation on diel and seasonal basis by using moisture, salinity and granulometric cues, depending on the species (Tongiorgi 1969; Aloia et al. 1999; Colombini et al. 1994, 2002, 2005; Fallaci et al. 2002). In *Phaleria provincialis*, winter storms tend also to move the mean zonation landwards (Fallaci et al. 2002).

Astronomical orientation may be important in nocturnal species, and *Phaleria* spp. use it to return from displacement in normal conditions as well as under stress (Pardi 1956; Chelazzi & Colombini 1989). However, *Phaleria* species living on Mediterranean coasts (where tides are negligible) do not show orientation behaviors in relation to tidal phases, while the Atlantic species *P. cadaverina* (Fabricius, 1792) shows distinct seaward and landward tidal movements to track conditions of air humidity, soil moisture, air temperature and soil temperature which are suitable for burrowing and surface activity (Colombini et al. 1996).

Larval zonation can be different from those of the adults. The larvae of *Phaleria provincialis* tend to occupy a more landward area because: (1) their slower movements do not allow a fast zonal recovery during winter; (2) a more landward burrowing area may be safer for the pupal stage, which is immobile; and (3) landward zones could have temperature and moisture values more favorable to the metabolic needs of the larvae (Fallaci et al. 2002).

Although morphological differences among tenebrionid species associated with different zones of Mediterranean ecosystems did not evolve in consequence of competitive pressure (Martín Cantarino & Seva Roman 1991), adult and larval zonations may act as habitat segregation, thus reducing competition.

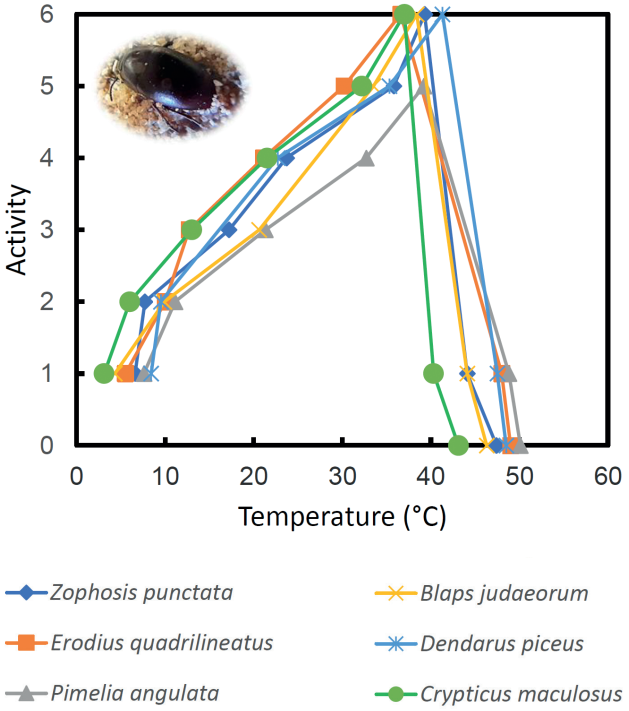

Fig. 1 – Relationship between activity and temperature in some tenebrionid species in Palestine investigated by Bodenheimer (1934). Activity intensity is expressed by the following rank scale: **(1)** cold-torpor, **(2)** only weak, occasional movements of legs and antennae, **(3)** crawling with interruptions, **(4)** normal activity, **(5)** high activity, **(6)** excited activity, **(1)** heat-torpor, **(0)** heat-death. Redrawn from Fattorini (2008) with corrections. Inset: *Zophosis punctata* (photo S. Fattorini).

Activity patterns

The diel activity of tenebrionids of arid environments is thermally opportunistic as it varies in response to variation in ambient temperatures. Diel activity patterns, during which the beetles burrow into the soil or emerge from their burrows, are an important feature of species inhabiting deserts (Costantinou 1988; Cloudsley-Thompson & Costantinou 1981, 1985; Dajoz 2002). This also applies to Mediterranean tenebrionids, especially diurnal species that are black colored. If a black surface may lead a rapid warm-up and activity, it would also lead to earlier retirement from activity as environmental temperatures rise. In a seminal paper on the ecology of tenebrionids in Palestine, Bodenheimer (1934) investigated the activity of various coastal species at different temperatures in laboratory experiments. The studied species showed a positive response of activity to increasing temperature, until an intolerable temperature is reached (Fig. 1). Field observations also proved that soil temperature was more relevant than ambient temperature in determining species activity, being very important in regulating the activity rhythms of *Pimelia angulata* Fabricius, 1775 and *Blaps judaeorum* Miller, 1861 on Tel Aviv dunes (Bodenheimer 1934). These species pass the night burrowed, are active at relatively high temperatures (more than 22 °C and 14 °C, respectively), but return into the soil when temperatures are too high (38 °C and 27 °C, respectively). In general, diurnal species of Mediterranean dunes (e.g., *Erodius siculus*, *Pimelia bipunctata*, *P. grossa*, *Tentyria grossa*, and *T. elongata* Waltl, 1839) are found buried when temperature are too low or too high, with some minimal thresholds needed to enable individuals to terminate diapause or to become active during the day (Brun 1970; Alicata 1979; Martín Cantarino & Seva Roman 1992; Fallaci 1997; Di Stefano & Fattorini 2000; Fattorini & Di Stefano 2004). Their locomotory activity tends to increase with increasing temperatures, but too high temperatures have a negative influence (Fig. 2A), and activity patterns can shift from unimodal to bimodal, with a drop in the central part of the day, when temperatures are higher (Colombini et al. 1994; Fallaci et al. 1997; Di Stefano & Fattorini 2000; Fattorini & Di Stefano 2004). This shift from unimodal to bimodal activity patterns is distinctly associated with changes in diel temperature variations during seasons. In desert environments, species that are diurnal in spring, can become nocturnal in summer (Cloudsley-Thompson 2001). On the Mediterranean dunes, species that show unimodal activity patterns in spring, can shift to bimodal patterns in the hottest months, when they may extend their activity to the nocturnal hours or can become even nocturnal (Fallaci et al. 1997; Di Stefano & Fattorini 2000; Fattorini & Di Stefano 2004). The diel activity of *Pimelia bipunctata* in Latium clearly illustrates how this species shifts from unimodal to bimodal activity patterns (Colombini et al. 1994; Fallaci et al. 1997) depending on temperatures (Fattorini & Di Stefano 2004) (Fig. 2 B, C). Since a temperature of 23-25 °C may enable individuals in winter diapause to become active (Brun,

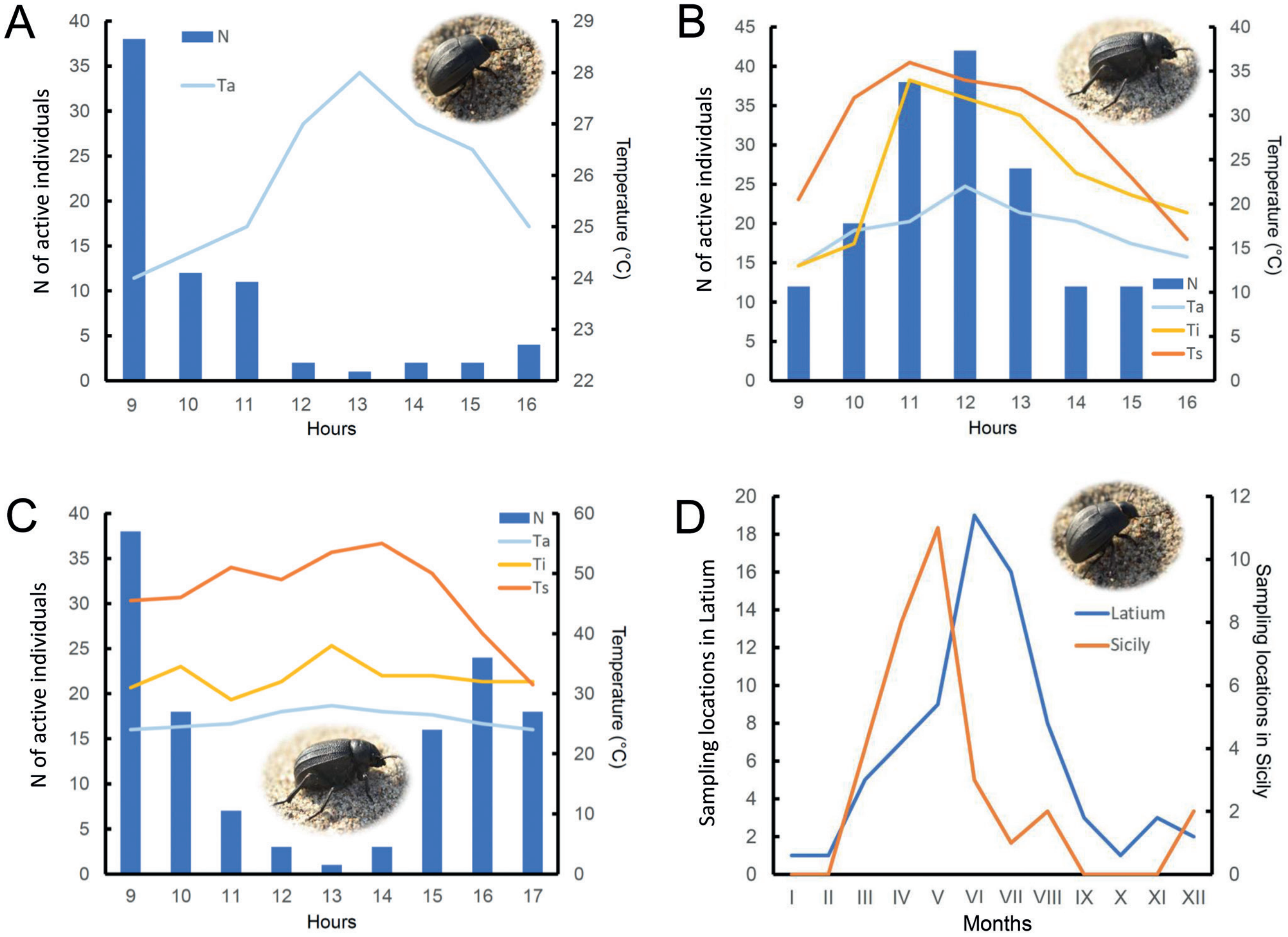

Fig. 2 – Diel and monthly activity patterns of tenebrionid beetles of Mediterranean dunes. **A**, diel activity of *Erodius siculus* in Latium (Central Italy) in May 1997; **B**, diel activity of *Pimelia bipunctata* in Latium (Central Italy) in March 1997; **C**, diel activity of *Pimelia bipunctata* in the same locality in May 1997. In these experiments, activity was measured as number of individuals intercepted by pitfall traps per hour in single days. After counting, beetles were immediately released. N: number of trapped individuals per hour. Ta: ambient temperature (°C), Ti: soil internal (3-4 cm depth) temperature (°C), Ts: soil surface temperature (°C). **D**, Phenological patterns of *Erodius siculus* in Latium (Central Italy) and Sicily (Southern Italy). Phenologies are expressed as number of locations in which the species has been recorded in each month over a period of a century (from 1897 to 1997). A and D are based on Di Stefano & Fattorini (2002). B and C are based on Fattorini & Di Stefano (2004). Photos: courtesy of L. Di Biase.

1970), it is probable that 24 °C is a thermal optimum for the activity of this species, whereas too hot sand temperatures (which can surpass 50 °C in its Italian range) inhibit movements. Similar seasonal shifts from unimodal to bimodal patterns have been observed in *Pimelia grossa* in Sicily (Alicata 1979), *Tentyria elongata* in Southern Spain (Martín Cantarino & Seva Roman 1992) and *T. grossa* in Tuscany (Colombini et al. 1994).

In fact, the activity patterns of diurnal tenebrionids on Mediterranean dunes is influenced by numerous factors, including light:dark cycle, air temperature (in sunlight and in the shade), air humidity, global radiation, and temperatures on the sand, under the sand, and on the sand under plants they can use to find shelter, with differences among species and seasons (Fallaci et al. 1997). In desert environments tenebrionids tend to prefer vegetation over open sands, not only for thermoregulation, but also because vegetation may offer greater food resources, better protection from predators, better oviposition sites, and higher relative humidity (Ismail & Bartholomew 2020), and the same applies to species living on Mediterranean dunes. It is worth mentioning that, while most tenebrionids have defensive glands, most of the diurnally active tenebrionids of Mediterranean dunes belong to the subfamily Pimeliinae, which lack these glands (Doyen 1993) and are therefore potentially exposed to high predation (Ayal & Merkl 1994; Fattorini 2000).

Nocturnal species like those of the genus *Phaleria*, being not exposed to intolerably high temperatures, have typical unimodal patterns, or are active all the night round depending on the season (Tongiorgi 1969; Colombini et al. 1994), but show the ability to change their burrowing depth according to the hour of the day (Aloia et al. 1999).

Seasonal changes in temperatures also influence tenebrionid phenological patterns. For example, *P. bipunc-*

tata in Latium is present all year round, being however particularly abundant in spring and autumn, with drops in summer (when temperatures are too high) and winter (when temperature are too low and inactive, buried individuals are found) (Fattorini & Di Stefano 2004). This pattern is consistent with the biological cycle observed in France by Brun (1970). Nocturnal species tend to show broader phenologies. *Xanthomus pallidus* and *X. pellucidus* (which prefer relatively low temperatures) are active in autumn and winter, whereas more thermophilic species, like *Halammobia pellucida*, *Phaleria bimaculata* and *P. provincialis*, are active throughout the whole year or in spring/summer (Aloia et al. 1999).

As water availability is an important limiting factor in arid environments, peaks of abundance in autumn observed in several coastal tenebrionid species may be related to the water input provided by restarting precipitation (Fattorini 2008). This parallels the biology of tenebrionids of hot, dry deserts, whose adults usually emerge and/or became active at the time of the rains, when the weather is cooler and food is more abundant (Cloudsley-Thompson 2001). However, phenological patterns can show geographical differences according to local climate. For example, the phenological peak of *Erodius siculus* which occurs in summer in Central Italy is anticipated to spring in Sicily, where the climate is warmer (Fig. 2 D) (Di Stefano & Fattorini 2000).

It is possible that interspecific differences in diel and seasonal activity patterns may help species to reduce competition (Draney 1993). For example, in Central Italy, while *Tentyria grossa* is more active in the morning and in the evening, *Pimelia bipunctata* is more active in the central part of the day (Fallaci et al. 1997). Competition, however, might be avoided by differences in spatial and trophic niches. For example, *Phaleria bimaculata* and *P. provincialis*, which are sympatric on the Tyrrhenian seashore, show similar circadian activity rhythms (Colombini et al. 1994), but *P. provincialis* tends to forage in a more seaward area (Aloia et al. 1999). The two species may also differ in the trophic niche. Although *Citrobacter* and *Hafnia* are usual components of the gut microbiome of both species, *P. bimaculata* shows a higher microfloral biodiversity, which suggests differences in foraging areas and/or sensitivity to moisture and salinity (Barberio et al. 2001). Also, their life cycles are slightly shifted, and the two species are differently adapted to the beach environment (*Phaleria provincialis* is more thermophilous than *P. bimaculata*) (Fallaci et al. 2002).

Similarly, *Xanthomus pallidus* and *X. pellucidus*, which have an overlapping unimodal activity in the winter months, differ in their zonation (*X. pallidus* is more halophilous than *X. pellucidus*), trophic preferences (*X. pallidus* feeds on detritus, especially *Zostera*, as well as on seeds of *Ammophila arenaria* (L.), whereas *X. pellucidus* seems to be phytosaprophagous), and foraging behaviors (*X. pellucidus* spends more time buried, and less time wandering in search of detritus) (Colombini et al. 1994; Aloia et al. 1999).

In summary, it is apparent that diel and seasonal changes in temperature regulate tenebrionid activity patterns on the Mediterranean coastal dunes, since activity rhythms are positively influenced by temperature, but too high temperatures have an opposite effect, being intolerable even for thermophilous species.

Climate change

In theory, insects might track the climate change by moving towards higher latitudes or higher elevations to find cooler environments (Hickling et al. 2005; Crozier & Dwyer 2006; Wilson et al. 2007; Colwell et al. 2008; Sunday et al. 2011, 2104; Pélissié 2022). The ability of tenebrionids inhabiting Mediterranean dunes to track a suitable climate is however limited by their high specialization to warm and arid sandy environments (illustrated in Section Morphological and physiological adaptations of this review). Species that are strongly adapted to sand cannot disperse over different types of substrates, which limits their latitudinal movements, because sandy coasts in the Mediterranean are continuously interrupted by rocky shores (Fattorini 2022). Elevational changes are also impossible because of geographical constraints, since coastal dunes obviously occur only at sea level. Thus, species associated with coastal sandy areas cannot track the climate change, neither latitudinally (i.e., moving northwards) nor vertically (i.e., moving upwards). This confinement will expose these species to the effects of climate change with no escape route, with many negative consequences (summarized in Table 1).

In general, the ongoing climate change is too fast to be efficiently tracked by changes in geographical distributions (Román-Palacios & Wiens 2020; Poloni et al. 2022), especially for species living in flat areas, as change velocities are higher there (Loarie et al. 2009). This is especially true for the Mediterranean basin, which is already experiencing an astonishingly rapid increase in the average temperature, and these changes will be particularly dramatic on coastal areas (Prisco et al. 2013; Cramer et al. 2020). In principle, insects might respond to climate change through adaptation, but the velocity of the anthropogenic climate change makes unlikely that most species will adapt to it (Kellermann & van Heerwaarden 2019; Poloni et al. 2022). This possibility is further reduced in species living near their physiological limits (Hoffmann & Sgro 2011), a situation that characterizes tenebrionids living in hot and dry environments. As a result, their climatically suitable areas will be rapidly reduced and fragmented, and hence their populations will become progressively smaller and more isolated (Table 1).

At the habitat level, climate changes may have profound impacts on the species distributions across the different zones of the beach-dune system. A large body of ecological and behavioral research on tenebrionids living in Mediterranean dunes indicates that they are distributed along the sea-inland gradient according to peculiar zonations, which can be modulated on diel or seasonal basis according to changes in environmental characteristics (see Section Zonation of this review). Since climate change in the Mediterranean coastal areas will lead to sea level rise and coastal erosion (Cramer et al. 2020; Gutiérrez et al. 2021), this will interfere heavily with zonation patterns. Sea level rise, in conjunction with increased frequency and intensity of flooding, as well as increased magnitude and duration of extreme sea level events (Cramer et al. 2020), will produce rapid and severe alterations in the zonation of the environmental characteristics of the beach-dune systems, and such changes will negatively impact tenebrionid zonations. An increase in mean sea level in association with climate variation may have profound effects on the spatial distribution of dune plant species (Mendoza-González et al. 2013). These alterations in the plant distribution may have important consequences for the spatial organization of tenebrionid communities, in which different species are associated with specific sectors of the dune (Carpaneto & Fattorini 2001, 2002; Fattorini & Carpaneto 2001), with possibly serious consequence on the whole community structure and functioning, as zonation might be important for reducing competition (Table 1). Coastal erosion is already one of the major threats to the conservation of insects of Mediterranean coastal areas (Fattorini 2022), and an accelerated sea level rise will obviously affect coastal tenebrionids by reducing the space available to these insects (Table 1).

Climate change can negatively affect many aspects of life cycles (see Section Species life cycles of this review) of tenebrionids inhabiting the Mediterranean dunes. The most obvious feature of the anthropogenic climate change is the ongoing global warming. For example, along the Italian coasts, mean temperatures are predicted to increase on average between +1.59 °C and +3.85 °C by 2050 (Prisco et al. 2013). As a result of increased average temperatures, species might change significantly their phenological patterns (Table 1). Change in phenology is one of the best documented aspects of insect response to climate change, with shifts toward earlier seasonal activity being widely recorded (Forrest 2016). However, increased temperature may also change overwintering strategies, which are particularly important for tenebrionids that overwinter buried in the sand. Tenebrionids living on Mediterranean coastal dunes have phenological patterns influenced by temperature (see Section Activity patterns of this review). A delay in the winter diapause induction might lead to a complete or partial additional generation in the autumn that cannot survive or enter diapause (Van Dyck et al. 2015; Kerr et al. 2020). This may have relevant impacts on the temporal organization of tenebrionid communities, since temporal segregation between autumn and summer specialists may be an important factor regulating tenebrionid communities in Mediterranean dunes (Carpaneto & Fattorini 2001, 2003).

For many insects, an anticipated phenology translates into an increase in the length of the activity period (Menéndez 2007), but some species do not show the expected advance in springtime (Forrest 2016). In the case of tenebrionids of Mediterranean dunes, too high temperatures in summer might lead many species, especially the summer specialists, to become inactive earlier, and if this is not compensated by a phenological anticipation, their phenology will be shortened. This contraction in their phenology might reduce the possibility to find food (and water), which is particularly harmful for insects living in environments poor in resources like the sand dunes.

Global warming might expose tenebrionids living in Mediterranean coastal dunes to summer temperatures surpassing the optima and possibly even the upper thermal limits of many biological processes. Thermal responses of biological activities follow performance curves (Nati et al. 2016), in which above the optimal temperature there is a rapid decline, until the upper lethal temperature limit is reached. The difference between the upper thermal limit and the upper environmental temperature is defined as the "thermal buffer" (Bennett et al. 2015). Increasing temperatures due to the climate change will easily erode this buffer. This will lead to an increased risk of experiencing temperatures that are higher than the optimal ones, or even exceeding the upper thermal limit (Table 1). Since thermal upper limits tend to be inevitably close to the thermal optima for species living in hot environments, even a small increase in average temperature might expose these species to lethal conditions.

Even if the average increase in temperatures might not exceed the thermal limits, these might be fatally surpassed during extreme events. Climate change does not simply consist in a general increase of average temperatures, but includes also an increase in the frequency, intensity, and duration of heat extremes (Arias et al. 2021), which may be fatal for populations that are already exposed to temperatures close to the maximum threshold. Even when temperatures remain below the lethal limit, they might be still too higher (or to low) for many biological processes, including reproduction (Table 1). Tenebrionids of Mediterranean dunes might be particularly affected by these threats. For example, in *Pimelia bipunctata*, there is no hatching when temperatures are too low (15 °C) or too high (41 °C) (Brun 1970), and these conditions might be easily reached during climate extremes. Even highly thermophilous tenebrionid species cannot survive to very high temperatures above their maximum limits. Thus, temperatures that surpass these thresholds, even for short periods, are expected to increase mortality rates (Table 1).

Although the average increase of temperature and the higher frequency and intensity of periods of excessively high temperature are the major source of concerns, the ongoing climate change might lead to an increase of occasional, short periods of excessively low temperatures (De

Table 1 – Impacts of climate change on the biology of tenebrionids living on Mediterranean dunes.

Change	Environmental consequences	Effects on tenebrionids	Consequences
Gradual long-term increase in temperatures	Changes in the extent of climatically suitable areas	Range contraction and fragmentation (for most species that occupy the warmest areas)	Reduction in population size; increased isolation between populations
Gradual long-term increase in temperatures	Changes in local climatic conditions	Range extension (for species that currently do not occupy the warmest areas)	Alterations in interspecific relationships
Gradual long-term increase in temperatures	Changes in local climatic conditions	Shifts and/or reductions in species phenologies	Alterations in temporal segregation; less time for mating and foraging
Gradual long-term increase in temperatures/Extreme events	Changes in local climatic/weather conditions	Alterations of biological processes regulated by temperature (e.g., fecundity and development) because of temperatures that are superior/inferior to the optima or the upper limits	Lower fecundity and higher mortality
Gradual long-term increase in temperatures/Extreme events	Changes in local climatic conditions	Alterations in diel and seasonal patterns of activity rhythms	Less time for foraging and mating
Gradual long-term increase in temperatures/Extreme events	Increased drought periods	Reduced access to water	Water deficits
Sea level rise, coastal erosion, increases in temperatures, etc.	Impacts on dune vegetation (plant zonation and productivity)	Alterations in species zonation, food and water availability	Alteration in habitat use; lower resources; increased competition

Luca et al. 2020; Hochman et al. 2022a, 2022b), which might be close to the lower thermal limits of some biological processes in tenebrionids of Mediterranean dunes (Table 1). It has been observed that the adults of *Blaps mucronata* Latreille, 1804, a species associated with humid and cool places in Central and Southern Europe, can survive only few hours when exposed to temperatures below 0 °C (Belcari et al. 1980). Thus, it can be expected that more thermophilous species, such as those that live on Mediterranean dunes, will be even more sensitive to short expositions to low temperatures. Further studies would be useful to extend our knowledge of the response of tenebrionid biology to exceptionally lower temperatures.

The diel and seasonal activity rhythms of most species, and especially the diurnal ones, are regulated by temperature, and even the most thermophilous species have behavioral adaptations to avoid exposure to high temperatures in the hottest hours of the day (as described in Section Activity patterns of this review). In summer months, individuals tend to be active in the morning or evening, when temperature and humidity are close to the optimum, with a resting phase at intolerable temperatures in the central part of the day. Therefore, increased temperatures will dramatically reduce the time available for these species for exploiting the habitat and for mating, thus potentially increasing mortality rates and reducing reproduction rates (Table 1). Since phenological partitioning may be a mechanism to regulate competition in tenebrionids (Fattorini 2008), climatic change might also have severe effects on their community structure.

In addition to higher temperatures, the increasing duration and intensity of prolonged drought due to the climate change can affect negatively insect biology, for example by reducing reproduction rates, as water is needed for egg formation and development (Wigglesworth 1972; Ofuya & Reichmuth 2002; Gillot 2005; Telfer 2009). It is important to stress that the Mediterranean biome is characterized by very warm summers during which rainfall is virtually absent. For this reason, tenebrionid communities on Mediterranean dunes may show a peak of abundance of certain species in autumn, when rainfall restarts (Carpaneto & Fattorini 2001, 2003). Rainfall reduction is an important aspect of climate change in the Mediterranean (Cramer et al. 2020; Gutiérrez et al. 2021, Noto et al. 2023). A reduction in autumnal rainfall may suppress or strongly reduce typical autumnal peaks in species abundance of tenebrionid species, thus altering their biological cycles, which are regulated by water inputs in addition to photoperiod and temperature. Increased drought will affect directly tenebrionids by reducing water availability, but also indirectly, because less rainfall will have negative effects on the dune vegetation (Prisco et al. 2013; Zunzunegui et al. 2022), and hence will reduce the amount of detritus on which tenebrionids typically depend (Table 1).

Climate change is also expected to increase the risk of large fires in the Mediterranean (Turco et al. 2014). Increased fires due climate change are considered an important source of threats for insects, and it has been observed that burnt areas close to sand dunes are rapidly colonized by tenebrionids adapted to arid environments, with a complete transformation of the community structure (Fattorini 2010).

Although some species might benefit from warmer conditions that increase survival rates or enhance voltinism, these positive responses are expected to be transient, because of the short-term stresses imposed by climatic extremes and the passing of species thermal optima for reproduction and survival. In the case of Mediterranean tenebrionids, increased temperatures might favor some thermophilous species in particular areas, allowing them to extend their range and/or diel and yearly activity rhythms and hence their densities (Table 1), with possibly negative implications for the food chains. For example, it has been reported that nests of the loggerhead turtle *Caretta caretta* (Linné, 1758) in Turkey were recently infested by tenebrionid larvae, with potentially substantial damage (Baran et al. 2001; Katılmışet al. 2006; Katılmış & Urhan 2007; Aymak et al. 2020). It can be speculated that increasing aridity could have favored thermophilous tenebrionids, or could have forced them to attack turtle eggs to obtain food and hence water. Thus, positive impacts of climate change on the biology certain tenebrionid species might lead to very negative consequences on community structure and ecosystem functioning.

Future directions

Tenebrionids living on Mediterranean sand dunes have peculiar adaptations which allow them to exploit hot and dry environments. However, their high specialization to harsh conditions make them particularly exposed to the negative effects of the ongoing anthropogenic climate change.

Based on species distributional data, current climate and climatic scenarios, it is possible to construct models of species climatic niches, and hence to evaluate how species distributions will be affected by climatic change in the next years (Bosso et al. 2013; Batalden et al. 2014; Barredo et al. 2015; Lemoine 2021; Sistri et al. 2021; Poloni et al. 2022). Studies on the effects of climate change on species distributions have paid special attention to cold-adapted species living on mountain peaks as they cannot further shift their range upward or northward (Sistri et al. 2021; Poloni et al. 2022), which makes them extremely vulnerable to increasing temperatures (Haslett 1997; Halsch et al. 2021). Tenebrionids of coastal areas have completely different characteristics, being warm-adapted species inhabiting lowland areas, yet they are highly threatened by climatic change for an analogous reason: they cannot keep pace with increasing temperature by moving vertically or latitudinally. Thus, the application of climatic niche modelling to these animals would be a very promising field of research and would be of paramount importance for conservation. Given the expected effects of climate changes on the coastal habitats, climate niche models might be complemented by information on the future evolution of coastal environments to produce the most reliable predictions of true habitat suitability. For example, coastal environments are not only subject to the effects of increasing sea level, but also to the increase in winter wave heights and increased storminess, which are determining dune retreat (Enríquez et al. 2019; Masselink et al. 2022). Combining climate-based predictions with data on shoreline responses to climate change might allow us to accurately predict the future changes in the extent of suitable areas for these insects.

To investigate species' responses to climate change, knowledge on physiology is extremely important, especially because of its relevance for the impact of climatic extremes. Comparing thermal tolerance limits with habitat temperatures provides indications about species vulnerability to extreme heat (Hoffmann et al. 2013; Pincebourde & Casas 2019), which is especially important for species that live close to their upper thermal limits, since insects have a weak ability to adjust their thermal limits to high temperatures (Weaving et al. 2022). Available information on species thermal upper limits of tenebrionids inhabiting Mediterranean coastal areas is, however, still very limited. While available information, and comparisons with allied taxa, are clearly illustrative of the sensitivity of these animals to high temperatures (despite their thermophilous preferences), more information on thermal tolerances might be useful to forecast the impact of increasing temperatures. Since prolonged exposure to mild heat stress may have negative impacts on insects' biology, establishing thermal optima might be even more useful than testing thermal limits. As illustrated in this review, temperature exerts a pivotal role in regulating behaviors, life cycles, ecology, and viability of tenebrionids inhabiting the Mediterranean: thus, all these aspects might be severely compromised by even relatively small departures from optimal values. In this regard, it should be stressed that these animals might be also very sensitive to excessively low temperatures. Although the general trend for the Mediterranean area is that of increasing temperatures, the climate change in this region can lead to an increase of events of exceptionally low temperature (De Luca et al. 2020; Hochman et al. 2022a, 2022b), and this might have important consequences on tenebrionids living on the Mediterranean dunes. Thus, further studies would be useful to extend our knowledge of the response of tenebrionid biology to exceptionally lower temperatures, and to incorporate this information in predictive models of the effects of climate change on these insects.

The available information reviewed in this paper indicates that the same species may show different phenological patterns in different parts of its range. Data are however very limited and there is no analysis specifically addressed to study this type of clinal variation. Expanding our knowledge on this aspect might lead to the detection of clinal patterns, and thus to improve our predictions about responses of local populations. This may be extremely important for species distribution modelling, because excluding intraspecific information may lead to underestimate or overestimate species tolerances to climate change (Pearman et al. 2010; D'Amen et al. 2013).

Field and laboratory work indicates that tenebrionids of coastal areas have characteristic zonations, modulated by many environmental variables (such as temperature, sand moisture, salinity, grain size, etc.). These zonations may be not stable, but may vary seasonally, and hence changes in climatic conditions may alter species zonations. Changes in species zonations induced by climate change may have profound influences on species' ability to exploit the habitat and on interspecific interactions that are however still unknown. Tenebrionids may have extremely dense populations on the Mediterranean dunes, with different species showing abundance peaks in different zones (Fattorini & Carpaneto 2001). Their massive presence on the Mediterranean dunes makes these insects especially important for nutrient and energy cycling, because in arid environments the decomposition of detritus by bacteria and fungi is strongly limited by the scarcity of water (Hanrahan & Seely 1990). Thus, further research on this topic would be beneficial to our understanding of the impact of climate change on the functioning of coastal dune ecosystems.

Current information synthesized in this review indicates that tenebrionid species have diel activity rhythms regulated by temperature, and that these rhythms change seasonally. Alterations in diel temperature fluctuations due to climate change may have important negative effects on insects (Paaijmans et al. 2013; Kingsolver et al. 2018; Duffy et al. 2022). This type of variation should be considered not only for its potential effects on the diel activity patterns of coastal tenebrionids, but also in niche modelling based on mean temperatures, since short-term fluctuations can expose tenebrionids to thermal stresses very different from those that can be deduced by average temperatures.

In general, it seems that community organization of tenebrionid species inhabiting Mediterranean coastal dunes is determined more by habitat preferences than interspecific competition (Fattorini et al. 2016), yet changes in species zonations imposed by climatic change may lead species to interact and hence to create new competitive relations. Despite the recognized importance of interspecific interactions, they are rarely addressed in climate change studies (Urban et al. 2016; Zhang et al. 2017; Tekwa et al. 2022). Thanks to the small number of involved species, tenebrionid communities of Mediterranean coastal dunes may offer excellent opportunities to study how alterations in species abundances and their distribution among different zones may have cascade effects on food webs.

Although still incomplete, current information on tenebrionids adaptations to the Mediterranean dunes clearly illustrates the enormous importance that these insects might have in climate change studies and should encourage new generations of ecologists to consider them as important and useful model organisms.

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