sustainability

MDPI

Review

Can the Beach–Dune Ecosystem Be Preserved Without Protecting the Beach? Ecological Assessment with a Focus on Specialized Beetle Fauna as Environmental Quality Indicators

Lorenzo Zanella * and Fabio Vianello *

Department of Comparative Biomedicine and Food Science, University of Padua, Viale dell'Università 16, 35020 Legnaro, Italy

* Correspondence: lorenzo.zanella@libero.it (L.Z.); fabio.vianello@unipd.it (F.V.)

Abstract: Anthropogenic development has historically concentrated in coastal areas to exploit resources from fishing and commercial navigation. In recent centuries, intensive tourism has added pressure on sandy shorelines, leading to their modification. This development model has led to the disappearance of most coastal sand dunes and their rich biodiversity, which includes specialized plant and animal species adapted to sandy substrates, harsh arid conditions, and variable levels of salinity. The European Community's conservation policies, particularly the Habitats Directive (Council Directive 92/43/EEC), have facilitated the preservation and restoration of the few remaining dune systems. However, these policies have unfortunately overlooked the protection of the adjacent beaches, which are integral to the coastal ecosystem. The loss of biodiversity typical of the beach–dune ecosystems is examined in relation to the anthropogenic disturbance factors, with particular attention to mechanical beach cleaning. Indeed, the metabolizable energy generated by this decomposer biomass is crucial for supporting a diverse trophic network of predators, ranging from insects to birds. The rapid disappearance of the specialized beetle fauna is examined, and some essential criteria for defining standard biotic indices suitable for monitoring these ecosystems are suggested. This approach aims to support more effective conservation programs for these fragile environments. We recommend revising the regulatory framework for safeguarding beach–dune ecosystems, while also proposing some key management principles to be incorporated into the protection guidelines.

Keywords: beach–dune systems; coleoptera; biotic indices; environmental protection policies; insects; endangered species

check for updates

Academic Editor: George P. Kraemer

Received: 9 December 2024
Revised: 17 February 2025
Accepted: 20 February 2025
Published: 24 February 2025

Citation: Zanella, L.; Vianello, F. Can the Beach–Dune Ecosystem Be Preserved Without Protecting the Beach? Ecological Assessment with a Focus on Specialized Beetle Fauna as Environmental Quality Indicators. *Sustainability* **2025**, *17*, 1922. https://doi.org/10.3390/su17051922

Copyright: © 2025 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).

1. Introduction

Beach and dune systems require decades or even centuries to develop [1] and represent highly selective environments characterized by intense sunlight, aridity, and unstable sandy soils [2]. Salinity levels vary from marine values at the shoreline to nearly zero in the inner dune sands. The entire ecosystem is exposed to salt aerosol, originating from the spray of seawater on windy days.

This is, therefore, an extreme environment, where highly adapted biocenoses thrive, featuring species with high degrees of trophic specialization and fidelity to the habitat [3,4]. For this reason, beach–dune ecosystems are invaluable reservoirs of unique biodiversity, threatened by extensive environmental alterations due to human activity. Awareness of the need to safeguard what remains of these unique habitats has led to their inclusion in several

international biodiversity protection regulations. Within the European Community, the relevant policy is the Habitats Directive (Council Directive 92/43/EEC of 21 May 1992), aimed at identifying and protecting a network of sites of particular naturalistic interest across Europe, known as Natura 2000. Coastal dunes have been designated as habitats of community interest, with their ecological characterization based on typical plant assemblages, as shown in Table 1.

Table 1. Dune habitats of community interest whose conservation requires the designation of special areas of conservation according to the Annex-I of the Council Directive 92/43/EEC of 21 May 1992 (updated version 2013). The code corresponds to the Natura 2000 code. The sign '*' indicates priority habitat types.

Code	Habitat
21.	**Sea dunes of the Atlantic, North Sea, and Baltic coasts**
2110	Embryonic shifting dunes
2120	Shifting dunes along the shoreline with *Ammophila arenaria* ('white dunes')
2130	* Fixed coastal dunes with herbaceous vegetation ('grey dunes')
2140	* Decalcified fixed dunes with *Empetrum nigrum*
2150	* Atlantic decalcified fixed dunes (*Calluno-Ulicetea*)
2160	Dunes with *Hippophaë rhamnoides*
2170	Dunes with *Salix repens* ssp. *argentea* (*Salicion arenariae*)
2180	Wooded dunes of the Atlantic, Continental, and Boreal regions
2190	Humid dune slacks
21A0	Machairs (* in Ireland)
22.	**Sea dunes of the Mediterranean coast**
2210	*Crucianellion maritimae* fixed beach dunes
2220	Dunes with *Euphorbia terracina*
2230	*Malcolmietalia* dune grasslands
2240	*Brachypodietalia* dune grasslands with annuals
2250	* Coastal dunes with *Juniperus* spp.
2260	*Cisto-Lavenduletalia* dune sclerophyllous scrubs
2270	* Wooded dunes with *Pinus pinea* and/or *Pinus pinaster*

Unfortunately, although this methodological approach has promoted national policies aimed at protecting many important dune systems, it has also entirely overlooked the adjoining beaches, which lack vegetation. Beaches, economically valuable for seaside tourism and subject to numerous human-induced stressors [5], are integral to coastal dune ecosystems, supporting the trophic web with essential organic detritus deposited onshore by marine currents. Among the main stressing factors, buildings along the beach profile, beach cleaning, presence of solid waste, vehicle traffic on the beach, and frequency of visitors can be mentioned [6]. Among the most important ecological functions of the beach, the drifted organic debris, primarily composed of macroalgal thalli and marine seagrass leaves, provides energy and nutrients to the beach trophic web, starting with the complex biocenosis of microorganisms and invertebrates [7,8]. The stranded wrack also increases the environmental heterogeneity and provides a complex microhabitat with optimal conditions of moisture, temperature, and shade for specialized invertebrate fauna. These microhabitats increase the abundance of prey, which in turn attracts shorebirds and mammals, such as foxes [9,10]. Systematic removal of organic detritus from beaches serves recreational purposes but deprives the ecosystem of its primary nutrient source, impacting not only beach-dwelling animal species but also certain dune-associated species, including some protected bird species [11,12]. Other potential trophic sources can originate from diatom microalgal biomass, which becomes particularly significant in the surf zones of certain sandy beaches, especially in oceanic environments. These microphytes can accumulate,

forming brown patches that, under specific wave energy conditions, are resuspended and eventually drift onto the lower beach [13–15].

Since legislation recognizes only dune environments as conservation-priority habitats, research has steered toward studying the predominant biocenoses of dunes rather than those of the beach. While significant contributions have advanced our understanding of macroinvertebrate communities within the broader beach–dune ecosystem, most of these concentrate on protected or well-preserved sites. In contrast, research documenting beach biodiversity loss is much scarcer, and studies analyzing the impact of beach urbanization on dune biocenoses are almost missing.

In the context of conservation challenges, invertebrate fauna is a key element for studying and understanding the ecosystem's ecological status. The decline of beach-dwelling insect species due to anthropogenic disturbances has been reported and analyzed in the literature, though often without considering the effects on dune habitats. An integrated approach for conserving the entire ecosystem remains absent. This review has the following main objectives:

1. Emphasize the urgent need to protect the biocenosis of specialized arthropods inhabiting natural beach habitats, which are at high risk of local extinction without effective protection policies;
2. Highlight the interconnected relationships between beach and dune biocenoses, demonstrating how these morphologically distinct habitats function as complementary components of a unique ecosystem;
3. Underscore the ecological role of specialized beetle fauna and the zonation of their respective species across different ecosystem habitats. These characteristics make beetles highly effective bioindicators for evaluating ecological conservation status;
4. Highlight the urgent need to implement protection and monitoring plans for beach–dune ecosystems, utilizing selected indicator species from specialized beetle communities to guide conservation efforts.

The discussion highlights the ecological functionality of these specialized beetles, underscoring the necessity of preserving trophic chains dependent on stranded organic detritus to ensure effective ecosystem protection. The novelty of this approach lies in interpreting beaches as integral components of sandy coastal dune ecosystems, rather than as connected but distinct environments. This ecological perspective emphasizes the need to revise protection criteria for beach–dune ecosystems to ensure their effective conservation.

This review, furthermore, provides valuable insights for defining standardized biotic indices composed of species linked to the microhabitats distributed throughout the entire ecozone profile, from the intertidal zone to the dunes. To date, the lack of standardized biotic indices represents a major obstacle to the comparative analysis of coastal ecosystem conservation on a global scale. In contrast, the use of these tools is recommended here as the most effective approach for monitoring programs associated with the implementation of conservation policies.

Despite efforts to extend the geographical coverage of this review, the analysis reflects the limited number of research groups studying beach–dune insects. Consequently, the typical beetles cited as examples mainly belong to Euro-Mediterranean habitats, unless otherwise stated.

2. Morphological and Environmental Overview of Beach–Dune Ecosystems

Before delving into specifics, it is useful to clarify some definitions that have been variably interpreted in the literature, leading to potential misunderstandings. Here, we refer to the following definitions [16,17]:

- Habitat, as the physical place characterized by environmental conditions in which a species lives (e.g., temperature, salinity, humidity, etc.);
- Biotope, as the combination of physical parameters and biotic components that define a particular environment;
- Ecosystem, as a combination of one or more habitats, the living species present, and the biogeochemical cycles that take place within it.

Coastal dunes are found worldwide across all latitudes, exhibiting diverse morphological characteristics and conditions, including variations in humidity, sand supply, marine aerosol levels, and vegetation [2]. The morphology of beach–dune ecosystems results from dynamic processes driven by the movement of sand through wave and wind energy. The variation of dune morphologies reflects the complexity of the factors controlling their formation. Despite numerous mathematical models developed to analyze dune formation and evolution, these processes remain subjects of ongoing study [1,18–21].

The beach–dune profile reflects this dynamic process: embryonic dunes form along the upper edge of the beach, while white dunes develop just behind them, mirroring the gradual reduction of energy responsible for sand movement [21]. This balance is inherently dynamic, with coastal foredunes accumulating and releasing sand through exchanges with the beach, influenced by interactions among wind-wave impacts, external sediment inputs, and vegetation growth [20,21]. Consequently, although many authors have regarded dunes as discrete ecosystems in their own [2], they maintain a continuous exchange of sand with the beach and submerged littoral, which becomes especially significant during storms, often leading to substantial reshaping of the beach–dune system profile [21]. This morpho-dynamic equilibrium has been conceptualized in the definition of the "littoral active zone" (LAZ), but it has only recently been revised in an extended interpretation that takes into account the migration of biotic components between the dunes and the beach [22]. As we will show, these migrations can occur at various times of the day, during feeding activity, seasonally, or in relation to developmental stages, such as the transition from larvae to adulthood. Invertebrates, in particular, are adapted to survive the challenging environmental factors and are often distributed in a zonal pattern, reflecting gradients of moisture, organic debris, plant distribution, sand mobility, and exposure to salt spray [3,4,23].

3. Zonation and Ecological Functionality of Beetle Fauna in Beach–Dune Ecosystems

In the literature, the zonation of beach–dune system profiles has been described using various terminologies (see also [18]), which sometimes has created challenges for comparison. Several criteria for zoning sandy coastal environments have been proposed, particularly concerning the beach and the adjacent shallow waters, identifying three or four zones ranging from the intertidal area to the base of the dunes. These classifications often aim to study the distribution of intertidal macrofauna [24–28] but do not always effectively capture the fine zonation of beach–dune habitats. This review references the zonation used in studies on the distribution patterns of terrestrial arthropods [29–31], along with clarifications that take into account the habitats identified by the aforementioned Habitat Directive:

- Intertidal zone: This is the wet beach area exposed to tidal flooding, characterized by high humidity and the accumulation of fresh wrack debris in the uppermost area, which is inundated only during spring tides (syzygy high tides);
- Dry aphytic zone: This zone features patches of wrack debris, inundated only during exceptional meteorological events. Notably, the lower part (supratidal) of this zone exhibits higher humidity and semi-humid wrack deposits, making it environmentally

similar to the upper intertidal zone. In contrast, the upper section accumulates drier wrack and driftwood, exhibiting microclimatic conditions that are more akin to those of the next zone;

- Embryonic shifting dunes: Also known as incipient dunes or antedunes, this zone corresponds to habitat EC 2110. It includes sandy areas sparsely vegetated by a few perennial plants (e.g., *Thinopyrum junceum*) and annual pioneer plants that develop during favorable seasons. This annual vegetation typically spreads a few meters onto the upper beach, and the community includes species listed under habitat EC 1210 (Annual Vegetation of Drift Lines) from the "12. Sea Cliffs and Shingle or Stony Beaches" category in the Habitat Directive. However, in this work, the annual vegetation is considered part of EC 2110 (see below), as these plants also develop consistently within the embryonic dune. Thus, it seems inappropriate to apply codes formally associated with other habitats, although the description of the plant communities associated with the various habitats in the Directive appears incomplete and sometimes inconsistent with the complex situation observed in the field. This transitional zone still hosts some beetle species associated with stranded detritus, while species linked to the white dune vegetation predominate;
- White dunes: Commonly also referred to as foredunes, these correspond to habitat EC 2120 and represent the highest and most active dune cordon. This zone is characterized in Mediterranean and European environments by the extensive development of *Ammophila arenaria*;
- Grey Dunes: These fixed dunes, characterized by herbaceous and shrub vegetation, correspond to habitat EC 2130. However, this habitat has not been considered in this work, which focuses on dune habitats closer to the beach and distinguished by loose sand.

Figure 1 shows an example of the eco-zonal profile observed in the beach–dune ecosystem. The factors defining the gradient of microclimatic and edaphic characteristics in these various zones also determine a zonation of the animal species associated with them. It should be emphasized that, while referencing morphologically distinguishable zones is necessary for the ensuing discussion, the division of sandy beaches into clearly defined faunistic zones is a contentious topic. Indeed, the zonal distribution of species is dynamic and changes in response to variations of environmental conditions, both circadian (light/dark cycles, tidal excursions, prey movements, etc.) and seasonal (temperature, reproductive periods or developmental phases, hibernation, etc.) [29,31–34]. For instance, in the northern Adriatic, the daily tidal range can vary between 40 cm and over 100 cm, depending on the lunar cycle, resulting in changes in the extent of the intertidal zone and the corresponding dry beach. Entomological communities will shift accordingly in response to variations in the salinity and moisture gradients and, consequently, sand temperature (LZ, personal observation). This latter aspect, even under similar tidal ranges, further varies with the intensity of solar radiation. During summer, many species migrate toward the intertidal zone due to desiccation and the extremely high daytime temperatures in the dry zone. Therefore, the above-defined dry aphytic zone can, actually, be divided into subzones encompassing highly variable environmental conditions. The significance of these subzones increases on wider beaches, while on narrower beaches, this variability becomes less pronounced.

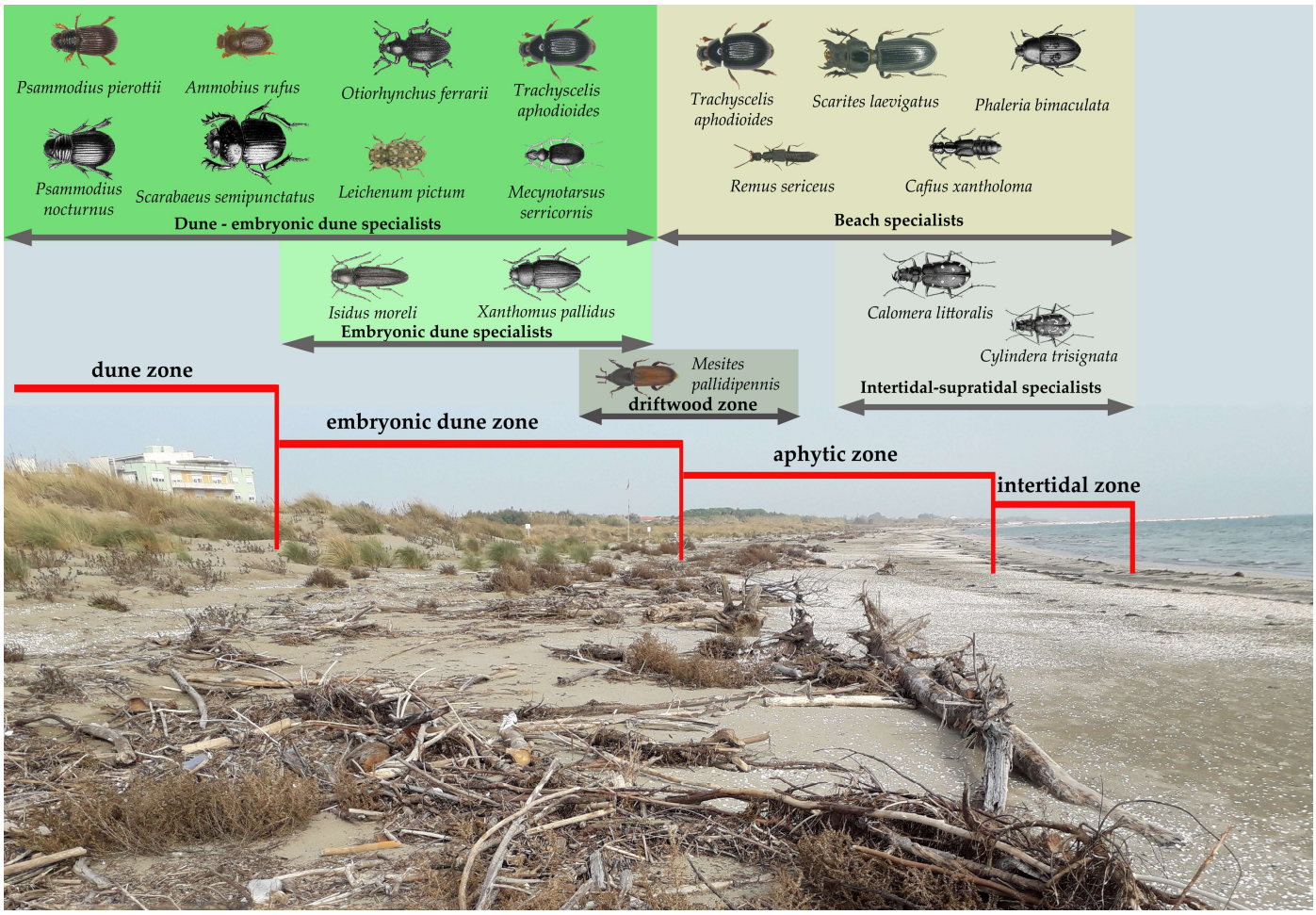

Figure 1. Zonal distribution of beetles typical of a beach–dune ecosystem on a protected Adriatic coastline (Italy). The red lines mark the zones as identified in the text. The upper part of the figure shows beetle assemblages typically occurring in dune and beach zones, respectively (excluding movements related to overwintering). Below, species with more restricted preferential zones are shown. The grey arrows indicate the preferred zonal range occupied by the different beetle assemblages. (drawings of insects by Gea d'Este, courtesy of the Museo di Storia Naturale di Venezia).

Even embryonic and white dunes can exhibit variability in their zonal transitions, with significant impacts on the gradient of physicochemical factors influencing the distribution of associated biocenoses. For instance, recent, low-lying white dunes may maintain some environmental conditions similar to those of embryonic dunes. In other cases, dunes rise several meters in height, resulting in substantial variations in wind exposure and the distance of the sandy surface from the phreatic water table, compared to the lower embryonic dunes in front of them. Entomological species, particularly beetles, which include numerous highly adapted species, tend to occupy well-defined ecological niches within the succession of microhabitats present in the beach–dune ecosystem. However, as just discussed, the zonal distribution of these ecological niches must be contextualized to the specific site and the seasonal conditions under consideration.

While other arthropod groups, such as crustaceans, arachnids, and hymenopterans, play essential roles in beach–dune ecology, this review focuses on beetles. However, references to other taxa that play a significant role in the biogeochemical cycles upon which beetle ecology depends, such as amphipod crustaceans and diptera, will necessarily be included.

Furthermore, the discussion will concentrate on the zones between the intertidal area and the white dunes, where the most pronounced gradient of physical and chemical factors operates selectively on the survival capacity of insects. The extensive area of grey dunes maintains a distinctive but less selective beetle community, with a more homogeneous distribution. A study on the succession of beetle recolonization carried out on reconstructed dunes showed that after the first year, with the stabilization of the inner dunes, species associated with sandy soils increased, surpassing dune-specialist species in dominance [35]. Furthermore, within the grey dunes, wet depressions may be present, hosting hygrophilous species that are shared with other humid and/or brackish environments (e.g., salt marshes).

4. Beach Habitat: Intertidal Zone and Upper Dry Beach

The intertidal zone, periodically flooded by tides, serves as a transition area between submerged and emerged coastal environments. The lower band of this zone, i.e., the closest to the low tide line, is more suitable for aquatic organisms, such as crustaceans, rather than terrestrial arthropods, like insects. Beetles inhabiting this zone are thus highly adapted to endure stressors, such as high salinity and occasional submersion (for instance, species from the genera *Cafius*, *Phytosus*, *Cercyon*, *Phaleria*, *Dyschirius/Dyschiriodes*, *Bledius* [36,37]). In the upper band of the intertidal zone, most of the organic debris carried by tides accumulates, consisting mainly of remnants of macroalgae and seagrasses. This material is commonly termed "wrack cast" or "beach cast" [38], but more often simply referred to as "wrack". It fulfills two essential roles in the beach habitat: providing the main source of organic carbon and energy fueling the food web and creating a microhabitat suitable for the specialized invertebrate fauna [8,12,39–41], as will be discussed in detail below. Among arthropods associated with wrack, talitrid amphipods are particularly abundant and act as primary herbivores, though they can also feed on other dead organic matter [7]. Due to their substantial biomass, these amphipods play a crucial role in transferring organic carbon and metabolizable energy to higher trophic levels, especially to insects (e.g., carabids and cicindelids, see below) and shorebirds [12,42–46].

Although crustaceans dominate the beach arthropod community in terms of abundance, Coleoptera typically represents the most diversified and specialized group [47,48] and, often, are the second most abundant component [49]. This group includes herbivorous, detritivorous, saprophagous, and predatory species. In the Mediterranean, among the particularly stenotopic species sensitive to environmental impacts are certain carabids, such as *Scarites laevigatus* (Figure 2a), a nocturnal predator adapted for hunting sandhoppers within their burrows dug into the sand [50,51], and *Eurynebria complanata* (Figure 2b), a nocturnal runner-predator now extirpated from many Mediterranean beaches [23,52–54]. Among diurnal and heliophilous beetles, cicindelids—likewise predators—are represented in the Mediterranean by characteristic species, such as *Cylindera trisignata* (Figure 2c), *Calomera littoralis* (Figure 2d), and *Cicindela concolor* (west Mediterranean) [50,55,56]. Less easily observed, instead, are the numerous small predators (1–10 mm) that hide within the stranded wrack, feeding on flies, nematodes, and other saprophytic invertebrates.

Among these, staphylinids from the genera *Cafius* and *Phytosus* are some of the most abundant and widely distributed. The genus *Cafius*, particularly *C. xantholoma* (Figure 2e), preys on dipteran larvae and adults, enchytraeids (phylum Annelida), and small maggots [7,57]. This beetle has been observed partially buried in the surface sand layer beneath wrack, exposing only its extended mandibles to catch passing preys [58]. *Remus sericeus*, another staphylinid with similar habits but more sensitive to environmental alterations, is smaller and preys on dipteran larvae and collembolans [50,59] (p. 334).

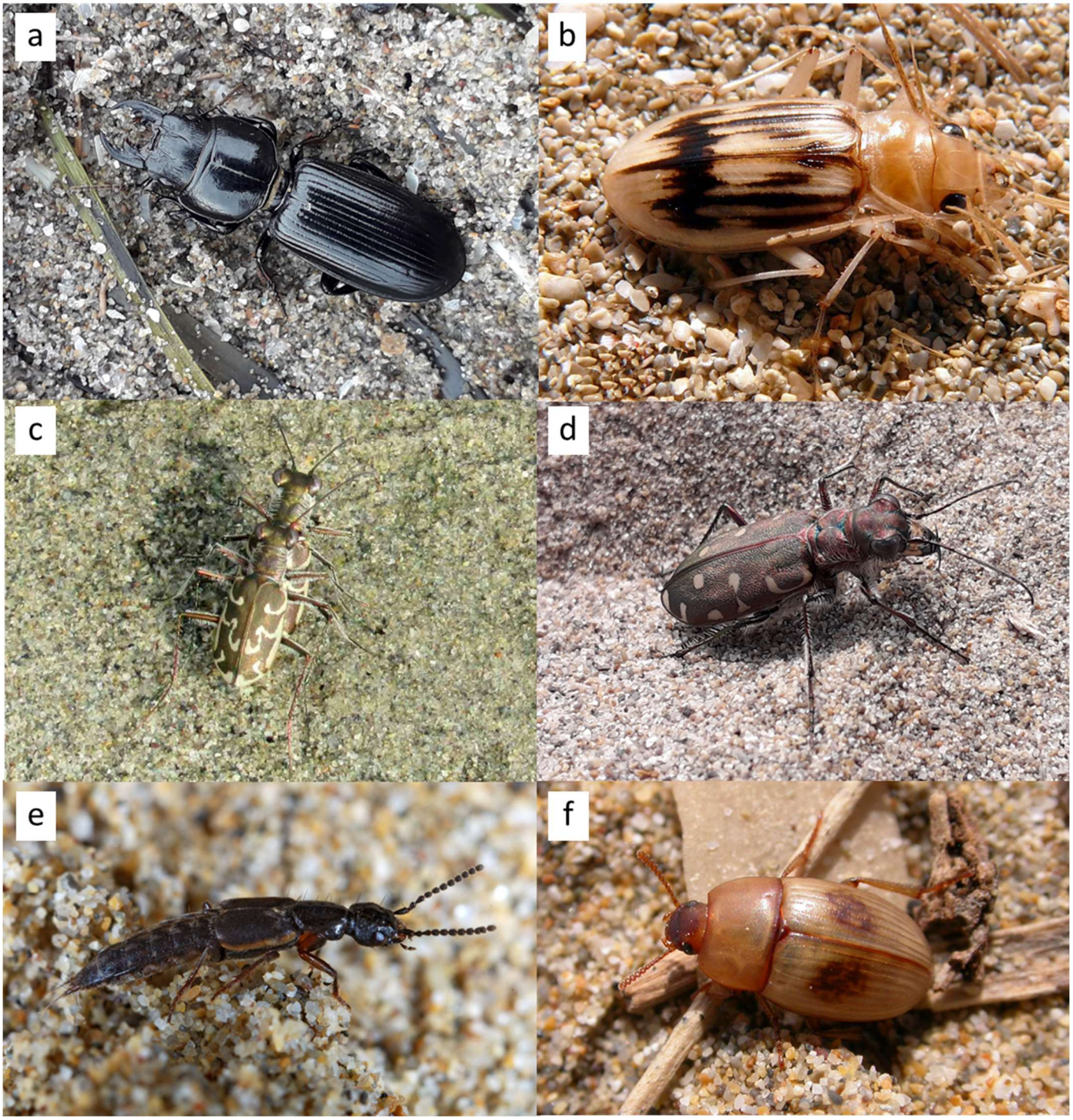

Figure 2. Coleoptera species suitable for use as indicators of the environmental condition of the beach in the Mediterranean coast: (**a**) *Scarites laevigatus* (ssp. *venetianus*); (**b**) *Eurynebria complanata* (image: courtesy of the author, M. Romano); (**c**) *Cylindera trisignata* (image: courtesy of the author, M. Baldin); (**d**) *Calomera littoralis*; (**e**) *Cafius xantholoma* (from Zanella et al. [50], with permission of the author, F. Barbieri); (**f**) *Phaleria bimaculata*.

The genus *Phytosus*, including *P. spinifer*, *P. balticus*, and *P. nigriventris*, comprises very small beetles (2–3 mm) that are sometimes very abundant in wrack layers near the sand [34,60,61], though little is known about their diet. While some authors consider *Phytosus* species as predators [62] or phytophagous [63], the majority classify them as scavenger

beetles [64] that also feed on fungal hyphae associated with aged organic detritus [33,34], which likely explains their abundance in moist, fermenting wrack biomass.

In the upper reaches of the intertidal zone, where tidal inundation occurs only during spring tides, wrack has already undergone significant degradation and substantial development of saprophytic microbiota. This wrack biomass, often lighter due to dehydration and decomposition, tends to be blown towards the dry beach by wind, forming patches of varying sizes that can remain for long periods. This semi-dry material is less attractive to amphipods but is colonized by abundant dipteran larvae and less hydrophilic, more thermophilic beetles. Although amphipod crustaceans are the primary decomposers of stranded wrack [65], tenebrionid beetles also contribute significantly, reaching high abundances [39,48,66–68]. Mediterranean tenebrionids like *Phaleria bimaculata* (Figure 2f), *P. acuminata*, and *P. provincialis*—vicariated by ecologically similar species on beaches in other regions—are among the most abundant and move between the intertidal zone and the dry beach [30,34], reaching as far as the dunes under certain conditions [69,70].

The community of specialized arthropods associated with stranded wrack is severely disrupted and impoverished by mechanical beach cleaning for recreative purposes [5,8,71], impacting higher trophic levels such as birds, particularly plovers [8,11,12,72,73].

4.1. Ecological Importance of Organic Debris Input

Stranded organic debris is a complex microhabitat containing several ecological niches defined by physical (temperature, sand substrate granulometry, etc.) and biological factors (plant and animal species from which the biomass originates, along with the interactions and successional dynamics involving microbiota and macrofauna species) [7,8,40,42]. Wrack input can vary considerably in quantity and composition, depending on the primary productivity of the submerged coastal belt and/or inputs from nearby river mouths or lagoons [40,67]. Given the variability in wrack distribution on beaches influenced by macrotidal and microtidal conditions, wrack input is typically measured as biomass per linear meter of shoreline rather than per unit area, following the approach of McLaughlin et al. [74].

Macrophyte wrack contributions vary seasonally and between sites, with values increasing with the shoreline/beach-area ratio [75]. For instance, Griffith et al. [45] estimated wet weight (W.W.) biomass inputs of approximately 2179 kg m^{-1} yr^{-1} on sandy beaches along South Africa's southwest coast. In north-western Atlantic Spain, Barreiro et al. [75] estimated wrack inputs between 0.2 and 110 kg m^{-1} yr^{-1} dry weight (D.W.), consisting mainly of brown algae debris, though composition varies by origin. The plant component is generally predominant and can include, in varying proportions, both remnants of marine angiosperms (*Posidonia oceanica*, *Zostera marina*, *Cymodocea nodosa*, etc.), which are particularly rich in cellulose, and macroalgae (Phaeophyceae, Rhodophyceae, Chlorophyceae), whose thalli contain a variety of complex polysaccharides.

Herbivorous macrofauna generally prefer macroalgae, despite their polyphenol content affecting palatability, over angiosperms, which are rich in cellulose and possess thick vascular structures [7,8,76,77]. Stranded wrack is subjected to a variety of processes, including in situ consumption by beach herbivores, meiofaunal and microbial degradation, and export by tides and currents [8,75,76]. The development of nematodes appears to play a crucial role in the initial degradation of macroalgae, also preventing the development of molds that would interfere with herbivore activity [58].

After deposition on the sand, the wrack undergoes a rapid development of microbial communities, which varies with the composition of the wrack and the environmental context in which it develops, including bacteria, microalgae, fungi, and protists [8]. Bacterial and fungal biomass, in addition to contributing to the decomposition of organic detritus, becomes a source of food for herbivorous and saprophagous macrofauna. Each

detritivorous species consumes dead organic matter with specific moisture content and decay stages [7,65,78]. Colonization of wrack by different species follows a succession pattern depending on the site and wrack composition, requiring a natural decay period. For instance, Colombini et al. [42] observed the absence of Nematoda, Oligochaeta, and Collembola in the wrack of a tropical beach, suggesting that this phenomenon may be attributed to the short residence time of wrack caused by frequent storms. In another study, a positive and significant relationship between wrack-associated macrofauna and bacterial assemblage descriptors has been reported, highlighting the crucial role of macrofauna in optimizing conditions for bacterial mineralization and microbial activity [79]. Some beetles, occasionally very abundant, such as the tiny Ptiliidae (0.5–0.6 mm), colonize the wrack but seem to feed almost exclusively on fungal hyphae and conidia [7,40]. Furthermore, mechanical fragmentation and partial digestion of detrital material by herbivorous and saprophagous fauna enhance microbial colonization efficiency within the abundant fecal material released, accelerating the overall decay rate of the wrack mound [7,80]. Thus, the decomposition of stranded material is a complex process involving reciprocal interactions between microbiota and macrofauna. Studies carried out on detritus from *Zostera marina* leaves along the beaches of the Baltic Sea suggested that microorganisms and leaching play a more significant role than the meiofauna and macrofauna communities in the overall degradation process, although microbial activity tends to decrease significantly under low humidity conditions [76]. Other studies, conducted in different environments and using different methodologies, indicate that amphipods are the primary herbivores capable of consuming more than 50% of kelp wrack [8] and can reach densities exceeding 10,000 ind. m^{-1} [65]. Griffith et al. [45] calculated that, on a beach in South Africa, amphipods of the genus *Talorchestia* could consume 53% of the wrack, while dipteran larvae accounted for approximately 14.5%, and beetles contributed only 3.5%, with the remaining portion (about 30%) being degraded by the microbial community and meiofauna. The factors regulating the interaction between organic detritus and arthropods are numerous, and the resulting ecological dynamics are complex. Each macroalga present in the wrack exhibits a composition that influences its palatability and, consequently, the preference of saprophagous macrofauna. For instance, polyphenols, which are particularly abundant in Phaeophyceae and tend to decrease with the wrack aging, can deter herbivores, although the correlation with consumption rates appears unclear [81]. Nonetheless, there is strong evidence of a preference among specialized herbivores for aged, stranded seaweeds over fresh seaweeds [82].

Patterns of macrofaunal assemblages can vary among sites and through time in relation to successional colonization [44,66] and/or seasonality [33,34,49,63], as well as to the distance from the shoreline [67,83] and the size of wrack patches [66]. The colonization of detritus occurs at different rates depending on the species involved. Amphipods quickly colonize the wrack, followed by dipteran larvae, whereas beetle macrofauna, including both herbivorous and predatory species, develops progressively and can persist even after the decline of amphipods and dipterans, which occurs with the desiccation of the detritus [33,44]. The presence of amphipods, in particular, declines drastically as the moisture content of the wrack falls below 50% [39]. Among beetles playing a significant role in wrack decomposition, *Phaleria* spp. are mid-successional invaders, while *Trachyscelis aphodioides* is a late-successional invader, with both taxa preferring supratidal and less humid wrack [39]. While dipteran larvae play a significant role in the decomposition of detritus, they also serve as primary prey for staphylinid beetles and other small predators, such as the larvae of *Cercyon littoralis* (Hydrophilidae) [84–86]. Cicindelids also actively prey on both fly larvae and adults [87].

Regarding zonal distribution, different species exhibit distinct preferences, which may vary in response to various factors. On a sandy beach of Somalia (Indian Ocean), Colombini et al. [42] found that juvenile amphipods of the species *Talorchestia martensii* are more abundant in the wrack deposited landward compared to that which is dominated by adults, likely as a strategy to avoid tidal inundation. On the beach of Isola Varano (Apulia, Italy), the two *Phytosus* species abundant under wrack, *P. spinifer* and *P. balticus*, exhibited significant differences in their mean zonation, with *P. spinifer* occurring more landward than *P. balticus* [34]. In the same environment, the scavenger tenebrionid *Phaleria acuminata* exhibited seasonal shifts in its median zonation, influenced by microclimatic variations in sand temperature and humidity. Specifically, it shifted seaward from spring to summer compared to early spring and autumn, while consistently maintaining its preferred foraging zone at mid-beach throughout the year [34].

Another important aspect worthy of attention is the distribution of macroinvertebrates within the biomass of wrack, which some studies have highlighted as heterogeneous, varying with the species considered and, in some cases, according to the life stage. Size and thickness of wrack deposits are significant factors in this regard, although these two variables are often interdependent. Long-term monitoring of some beaches along the northern Adriatic coast revealed ecological differences between two closely related staphylinid beetles, *Cafius xantholoma* and *Remus sericeus*, which were once abundant. *C. xantholoma* remains common on beaches where at least small amounts of wrack persist, whereas *R. sericeus*, along with the small histerid *Halacritus punctum* and staphylinids of the genus *Phytosus*, thrives exclusively in thick wrack deposits with underlying layers of moist, fragmented detritus (personal observation, LZ).

Olabarria et al. [66] investigated macrofaunal distribution on a Spanish beach, finding that large (0.49 m^2; 5 kg W.W.) and medium wrack patches (0.25 m^2; 3 kg W.W.) hosted a greater number of species and individuals compared to small patches (0.09 m^2; 1 kg W.W.) with equivalent detritus biomass. On a South African beach, Griffiths and Stenton-Dozey [44] showed that individual fronds of the brown alga *Ecklonia maxima* degraded much more slowly than the equivalent biomass deposited in flat banks of 2 m^2 and 15–20 cm thick. Individual algal fronds desiccate rapidly compared to the thicker deposits, negatively impacting the abundance of dipteran larvae and influencing the succession of arthropods associated with wrack decomposition. The impact of wrack mound thickness, predominantly composed of phaeophytes, was also studied on the English coast by Hodge and Jessop [84]. They identified three distinct layers: (i) a thin surface layer that dries out and tends to form a crust; (ii) a 15–20 cm intermediate layer in which the material is highly fragmented by detritivores; and (iii) a deep layer where the material degrades more slowly and under anaerobic conditions. According to these authors, the distribution of dipteran larvae is primarily concentrated in the intermediate layer, whereas beetles prefer the surface and intermediate layers. Phillips and Arthur [86] observed that larvae of the dipteran genus *Coelopa* prefer higher temperatures and tend to concentrate in the deep layer, benefiting from the heat generated by anaerobic decomposition. Conversely, salt hoppers are negatively affected by temperature and show no preference regarding the depth of the colonized layer. In the same study, the distribution of the staphylinid *Cafius xantholoma* was more closely correlated with the distribution of its prey than with other microhabitat factors [86]. Therefore, the thickness of wrack biomass plays a crucial role in defining the ecological niches present within it, subsequently influencing the development of the invertebrate community.

A general comment regarding the ecological functionality of beetles, based on the above considerations, is that they play a primary role in the decomposition and metabolization of stranded organic detritus, intervening at various stages of the process, although our

current knowledge remains very limited. Detritivores contribute by fragmenting macrophyte remains and simplifying their composition through digestive processes, thereby accelerating microbial activity. Certain microphagous and mycetophagous species interact with the development of saprophytic microflora, likely in a complex and potentially selective manner. These trophic levels are crucial for transferring a significant portion of metabolizable energy to predatory species, both invertebrates and vertebrates. Predatory beetle activity may also play an important role in controlling the overgrowth of saprophagous species. Although the scarcity of studies limits the availability of representative cases, the impact of such predatory activity could be substantial. For instance, Orth and Moore [88] reported that declines in rove beetles of the genus *Cafius*, in North American coastal environments, were linked with the overdevelopment of detritus-associated dipteran populations.

4.2. Driftwood: A Microhabitat Hosting Threatened Invertebrates

In the innermost zone of the dry beach, and partially within the embryonic dunes, driftwood tends to accumulate. This material serves as a particularly resilient reservoir of organic carbon that, in the absence of entomological activity, would undergo extremely slow decomposition. At the same time, it provides a natural reinforcing structure for foredunes and creates microhabitats for a surprising variety of animals and plants [40,89,90]. In Mediterranean environments, driftwood soaked in saltwater is attacked by the weevil *Mesites pallidipennis* (Figure 3a), whose larvae burrow into the wood [91,92]. This species is replaced on some Atlantic–Mediterranean beaches by its congener *Mesites aquitanus*, which exhibits similar biology [54,62,64,93].

Delnatte [94] highlighted the importance of driftwood for the survival of *Isidus moreli* (Figure 3b), an elaterid beetle strictly associated with Mediterranean beaches. Its larvae have a 3–4-year lifecycle in decaying driftwood, preying on saproxylic beetle larvae, such as *Mesites pallidipennis*. This zoophagous diet, which also includes cannibalism, is supplemented with wooden compounds, fungi, or organic debris [95]. The adult beetle is rarely observed as it remains buried in the sand, emerging at dusk for mating during June and July [96]. Once abundant, this species has become increasingly rare due to the systematic removal of driftwood from beaches [91,94,95].

Other specialized beetles are also associated with beach driftwood, including the weevil *Styphloderes exsculptus* and its specialized predator *Brachemys brevipennis* (family Melyridae, Figure 3c), now rare and found only in a few localities along the French Mediterranean coast, Spain, Sardinia, and Sicily [40,97,98]. The genus *Brachemys* also comprises five other species (in addition to *B. erichsonii*, currently considered of dubious status), divided into two subgenera (*Brachemys* and *Atelestodes*) [98]. All exhibit similar ecological traits, being stenotopic and confined to specific regions of the Mediterranean coast [98]. These species are increasingly threatened by environmental changes on beaches, primarily driven by recreational activities.

Among the species whose larvae inhabit and feed on driftwood, particular mention should be made of the scarab beetles of the genus *Calicnemis* (Scarabaeidae: Dynastinae), now very rare and locally extinct on many beaches where they were once recorded [23,62]. According to Caussanel [64], both larvae and adults also feed on *Thinopyrum junceum* as well. This genus includes *C. latreillei*, occurring in Italy, France, and Spain, and *C. obesa*, with its nominotypical form *C. obesa obesa* widely distributed in the western Mediterranean region, as well as an endemic subspecies from Sardinia (*C. obesa sardiniensis*, Figure 3d) [4,54,62,99,100].

The ecological role of beetles associated with driftwood may seem relatively marginal compared to that of species associated with marine macrophyte debris. However, in many

areas near river mouths, and in the absence of human intervention, driftwood tends to accumulate in substantial quantities. As wood represents a slow-degrading organic carbon load, the activity of saproxylic insects assumes a pivotal role. These insects can thrive in exceptionally large populations, maintaining a dynamic equilibrium with their predatory beetle counterparts. Their tunneling activity creates dense networks within the wood biomass, significantly increasing the surface area available for colonization by cellulolytic microorganisms. Meanwhile, the wood ingested by beetles is converted into proteins that become available to predators. Under natural conditions, this process accelerates the breakdown of otherwise recalcitrant organic carbon, enabling its metabolization within years rather than decades (LZ, personal observation). This activity has a profound impact on the biogeochemical cycles of the transitional zone between the upper beach and embryonic dunes.

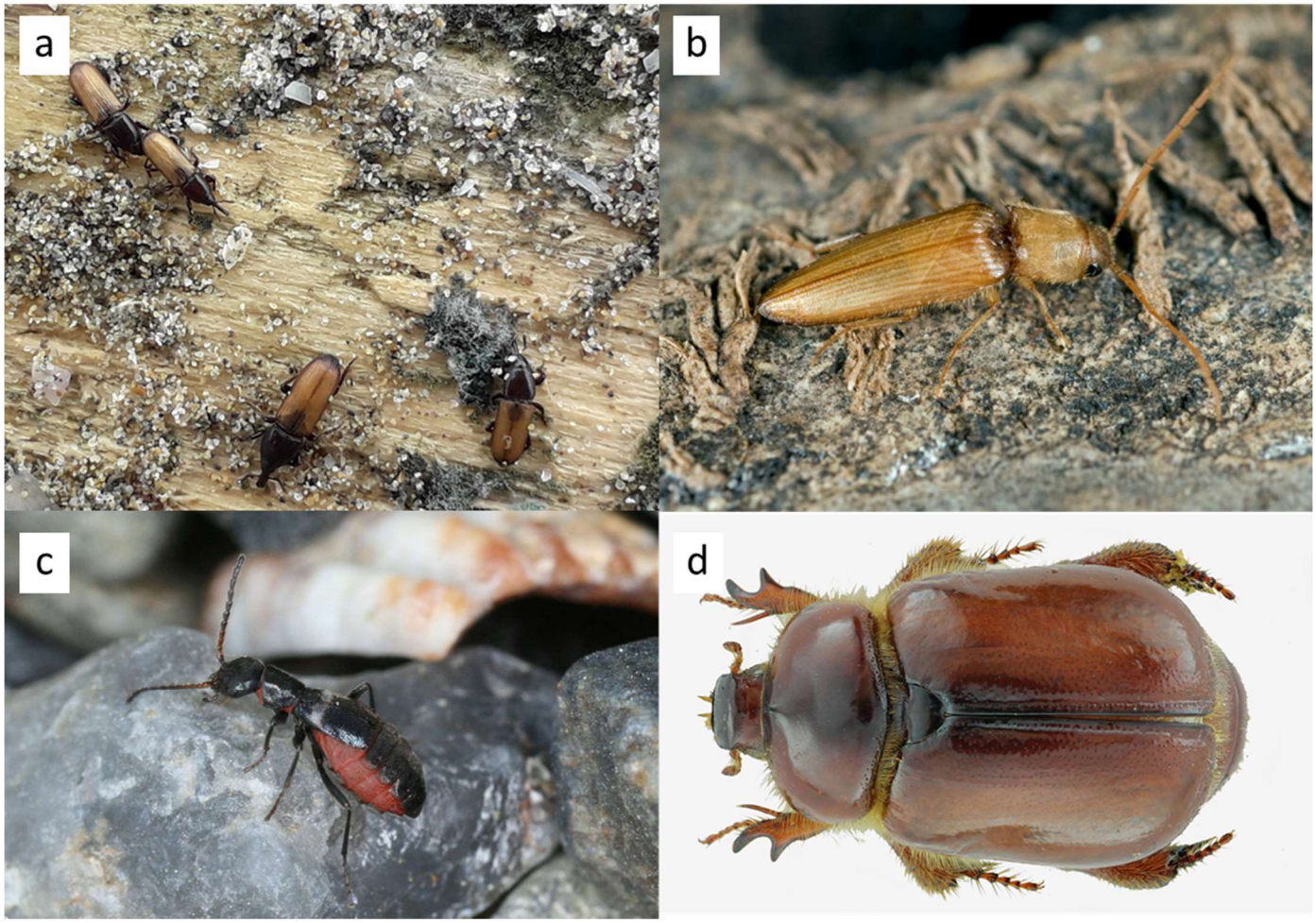

Figure 3. Coleoptera species suitable for use as bioindicators of the environmental condition of the beach in the Mediterranean coast: (**a**) *Mesites pallidipennis*; (**b**) *Isidus moreli* (from Zanella et al. [96], with the permission of the author F. Barbieri); (**c**) *Brachemys brevipennis* (from https://inpn.mnhn.fr/espece/cd_nom/235185; with the permission of the author, H. Bouyon); (**d**) *Calicnemis obesa sardiniensis* (from Ballerio et al. [101], with the permission of the author, A. Ballerio).

5. Embryonic Dunes and White Dunes

The transition zone between the dry beach and the white dune, referred to here as the embryonic dune, is characterized by the presence of pioneer plants with a low fraction of ground cover. This zone may develop as a sandy plain that gradually rises into low undulations or appears as a series of small sandy mounds, which remain unstable and

subject to wind reshaping. This area often contains driftwood, as previously mentioned, along with its associated fauna, forming a continuum with the innermost aphytic section of the beach. Ecologically, this zone can also include part of the upper beach, where transient populations of annual pioneer plants establish. This zone hosts a limited number of plant species, but, interestingly, these have the highest proportion of rare and endangered plant taxa of the beach–dune ecosystem [102].

In the Mediterranean, typical plants in this zone include predominantly annual species, such as *Cakile maritima*, *Salsola kali*, and *Xanthium orientale* var. *italicum*, as well as a few perennial species, such as *Thinopyrum junceum* (syn. *Elymus farctus*, *Elytrigia juncea*) [103,104]. The landward adjacent zone is occupied by the white dunes, also known as foredunes, which represent the first relatively stable dunes, though they remain somewhat susceptible to wind reshaping due to their composition of fine, loose sand. These dunes can reach heights of 6 m or more and are characterized by the presence of *Ammophila arenaria*, a plant species essential to dune morphogenesis [105]. Accompanying this key species are other typical plants, including psammophilous species such as *Crucianella maritima*, *Echinophora spinosa*, *Calystegia soldanella*, and *Eryngium maritimum* [103].

The embryonic dune and the white dune share common features, such as vegetation and a mobile sandy substrate, and as a result, they also share many specialized psammophilous insects. Predatory insects are relatively few in this environment, including antlion larvae (Order: Neuroptera, Family: Myrmeleontidae), which lie in wait for prey at the bottom of sand pit traps. Among specialized carabid predators, *Scarites buparius* (central-western Mediterranean, Figure 4a), a large ground beetle (24–38 mm) now in decline, and the heliophilous tiger beetle *Lophyra flexuosa* (Atlantic-Mediterranean), an excellent runner and flier, are particularly noteworthy. Additionally, small predators from the family Histeridae, such as *Hypocaccus rugifrons*, *H. crassipes*, and *H. rubripes* (1.5–4 mm), hunt tiny prey on dung, carcasses, or decomposing vegetation [62]. Under specific conditions, some of these species can also be observed in stranded beach debris [63,66]. However, in dune environments, beetles that feed on plants or dead organic matter prevail, although their biology is often still poorly understood. In the Mediterranean, among the characteristic phytophagous species are small chrysomelids (2.6–3.5 mm), such as *Psylliodes marcida*, which develops at the expense of its host plant, *Cakile maritima*, or the congeners *P. puncticollis* and *P. maroccana*, whose distribution is only partially overlapping [3]. Among Curculionidae, a family predominantly consisting of phytophagous species, notable mentions include *Otiorhynchus ferrarii*, an endemic species of the northern Adriatic that feeds on various plant species [50,96], and *O. juvencus*, which replaces the former in the western Mediterranean, along with other small weevils (genera *Sitona*, *Baris*, etc.) associated with psammophilous leguminous plants of the dunes [4].

The family with the largest number of species adapted to dune environments is certainly Tenebrionidae. This family includes highly specialized elements adapted to arid and sandy habitats [106], some with localized distributions and others found across large Mediterranean areas, in some cases extending to the Atlantic coasts. Among the frequent and sometimes abundant tenebrionid species, the conspicuous species of the genera *Pimelia*, *Tentyria*, and *Erodius* (Figure 4b) are worth mentioning. These opportunistic saprophages, with body sizes typically ranging between 10 and 20 mm, are active on the sandy surface [106]. Interestingly, some of these tenebrionid beetles occasionally exhibit predatory behavior, attacking other insects in distress or defenseless larvae [70,100].

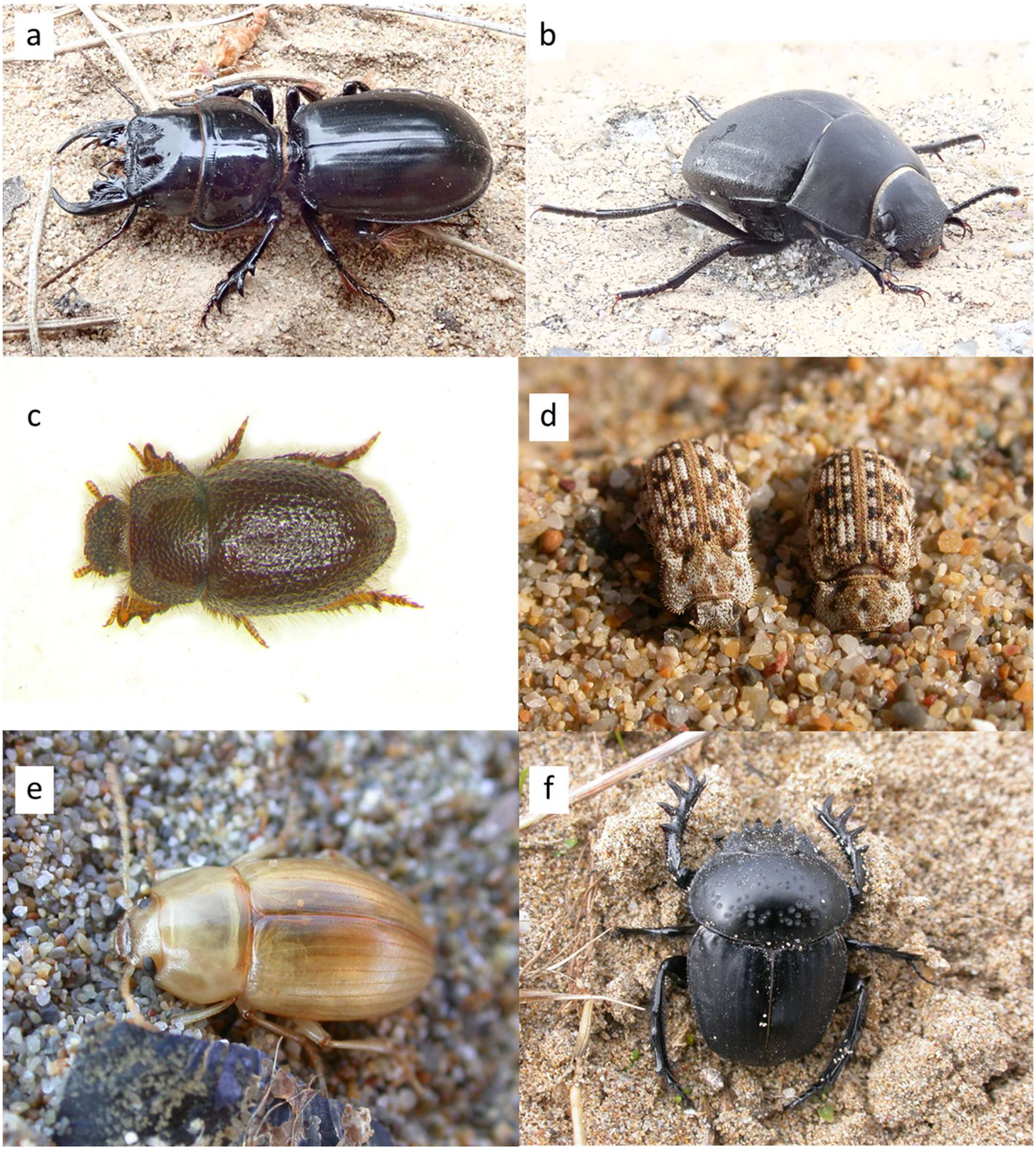

Figure 4. Coleoptera species suitable for use as bioindicators of the environmental condition of the beach in the Mediterranean coast: (**a**) *Scarites buparius* and (**b**) *Erodius siculus* (both images by Siga, use allowed under Creative Commons Attribution-Share Alike 4.0 International license); (**c**) *Ammobius rufus*; (**d**) *Leichenum pictum*; (**e**) *Xanthomus pallidus*; (**f**) *Scarabaeus semipunctatus*.

Among burrowing species, some small tenebrionids (3–5 mm), such as *Ammobius rufus* (Figure 4c), which is generally found in dunes, and *Trachyscelis aphodioides*, which also occurs among upper beach wrack, are particularly common [96,107–109]. Some evidence suggests that these small insects feed primarily on fungi that develop on plant detritus [40].

Characteristic psammo-xerophilous beetles include the small *Leichenum* species (4–5 mm in length), whose color pattern provides excellent camouflage with sandy environments. These are represented by *L. pictum* (Figure 4d), found in central and southern Europe and the central-western Mediterranean, and *L. pulchellum*, occurring in the eastern Mediterranean. Some tenebrionids, with diverse ranges spanning the Mediterranean and, in some cases, Atlantic coastal regions, are characterized by an autumnal phenology. Examples include *Halammobia pellucida* (4–5 mm), *Pseudoseriscius helvolus*, and *P. pruinosus* (4–6 mm), and species of the genus *Xanthomus* [4,34,40,56,62,106,110]. Among these latter, *X. pellucidus* and *X. pallidus* (Figure 4e) are associated with the embryonic and white dunes but can also be found among beach wrack, which appears to be the preferred microhabitat of *X. pallidus* [30,107,109,111,112]. These species are considered good indicators of environmental quality due to their sensitivity to anthropogenic impacts [113]. Generally, *X. pallidus* prefers embryonic dunes and is frequently found in the upper beach beneath plant debris, while *X. pellucidus* is more abundant on white dunes and occurs further landward [34,96,114,115]. Ferrer and Whitehead [113] interpret their diet as primarily omnivorous, while Caussanel [112] suggests that *X. pallidus* mainly feeds on organic detritus, distinguishing it from its congener *X. pellucidus*, with which it can coexists in some regions, and which often feeds on seeds [30]. In captivity, *X. pallidus* has been observed feeding on dead wood and, to a lesser extent, on remains of *Ammophila* spikes, although the seeds of these plants were not consumed [50].

In general, the diverse family of Tenebrionidae includes detritivorous and/or saprophagous insects that play a significant role in transferring metabolizable energy to higher trophic levels. However, it should be noted that the knowledge of their diet is still quite rudimentary, and thus our understanding of their ecological functionality remains limited. Lagar et al. [114] observed differences in the enzymatic composition of the intestines of detritivorous/saprophagous arthropods found in beach–dune ecosystems, particularly with regard to glycosidases, which is consistent with differential specialization in food preferences, presumably aimed at the segregation of their respective feeding niches.

The Scarabaeidae family also includes some important species associated with dunes. Among those with a Mediterranean distribution, in some cases extending to the Atlantic coasts, are small Aphodiinae of the genus *Psammodius* (e.g., *P. pierottii*, *P. nocturnus*, *P. porcicollis*, *P. basalis*), which are both psammophilous and rhizophilous. These species live burrowed at the base of plants [40,56,62].

While they are considered herbivores that feed on both leaves and roots [116] or saprophagous [101], their feeding habits are poorly understood, and there is some evidence of mycetophagous activity, at least for *P. porcicollis* (P. Ponel in [40]).

Among iconic species, some large dung beetles are easily observed while moving across the sand, rolling a dung ball, which they later bury and deposit an egg inside. These include the Mediterranean species *Scarabaeus semipunctatus* (14–28 mm, Figure 4f), which is in significant decline [4,53,96,117,118].

The embryonic and white dunes also host some tiny Anthicidae (1.6–3.5 mm), which are psammophilous and thermophilous, and about whose diet little is known. Characteristic species, considered polyphagous by Labatut et al. [62] and detritivorous by Caussanel [64], include *Mecynotarsus serricornis*, *Anthicus fenestratus*, and *Stricticomus transversalis*, with the latter two also occurring among upper beach wrack [91,107] (LZ, unpublished data).

Although the beetle community described here is characteristic of embryonic dunes and white dunes, it should be noted that many of the species mentioned can migrate into the beach at certain times of the day or year. Many typical beach beetles, on the other hand, burrow among plant roots to survive the winter or adverse climatic periods (LZ, personal observation). The separation between dune and beach associations is therefore regulated by

a dynamic balance, further highlighting that these are complementary habitats within the same ecosystem, rather than distinct ecosystems. The beetle assemblages described above play critical ecological roles within the trophic network of dune habitats, which, despite supporting primary production, are characterized by arid conditions and extreme summer temperatures. Unfortunately, the scarcity of studies allows only a limited understanding of their dynamics, leaving room for a few essential concepts and some speculative inferences. For instance, the disappearance of some aforementioned tenebrionids deprives insectivorous organisms of substantial prey that feed on organic detritus and, potentially, seeds and plant material. Similarly, phytophagous Chrysomelidae and Curculionidae, by feeding directly on dune vegetation, contribute to enhancing the availability of animal proteins for zoophagous fauna.

The activity of coprophagous scarab beetles facilitates the rapid transformation or burial of feces, preventing desiccation, which would otherwise occur rapidly in these habitats, rendering the feces unpalatable to most macroinvertebrates [119]. This ensures the swift and efficient recycling of macro- and micronutrients contained in feces, which are precious in these nutrient-poor, low-organic-matter sandy soils.

The small yet often abundant rhizophilic Scarabaeidae (e.g., *Psammodius* spp.) and fossorial tenebrionids (e.g., *Ammobius rufus*) interact with the rhizosphere in ways that remain poorly understood but are likely significant. For instance, these species are probably active mycetophages [40], contributing to the biological cycling of arbuscular mycorrhizas, which, in turn, play a key role in the biology of dune plants [120].

6. Overview on the Conservation of Beetle Fauna Associated with Dune–Beach Ecosystems

Although coastal dunes have benefited from protection and restoration plans for several years, the number of well-preserved beach–dune ecosystems remains insufficient. According to data updated in the late 1990s, the European Union for Coastal Conservation reported that the area of coastal dunes in central and western Europe has declined by approximately 75% over the past century, with an even more pronounced reduction of 80% in Italy alone [121]. Similarly, in Catalonia, Garcia-Lozano and Pintó [122] estimated that 30% of the beaches possess characteristics suitable for the development of dune systems, and, at the beginning of the 20th century, dune systems were present in 90% of these suitable sites, but their presence has now declined to just 40%.

The condition of beaches is even more concerning. In sites where dune systems are still preserved or have been restored, the beach is generally regarded as a habitat of limited ecological interest, and its management remains focused on maximizing recreational use. The anthropogenic disturbances include the following:

- Urbanization. It involves the physical transformation of natural beaches to accommodate human activities, structures, and services. It leads to a decline of macrofauna community structure descriptors as the level of local urbanization increases [123]. Among the case studies on specialized beetles, in Turkey, the tiger beetle *Calomera concolor* has shown a dramatic decline in both its adult and larval stages on heavily utilized beaches compared to natural, undisturbed ones [55].
- Human trampling associated with recreational activities. It impacts the behavior of beach macrofauna, disrupting its ecological functioning [124]. In the USA, for instance, studies on *Cicindela oregona* and the rare *C. hirticollis* demonstrated that repeated human and non-human trampling compacts the sand and disrupts low-lying vegetation. This interference affects cicindelid oviposition, leading to a reduction of the number of larval burrows [125];

- Exposure to off-road vehicle traffic. Many burrowing invertebrates are exposed to this stressor on the middle to upper beach. Impacts on vegetated habitats are even more severe, with embryonic dune plants showing some capacity for faster recovery, while fixed dunes are significantly more sensitive to damage caused by vehicle stress [126,127].
- Use of artificial light at night. This stressor can disrupt various life history traits, including species orientation, locomotor activity, foraging, predator–prey interactions, reproduction, and settlement [128].

Among the most widespread and impactful activities is the regular and thorough removal of organic debris and stranded litter, or "grooming," which is typically performed daily using mechanical equipment. The complete removal of wrack and driftwood eliminates key food sources and microhabitats, critically impacting the diverse macrofauna associated with these environments (Figure 5a,b). Even less intensive management practices, where only limited amounts of wrack are left or grooming interventions are sporadic, negatively affect the associated biocenosis [129]. As discussed above, studies show that both the thickness of wrack deposits and the area they cover influence the microenvironmental conditions within the biomass, thereby shaping the structure and composition of associated biocenosis.

Figure 5. Impact of the cleaning interventions: (**a**) Deposit of stranded wrack (mainly composed of *Zostera marina* leaves) in the intertidal zone; (**b**) Mechanical beach cleaning operations (grooming) in the beach; (**c**) Pioneer vegetation freely developed on the embryonic dunes; (**d**) Embryonic dune alteration as a result of cleaning activities.

Additionally, grooming activities often extend to the base of white dunes, removing pioneer vegetation and destroying embryonic dune habitats (Figure 5c,d). Although this habitat is protected under the Council Directive 92/43/EEC (code 2110) and serves as a nesting area for the Kentish Plover (*Charadrius alexandrinus*) [130,131], a priority species, the embryonic dune is often not recognized by beach operators as a valuable dune environment. Grooming in these areas also removes heavy driftwood, crucial for the development of highly specialized beetles, such as species of the genera *Calicnemis*, *Isidus*, *Mesites*, and *Brachemys*.

While studies on arthropod macrofauna associated with beach–dune ecosystems have increased since the early 2000s, as highlighted above, long-term monitoring aimed at assessing the conservation status of specialized beetles remains scarce [50,56,92,96,132–134].

7. Are the Beach and Dunes Habitats Within the Same Ecosystem?

Dunal environments and beaches have generally been treated as distinct ecosystems, primarily based on their differing morphology and on the contrasting ecological processes that dominate in each one. A comprehensive description of the ecology of beach–dune ecosystems was published by Bigot et al. [135] and Audisio et al. [136]. In dunes, primary production prevails, while beaches are aphytic, with food webs sustained by organic debris transported and deposited by tidal movements. [2,60,137]. The presence of specialized plant communities has been used as a criterion for identifying priority habitats protected under the EU Habitats Directive, which, however, largely overlooks habitats found on sandy beaches. The division of beach and dune habitats into two separate ecosystems becomes questionable when considering the exchange of matter and living organisms between these two habitats. From a geomorphological perspective, dune systems rely on the supply of sand from the beach, some of which returns to the littoral zone, especially during storm events, in a dynamic equilibrium [20,21]. As above mentioned (cf. Section 2), the concept of an ecosystem assumes that the biological cycles defining it occur within its boundaries. In this regard, while vegetation presence allows for a clear separation between dunes and the beach, this division becomes less coherent when the life cycles of animal species typical of the beach–dune ecosystem are considered. Figure 6 presents a simplified trophic chain related to coleopterans. For the sake of clarity, the relevant roles of other insects, arachnids, and marine macroinvertebrates have been omitted.

It is evident that beetle fauna plays a crucial role in transferring organic carbon and energy from dead organic matter to higher trophic levels, particularly due to their function as decomposers of organic debris and wood. Macroinvertebrate decomposers transform stranded wrack, primarily plant-derived, into animal prey, which in turn serves as a food source for intermediate and top predators. The latter consists mainly of birds that nest in the foredune and mammals inhabiting the dune and backdune areas, both of which rely on the beach as their primary (birds) or complementary (mammals) hunting ground. Given that the annual deposition of stranded organic litter on beaches can range from a few kilograms to several hundred kilograms per linear meter of shoreline (see Section 4.1), the destruction of this microhabitat—densely populated by specialized entomofauna—undeniably deprives the entire ecosystem of a vital source of metabolizable energy. On the other side, the decline of insect populations is increasingly recognized as a global ecological crisis, threatening the functionality of ecosystems worldwide, including agroecosystems essential for human food security [138,139].

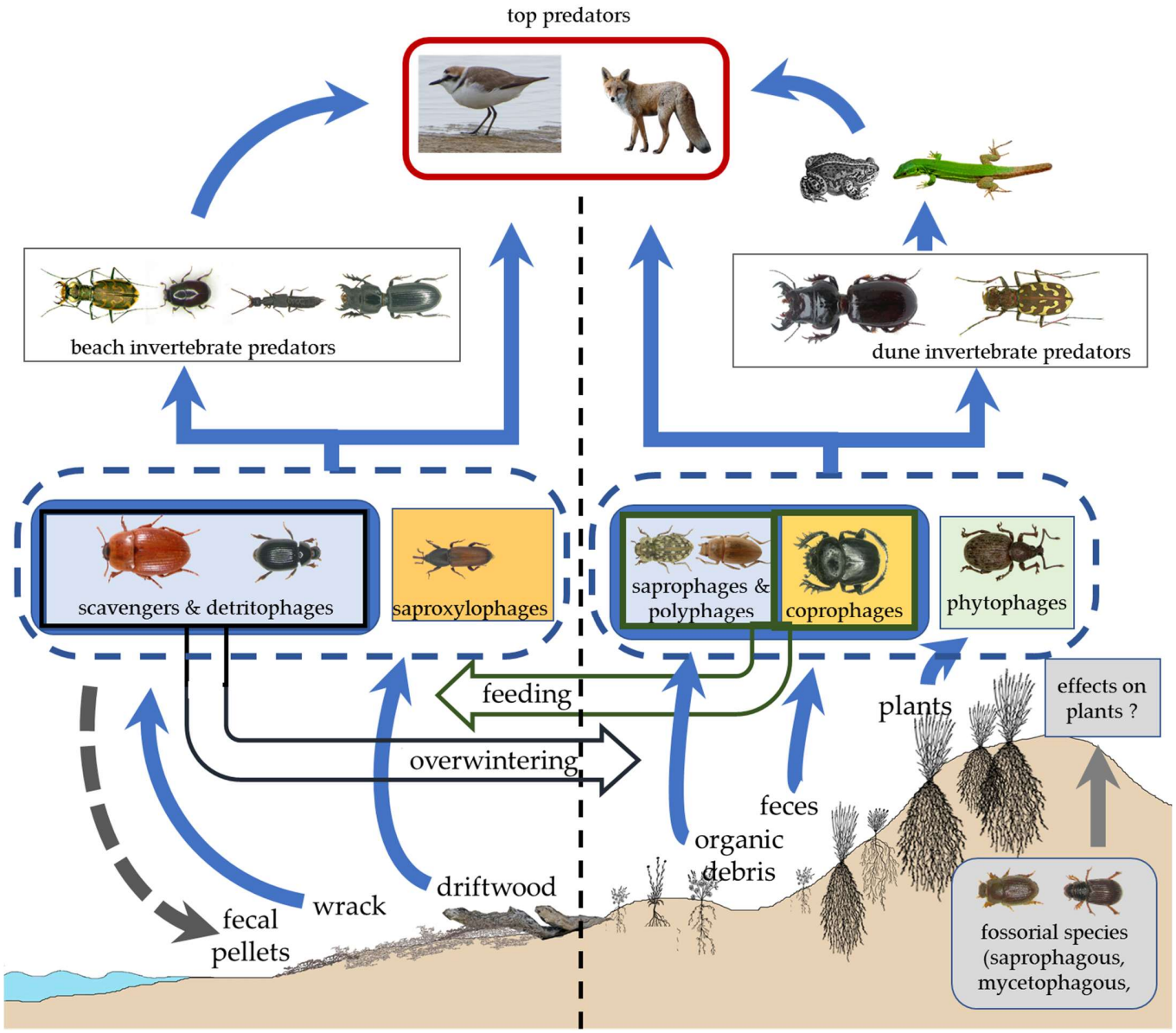

Figure 6. Schematic diagram of the primary trophic interactions involving the beetle fauna of the dune–beach ecosystem. Blue arrows indicate the flow of metabolizable energy and organic carbon through the trophic chain. The dashed grey arrow indicates the significant amount of shredded and partially digested organic matter, enriched with bacteria, that detritivorous beetles reintroduce into the environment in the form of fecal material. The dashed line boxes group together beetles that serve as food for intermediate predators and, at least partially, for top predators. Horizontal empty arrows indicate the movement of specific beetle groups beyond their typical activity zones for feeding or overwintering. The interactions between fossorial saprophagous/mycetophagous beetles and the plant biota remain to be understood. The images used, unless owned by the authors or used with permission, have been made available for free use by their respective creators without attribution requirements under the Pixabay.com license.

Regarding the movement of beetles between the beach and the dunes, these shifts are generally driven by two main factors: seeking shelter in the dunes to survive winter and/or moving toward beach wrack to feed. Both aspects are essential for completing the life cycle of the involved species. The wrack, especially the aged deposits in the upper part of the beach, serves as a food source also for many dune-dwelling beetles, which temporarily move to the beach for feeding. Chelazzi et al. [34] studied the zonation of the coleopteran community within a dune–beach system in southern Italy, reporting

significant overlap between the list of specialist beetles recorded in the dunes and those on the beach, albeit with varying levels of abundance. Specifically, the dune specialists *Ammobius rufus*, *Trachyscelis aphodioides*, *Psammodius basalis*, and *Psammodius nocturnus* were frequently observed also on the beach, whereas the beach specialist *Phaleria acuminata* was also found in the dunes, in addition to being the most abundant species on the beach (cf. Table I in [34]). Although no definitive interpretations are offered in this regard, it is highly likely that these movements of dune specialists towards the beach are driven by the search for food, which thus represents a significant contribution to the biological cycles of the dune habitat. The movement to the beach was also reported for the autumnal tenebrionid *Xanthomus pallidus*, likely driven by foraging. Conversely, *P. acuminata* was observed in the dunes during the cold months, likely seeking winter shelters. Table 2 shows some examples of species whose life cycles extend across the two habitats considered here. These examples suggest that beetles characteristic of both dunes and beaches complete their life cycles by moving between these habitats, which should therefore be considered complementary and part of the same ecosystem.

Table 2. Some examples of Coleoptera with life cycles distributed between the beach and dunes, or that inhabit embryonic/white dunes and are affected by anthropogenic disturbances on the beach.

Species	Feeding Habit	Life Stage on the Beach	Life Stage on the Embryonic Dunes or Dunes	Comment
Cicindela maritima	Predator	Imago	Larvae occur preferentially in embryonic dunes	A key Cicindelidae in beach food chains. It serves as a primary consumer of flies, which are hunted during the day. Adults retreat at night to shelter burrows dug into the dry sand on the seaside slope of the dunes, where also are concentrated their larvae [87].
Cylindera trisignata	Predator	Imago	Adult, temporary refuges (larvae zone?)	This species moves to the embryonic dunes in the evening [140].
Calomera littoralis	Predator	Imago	Overwintering	Adults overwinter among the roots of dune plants and re-emerge in April–May of the following year [50].
Eurynebria complanata	Predator	Imago	Overwintering?	The conservation status of the remaining populations of this beach-associated species was found to be correlated with dune quality. It is hypothesized that overwintering occurs among the dunes [141].
Phaleria spp.	Scavenger	Larvae and imago	Overwintering	The scavenger tenebrionids from this genus feed mainly on the supratidal wrack but move to the dunal areas during the autumnal seasons [34,96].
Xanthomus pallidus	Detritivorous and seed-eater, possibly saprophagous	Imago (feeding)	Larvae and imago	An indicator species of dune quality with autumnal phenology, which moves to the upper beach zone where it feeds on debris [60,104,107]. It has been observed climbing *Ammophila* plants [109], possibly to feed on their seeds, a feeding behavior very common in its congener, *X. pellucidus* [30].
Trachyscelis aphodioides	Detritivorous	Imago	Larvae and imago	This Tenebrionidae predominates in association with antedunal and dunal plants [56,70], where it overwinters among plant roots and is found in its immature stage in late summer and early autumn (LZ, unpublished data). It moves to the upper beach to feed on semi-dry wrack (LZ, personal observation; [39]). The analysis of beetle communities sampled from 14 dunes along the French Mediterranean coast showed that this Tenebrionidae is strongly affected by anthropogenic disturbances related to intensive recreative use of the beach [142].
Calicnemis spp.	Saproxylic and possibly phytophagous	Larvae	Larvae and imago	Larval development takes place in deadwood, which serves as their food source, both in the upper beach—where driftwood primarily accumulates—and in embryonic dunes [23,62]. The diet of adults is not well understood; it may be phytophagous, with a preference for *Thinopyrum junceum*, according to Caussanel [64].
Isidus moreli	Predator (larvae) and saproxy-lophagous (imago)	Larvae	Imago	In its adult stage (that lasts few months), this Elateridae spends the day buried in the sand, especially among the roots of plants (cakiletum is the preferred microhabitat), emerging at dusk for nuptial flights. The larval stage lasts 3–4 years and takes place in the driftwood [94,95]. This can occur in the dunal environment or in the upper beach, but the latter zone is the main driftwood zone. Critically declining everywhere, it resulted in close extinction on beaches subjected to mechanical cleaning, while they persist on beaches with stranded wrack and driftwood [96].
Otiorhynchus ferrarii	Phytophagous		Larvae and imago	A North Adriatic endemic Curculionidae species that lives and feeds on dune plants. Despite its stable zonation within dunes, *O. ferrarii* exhibited significantly lower abundance in a site where the beach was cleaned daily, compared to two nearby sites where the beach remained uncleaned [96].

Importantly, the functional integration between the beach and dunes is also reflected in the life cycle of other arthropods, on which the survival of specialized zoophagous beetles depends, such as in the case of amphipods. These amphipods serve as preferential prey for important beach beetles, threatened with extinction, such as *Scarites laevigatus*, *Eurynebria complanata*, and Cicindelidae in general. Amphipods migrate to embryonic and even stable dunes for several reasons, depending on the stage of development, for moving to foraging or wintering zones, or to escape adverse climatic conditions [31,46,48,143]. Many beetle species typical of the beach also move into dune areas for overwintering (see Table 2). Regarding the transition zone between the beach and dunes, saproxylic and zoophagous species considered indicators of dune quality, such as those already mentioned from the genera *Isidus*, *Calicnemis*, and *Brachemys*, actually carry out a critical part of their life cycle in the driftwood of the upper beach.

If the ecology of the beach is connected to that of the dunes, it is logical to expect that activities disrupting the beach habitat will also impact the dunes. Unfortunately, despite numerous studies on beetle zonation, research specifically addressing this issue remains scarce. Specifically, there is a lack of studies quantifying the energy transfer from beach wrack to dune biocenoses.

Nevertheless, it is evident that wrack influences the dune environment in various ways. For instance, interestingly, the impact of stranded wrack extends beyond the microbial and faunal biocenosis of the beach to also influence the plant community of the dunes. Indeed, seagrass wrack has been shown to positively affect both the area coverage and species richness of dune plant communities, particularly in vegetated zones close to the shoreline [144]. Furthermore, seagrass wrack transported by tides and winds to the upper beach zone mitigates the effects of reduced precipitation, enhancing the resilience of dune vegetation to climate change [145].

The impacts of beach disturbances on the beetle assemblages of dune was studied by Comor et al. [142], investigating 14 beaches along the French Mediterranean coast, finding that pressure factors on the beach significantly affect also the beetle communities occurring in dune systems. Other studies further support this finding. From 2007 to 2014, Zanella et al. [96] monitored three beach–dune ecosystems along the northern Adriatic coast, only one of which had been subject to beach cleaning since the early 2000s. In this disturbed beach, in addition to the near-total disappearance of beach-dwelling species, the eight dune-associated indicator species also experienced a sharp decline in abundance.

The arguments above outlined raise the issue of revisiting the criteria used to define priority habitats within beach–dune ecosystems under current regulations. It appears inconsistent to promote biodiversity conservation by focusing solely on dune areas. This inconsistency is further highlighted by a substantial body of literature documenting the decline or local extinction of key species in sites where mechanical beach grooming is practiced, regardless of the conservation status of the dunes [40,96,129,146,147].

8. Use of Specialized Beetles as Bioindicators to Assess the Environmental Quality of Beach–Dune Ecosystems: Case Studies and Recommendations on Guiding Criteria

The use of living organisms as indicators of an ecosystem's conservation status requires the identification of stenotopic species closely associated with that ecosystem, i.e., that can live exclusively, or almost exclusively, under its specific conditions. Therefore, the selection of indicator species depends on their strong association with particular habitats within the ecosystem under consideration. It is essential to emphasize that the goal of this approach is to use bioindicators to safeguard the entire biotope to which they belong. In highly selective environments, such as those under consideration here, specialized beetles are particularly

well-suited as biological indicators. These beetles encompass a diverse array of species highly adapted to surviving in the various habitats and microhabitats of beach–dune ecosystems, providing a comprehensive means for assessing their ecological state.

The significance and opportunity of selecting sites worthy of special protection using biological indicators, specifically beetles adapted to dune environments, have been effectively discussed by Fattorini [3] (p. 211), who analyzed the ecological functionality of the Tenebrionidae family. However, documented cases of the practical application of this approach remain limited. One of such examples is the study of dune systems along the French Mediterranean coast carried out by Jaulin and Soldati [56]. They identified a list of indicator species from the Carabidae, Tenebrionidae, and Scarabaeidae families to define the conservation status of the dune habitat. These authors proposed an interesting biotic index, assigning a score between 1 and 3 to each species based on its rarity and habitat fidelity. The final scores for each site were then associated with a specific conservation status of the biocenosis, according to a reference numerical scale.

Fattorini and Vigna Taglianti [148] introduced two indices based on Carabid associations to evaluate the ecological value of coastal environments: the "Overall Chorological Index (OCI)" and the "Conservation Value Index (CVI)". Thomas [54] conducted extensive monitoring along the French coast, focusing on a wide range of specialized arthropods. He assigned an "abundance score" ranging from 0 to 4 to each indicator species, based on the number of recorded specimens, with a value of 4 given to findings of 10 or more specimens. Zanella et al. [50] adopted an approach based on semi-quantitative sampling, which included indicator species from both beach and dune habitats. In this case, the final index, named Entomological Index for Environmental Conservation (EIEC), is derived from a more complex calculation, taking into account multiple parameters, i.e., (i) species resilience to environmental disturbance, (ii) population abundance, and (iii) overall biodiversity. Specifically, the following elements were considered:

- Sensitivity factor (S) (values from 1 to 8): This factor expresses the "sensitivity" of a species to environmental alterations and disturbance factors. The higher the value, the greater the sensitivity. This indicator is derived from the sum of values assigned to three autecological elements: environmental exclusivity (score between 1 and 3); dispersal capacity, which facilitates recolonization from nearby populations (score between 0 and 1); sensitivity to anthropogenic disturbance (score between 1 and 3); and position in the food chain (score between 0 and 1). Regarding the latter point, it should be noted that predators, in addition to their own sensitivity to environmental disturbance factors, are also indirectly affected by the impacts these factors cause on their prey. Predator species are therefore particularly sensitive bioindicators, as they also reflect the environmental impacts that affect the lower levels of the trophic chain.
- Density factor (D) (values from 1 to 3): This is based on the abundance category observed during a single survey (the highest value recorded throughout the annual monitoring cycle): sporadic (i.e., <5), present (i.e., 5–20), or abundant (i.e., >20).
- Species richness (N): This reflects the level of biodiversity by assigning a score equal to the number of species recorded from those included in the list of indicator species.

The numerical values defined for the calculation of the EIEC index involve some arbitrary, and therefore debatable, assumptions based on the evaluation of the auto-ecological traits of the considered indicator species. These evaluations are made according to the experience of the specialists who proposed the index and are specifically referenced to the sites for which they were developed. The aim is to provide a tool that tracks changes in the ecological status of a particular site over time, rather than enabling comparisons with sites from other geographical regions. Indeed, coastal environments always exhibit unique traits, and the composition of the index should be adapted to each specific context.

Of course, various versions of an environmental quality index based on bioindicator beetles can be proposed, but the concepts outlined above—intended to differentiate the significance of the presence/absence of each indicator species—should be taken into account. Experience shows that species in altered environments do not all disappear simultaneously; some survive stress factors that others cannot tolerate, and therefore, their value as bioindicators should reflect this variation.

Among the cases of species highly threatened in the Mediterranean due to their high sensitivity to recreational beach use, even in sites where dunes are preserved, two predatory carabids deserve particular mention: *Eurynebria complanata* and *Scarites laevigatus*. The former has now disappeared from most of the Italian and French sites where it was once found [23,54,148,149], although other specialized beetles still survive there. *Scarites laevigatus* and its endemic subspecies from the northern Adriatic, *S. laevigatus venetianus*, are locally extinct in sites where mechanical beach cleaning is practiced, while they survive in beach–dune ecosystems where this activity is limited to the removal of stranded litter [51,96,150].

Cicindelidae: Predatory Beetles Associated with Beach–Dune Ecosystems of Special Ecological Interest and Threatened with Extinction

Since species that exclusively inhabit beach–dune ecosystems vary depending on the geographical region considered, it is not possible to define a universal list of bioindicator species to be used in all contexts. However, the family Cicindelidae includes a large number of species worldwide, many of which are adapted to beach–dune ecosystems. Approximately 2800 species of these elegant predators have been described across all major biogeographic regions, and in all cases, they are insects highly sensitive to environmental changes and exposed to extinction risks [151–155].

Among them, a large number of species are found exclusively, or predominantly, in beach–dune ecosystems, often with highly localized endemisms [152,156,157]. Therefore, this family offers a rich list of bioindicator organisms suitable for assessing the environmental quality of coastal ecosystems, and the inclusion of these species in conservation and environmental monitoring plans should be prioritized whenever possible (Table 3).

Table 3. Cases of endangered Cicindelidae species occurring in beach–dune ecosystems (some of which are not exclusive) around the world.

Species	Distribution	Comment
Calomera concolor concolor	East Mediterranean (Greece, Cyprus, Turkey, Syria) [55].	This species shows a significant decline on beaches with high anthropic pressure, with a risk of disappearance in the absence of regulation [55].
Cephalota vartianorum	Iran, Iraq, Israel, Jordan, Saudi Arabia, Syria, Yemen [158].	Middle Eastern species. Sensitive to the recreational use of beaches and likely locally extinct in some sites where it was historically reported [159].
Cicindela maritima	European Atlantic coast and Baltic Sea.	Critically endangered species. Locally extinct on beaches that are more intensely used for recreational purposes [160].
Cylindera contorta	Eurasian: from the Ponto–Turanic region to west Siberia and northern China [158].	The combination of various factors threatens the survival of the species: suitable sites of limited extent, loss of larval populations during exceptional flooding caused by storms, and coastal urbanization [161].
Cylindera contorta valdenbergi	Mediterranean coast from western Egypt to northern Israel.	Critically endangered in Israel due the anthropic impacts on the coastal beaches [159].
Cylindera trisignata trisignata	Mediterranean.	Declining due to environmental alterations related to the use of beaches for tourism and recreational purposes [91,156,162].

Table 3. *Cont.*

Species	Distribution	Comment
Cylindera trisignata siciliensis	Spain, Sicily, Malta, North Africa, and the Balearic Islands [163].	In decline due to excessive anthropic impact, such as the recreational use of beaches [163].
Lophyra flexuosa flexuosa	Mediterranean with a range extending to the French Atlantic coasts [163]	Associated with dunes and considered not threatened by Assmann et al. [159] based on reports for the Mediterranean basin. It is, however, in marked decline along the French coasts [164].
Lophyra flexuosa sardea	Sub-endemic to Sardinia, Sicily, and Tunisia [163]	In decline due to the intense recreational beach activities [163].
Habroscelimorpha dorsalis dorsalis	USA, NE Atlantic coast from Virginia to Massachusetts [165]	Extirpated from most of the areal distribution for loss of the suitable beaches and recreational use of beaches [153,165,166].
Habroscelimorpha dorsalis media	USA, Atlantic coast from Florida to New Jersey.	Lost from all but one site in New Jersey due to the intense recreational beach activities in these areas [153].
Ellipsoptera lepida	Quebec to southeastern Alberta (Canada), southward to Chihuahua (Mexico), central Texas, southern Louisiana, eastward to NE Atlantic coast (North Carolina to New Jersey), and westward to western Arizona and eastern Nevada [167,168].	It historically inhabited localized coastal and mainland dunefields with loose, light-colored sand, scattered throughout its extensive range. Due to its extirpation across much of this range caused by habitat loss [167,169], conserving the coastal dune habitats where it has been recorded is particularly important. It tolerates even intense human presence on the beach but requires suitable characteristic dunes.
Ellipsoptera puritana	USA, NE Atlantic coast from New England to Maryland [165]	Threatened by the alteration of larval development sites due to excessive growth of invasive vegetation [165].
Cicindela hirticollis gravida	USA, California [170]	Threatened by sand trampling due to human activity on the beach and by the development of invasive plant species. The population endemic to Marin County (California) is genetically distinct from all other U.S. forms of *C. hirticollis*, but its actual taxonomic status remains uncertain [170,171].
Cylindera nivea	Brazil, Argentina, Uruguay [172]	A species highly sensitive to human disturbance that survives only in well-preserved environments. Its use as an indicator species for monitoring beaches is recommended [152].

9. Conclusions

The conservation status of coastal natural environments in advanced economies, and increasingly in many developing countries, is characterized by the loss of most dune systems and their associated biodiversity. However, the ecological degradation of beaches is far more severe than that of dune systems and is not currently addressed in habitat protection regulations for priority interest areas. The arguments presented in this paper lead to the following conclusions:

- The beach is an essential part of the beach–dune ecosystem and hosts significant biodiversity that is exclusively found in its habitats;
- The conservation of stranded organic debris is crucial for the biological cycles that sustain the ecosystem, and mechanical cleaning or grooming activities should be prohibited in sites designated for protection. Compatibility with the recreational use of the beach is possible if the areas where cleaning is allowed are alternated with large zones where wildlife protection is prioritized;
- The conservation of heavy driftwood is part of the ecosystem protection criteria, as it supports the biological cycle of species that live exclusively in this microhabitat;
- The use of biotic indices based on beetle fauna is an effective approach for classifying and monitoring the ecological status of beach–dune ecosystems. Indeed, these indices encompass a high number of species that are exclusively or predominantly associated with the various ecological zones and microhabitats within these systems;

- The selection of indicator species inevitably involves a degree of arbitrariness. However, it should be grounded in a thorough study of the local site characteristics, considering historical knowledge of the populations there occurring. Furthermore, the list should include species suitable to track all relevant habitats of interest;
- The sampling method should include visual surveys of insects active on the surface, as well as sand sifting using appropriate sieves. Data collection could be performed quantitatively (see [56,70]) or semi-quantitatively (see [50]), depending on the available resources and the level of detail desired;
- The selected indicator species must possess characteristics allowing their easy identification in the field. This enables monitoring programs to be carried out by recruiting technical–scientific staff with specific training, but not necessarily highly specialized expertise.

The protection of beach habitats is currently overlooked and generally restricted to sites within integral nature reserves or natural parks. Excellent guidelines and management models have already been proposed to improve the integrity and functionality of sandy beaches while balancing recreational use and conservation [173,174]. Although these often include biological indicators related to threatened and iconic species, such as sea turtles and shorebirds, insects are generally overlooked.

However, in some conservation initiatives involving beach areas with high recreational and tourist activity, beetle fauna has been considered. On the Venetian coast, for example, the small but ecologically significant sites of Ca' Roman and Alberoni are managed by LIPU (Lega Italiana Protezione Uccelli) and WWF Italy, respectively. These organizations employ conservation-focused methods for beach cleaning while ensuring free access for recreational purposes. Monitoring surveys have highlighted the positive impact of these practices on entomofauna conservation, especially when compared to the nearby site of Punta Sabbioni, where effective dune restoration measures were implemented, but no beach protection efforts were undertaken [96]. These initiatives, carried out with the involvement of non-profit organizations, are based on management models aimed at minimizing direct costs, which are primarily associated with the manual collection of stranded litter. In contrast, mechanical cleaning on anthropized beaches incurs costs for both machinery operation and the disposal of the substantial organic material collected. The costs of beach management aimed at ecosystem protection are therefore primarily indirect, as they involve forgoing the intensive economic exploitation of the beach, including restrictions on the construction of buildings and tourist facilities. Despite these potentially significant costs, the beach protection should be guaranteed at least for NATURA 2000 sites of community interest.

Funding: This work did not receive external funding.

Acknowledgments: The authors are grateful to the colleagues who kindly allowed the use of images of their property for this publication: Hervé Bouyon (Colombes, France), Marcello Romano (Capaci, Palermo, Italy), Marco Baldin (Venice, Italy), Francesco Barbieri (Bordano, Udine, Italy), and Alberto Ballerio (Brescia, Italy). A special thanks also goes to Giacomo Masato and Anna Bogo for their assistance in obtaining part of the literature cited in this review, and to Luca Mizzan for granting permission to use some insect images (Museo di Storia Naturale di Venezia, Italy). Finally, special thanks are also given to three anonymous reviewers for their valuable contributions and numerous suggestions aimed at improving our manuscript.

Conflicts of Interest: L.Z., as a freelance professional, participated in various surveys on the entomological fauna of the Venetian coast as part of the mitigation efforts related to the construction of the mobile barriers for closing the inlets of the Venice Lagoon, a project also known as MOSE. Fabio Vianello declares no conflict of interest.

References

1. Sherman, D.J. Problems of scale in the modeling and interpretation of coastal dunes. *Mar. Geol.* **1995**, *124*, 339–349. [CrossRef]
2. McLachlan, A. Ecology of coastal dune fauna. *J. Arid Environ.* **1991**, *21*, 229–243. [CrossRef]
3. Fattorini, S. Lineamenti faunistici delle dune italiane. In *Il Ripristino Degli Ecosistemi Marino-Costieri e La Difesa delle Coste Sabbiose Nelle Aree Protette*; Onori, L., Ed.; Rapporti 100/2009; ISPRA: Roma, Italy, 2009; pp. 183–215.
4. Audisio, P. Litorali sabbiosi e organismi animali. In *Dune e Spiagge Sabbiose*; Quaderni Habitat; Museo Friulano di Storia Naturale di Udine: Udine, Italy, 2002; Volume 4, pp. 63–117.
5. Defeo, O.; McLachlan, A.; Schoeman, D.S.; Schlacher, T.A.; Dugan, J.; Jones, A.; Lastra, M.; Scapini, F. Threats to sandy beach ecosystems: A review. *Estuar. Coast. Shelf Sci.* **2009**, *81*, 1–12. [CrossRef]
6. Checon, H.H.; Corte, G.N.; Shah Esmaeili, Y.; Laurino, I.R.A.; Turra, A. Sandy beach bioindicators: How each benthic taxon tells its own story. *Ocean Coast. Manag.* **2023**, *240*, 106645. [CrossRef]
7. Backlund, H.O. Wrack Fauna of Sweden and Finland: Ecology and Chorology. *Opusc. Entomol.* **1945**, *5* (Suppl.), 1–236.
8. Hyndes, G.A.; Berdan, E.L.; Duarte, C.; Dugan, J.E.; Emery, K.A.; Hambäck, P.A.; Henderson, C.J.; Hubbard, D.M.; Lastra, M.; Mateo, M.A.; et al. The role of inputs of marine wrack and carrion in sandy-beach ecosystems: A global review. *Biol. Rev.* **2022**, *97*, 2127–2161. [CrossRef]
9. Davis, T.J.; Keppel, G. Fine-scale environmental heterogeneity and conservation management: Beach-cast wrack creates micro-habitats for thermoregulation in shorebirds. *J. Appl. Ecol.* **2021**, *58*, 1291–1301. [CrossRef]
10. Ricci, S.; Colombini, I.; Fallaci, M.; Scoccianti, C.; Chelazzi, L. Arthropods as bioindicators of the red fox foraging activity in a Mediterranean beach-dune system. *J. Arid Environ.* **1998**, *38*, 335–348. [CrossRef]
11. Speybroeck, J.; Bonte, D.; Courtens, W.; Gheskiere, T.; Grootaert, P.; Maelfait, J.; Provoost, S.; Sabbe, K.; Stienen, E.W.M.; Van Lancker, V.; et al. The Belgian sandy beach ecosystem: A review. *Mar. Ecol.* **2008**, *29*, 171–185. [CrossRef]
12. Dugan, J.E.; Hubbard, D.M.; McCrary, M.D.; Pierson, M.O. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. *Estuar. Coast. Shelf Sci.* **2003**, *58*, 25–40. [CrossRef]
13. Odebrecht, C.; Du Preez, D.R.; Abreu, P.C.; Campbell, E.E. Surf zone diatoms: A review of the drivers, patterns and role in sandy beaches food chains. *Estuar. Coast. Shelf Sci.* **2014**, *150*, 24–35. [CrossRef]
14. Campbell, E.E. The global distribution of surf diatom accumulations. *Rev. Chil. De Hist. Nat.* **1996**, *69*, 495–501.
15. Maria, T.F.; De Troch, M.; Vanaverbeke, J.; Esteves, A.M.; Vanreusel, A. Use of benthic vs planktonic organic matter by sandy-beach organisms: A food tracing experiment with 13C labelled diatoms. *J. Exp. Mar. Biol. Ecol.* **2011**, *407*, 309–314. [CrossRef]
16. Udvardy, M.F.D. Notes on the ecological concepts of habitat, biotope and niche. *Ecology* **1959**, *40*, 725–728. [CrossRef]
17. Costello, M.J. Distinguishing marine habitat classification concepts for ecological data management. *Mar. Ecol. Prog. Ser.* **2009**, *397*, 253–268. [CrossRef]
18. Hesp, P. Morphology, dynamics and internal stratification of some established foredunes in southeast Australia. *Sediment. Geol.* **1988**, *55*, 17–41. [CrossRef]
19. Bochev-van der Burgh, L.M.; Wijnberg, K.M.; Hulscher, S.J.M.H. Decadal-scale morphologic variability of managed coastal dunes. *Coast. Eng.* **2011**, *58*, 927–936. [CrossRef]
20. Zhang, W.; Schneider, R.; Kolb, J.; Teichmann, T.; Dudzinska-Nowak, J.; Harff, J.; Hanebuth, T.J.J. Land–sea interaction and morphogenesis of coastal foredunes—A modeling case study from the southern Baltic Sea coast. *Coast. Eng.* **2015**, *99*, 148–166. [CrossRef]
21. Psuty, N.P. The Coastal Foredune: A morphological basis for regional coastal dune development. In *Coastal Dunes: Ecology and Conservation*; Martínez, M.L., Psuty, N.P., Eds.; Springer: Berlin/Heidelberg, Germany, 2004; pp. 11–27; ISBN 978-3-540-74002-5.
22. Fanini, L.; Piscart, C.; Pranzini, E.; Kerbiriou, C.; Le Viol, I.; Pétillon, J. The extended concept of littoral active zone considering soft sediment shores as social-ecological systems, and an application to Brittany (North-Western France). *Estuar. Coast. Shelf Sci.* **2021**, *250*, 107148. [CrossRef]
23. Audisio, P.; Taglianti, A.V. Insecta Coleoptera. *Biol. Mar. Mediterr.* **2010**, *17*, 547–571.
24. Dahl, E. Some aspects of the ecology and zonation of the fauna on sandy beaches. *Oikos* **1952**, *4*, 1–27. [CrossRef]
25. Salvat, B. Les conditions hydrodynamiques interstitielles des sédiments meubles intertidaux et la répartition verticale de la faune endogée. *Comptes Rendus Hebd. Seances Acad. Sci.* **1964**, *259*, 1576–1579.
26. Janssen, G.; Mulder, S. Zonation of macrofauna across sandy beaches and surf zones along the Dutch coast. *Oceanologia* **2005**, *47*, 265–282.
27. Schlacher, T.A.; Thompson, L. Spatial structure on ocean-exposed sandy beaches: Faunal zonation metrics and their variability. *Mar. Ecol. Prog. Ser.* **2013**, *478*, 43–55. [CrossRef]
28. Wendt, G.E.; McLachlan, A. Zonation and biomass of the intertidal macrofauna along a South African sandy beach. *Cah. De Biol. Mar. Paris* **1985**, *26*, 1–14.
29. Fallaci, M.; Colombini, I.; Taiti, S.; Chelazzi, L. Environmental factors influencing the surface activity and zonation of *Tylos europaeus* (Crustacea: Oniscidea) on a Tyrrhenian sandy beach. *Mar. Biol.* **1996**, *125*, 751–763. [CrossRef]

30. Aloia, A.; Colombini, I.; Fallaci, M.; Chelazzi, L. Behavioural adaptations to zonal maintenance of five species of tenebrionids living along a Tyrrhenian sandy shore. *Mar. Biol.* **1999**, *133*, 473–487. [CrossRef]
31. Scapini, F.; Chelazzi, L.; Colombini, I.; Fallaci, M. Surface activity, zonation and migrations of *Talitrus saltator* on a Mediterranean beach. *Mar. Biol.* **1992**, *112*, 573–581. [CrossRef]
32. McLachlan, A.; De Ruyck, A.; Hacking, N. Community structure on sandy beaches: Patterns of richness and zonation in relation to tide range and latitude. *Rev. Chil. De Hist. Nat.* **1996**, *69*, 451–467.
33. Colombini, I.; Aloia, A.; Bouslama, M.; ElGtari, M.; Fallaci, M.; Ronconi, L.; Scapini, F.; Chelazzi, L. Small-scale spatial and seasonal differences in the distribution of beach arthropods on the northwestern Tunisian coast. Are species evenly distributed along the shore? *Mar. Biol.* **2002**, *140*, 1001–1012. [CrossRef]
34. Chelazzi, L.; Dematthaeis, E.; Colombini, I.; Fallaci, M.; Bandini, V.; Tozzi, C. Abundance, zonation and ecological indices of a coleopteran community from a sandy beach-dune ecosystem of the southern Adriatic coast, Italy. *Vie et Milieu* **2005**, *55*, 127–141.
35. Zanella, L. La colonizzazione entomologica delle dune ricostruite di San Nicolò del Lido di Venezia (Insecta, Coleoptera). *Boll. Mus. Stor. Nat. Venezia* **2017**, *68*, 31–44.
36. Doyen, J.T. Marine beetles (Coleoptera excluding Staphylinidae). In *Marine Insects*; Cheng, L., Ed.; North Holland: Amsterdam, The Netherlands, 1976; pp. 497–519.
37. Moore, I.; Legner, E.F. Intertidal rove beetles (Coleoptera: Staphylinidae). In *Marine Insects*; Cheng, L., Ed.; North Holland: Amsterdam, The Netherlands, 1976; pp. 521–551.
38. Chubarenko, B.; Woelfel, J.; Hofmann, J.; Aldag, S.; Beldowski, J.; Burlakovs, J.; Garrels, T.; Gorbunova, J.; Guizani, S.; Kupczyk, A.; et al. Converting beach wrack into a resource as a challenge for the Baltic Sea (an overview). *Ocean Coast. Manag.* **2021**, *200*, 105413. [CrossRef]
39. Colombini, I.; Mateo, M.Á.; Serrano, O.; Fallaci, M.; Gagnarli, E.; Serrano, L.; Chelazzi, L. On the role of *Posidonia oceanica* beach wrack for macroinvertebrates of a Tyrrhenian sandy shore. *Acta Oecologica* **2009**, *35*, 32–44. [CrossRef]
40. Boudouresque, C.; Ponel, P.; Astruch, P.; Barcelo, A.; Blanfune, A.; Geoffroy, D.; Thibaut, T. The high heritage value of the Mediterranean sandy beaches, with a particular focus on the Posidonia oceanica "banquettes": A review. *Sci. Rep. Port-Cros Natl. Park* **2017**, *31*, 23–70.
41. Colombini, I.; Fallaci, M.; Chelazzi, L. Importance of marine allochthonous inputs for terrestrial macroinvertebrates inhabiting sandy beaches: Challenges for disentangling strategies of zonal recovery and food webs. In *Marine Research at CNR*; Brugnoli, E., Cavarretta, G., Mazzola, S., Trincardi, F., Ravaioli, M., Santoleri, R., Eds.; National Research Council of Italy: Roma, Italy, 2011; Volume DTA/06-2011, pp. 943–956.
42. Colombini, I.; Aloia, A.; Fallaci, M.; Pezzoli, G.; Chelazzi, L. Temporal and spatial use of stranded wrack by the macrofauna of a tropical sandy beach. *Mar. Biol.* **2000**, *136*, 531–541. [CrossRef]
43. Olabarria, C.; Incera, M.; Garrido, J.; Rodil, I.F.; Rossi, F. Intraspecific diet shift in *Talitrus saltator* inhabiting exposed sandy beaches. *Estuar. Coast. Shelf Sci.* **2009**, *84*, 282–288. [CrossRef]
44. Griffiths, C.L.; Stenton-Dozey, J. The fauna and rate of degradation of stranded kelp. *Estuar. Coast. Shelf Sci.* **1981**, *12*, 645–653. [CrossRef]
45. Griffiths, C.; Stenton-Dozey, J.; Koop, K. Kelp Wrack and the Flow of Energy through a Sandy Beach Ecosystem. In *The Sandy Beaches as Ecosystems*; McLachlan, A., Erasmus, T., Eds.; Developments in Hydrobiology; Springer: Dordrecht, The Netherland, 1983; Volume 19, pp. 547–556. [CrossRef]
46. Bessa, F.; Cunha, D.; Gonçalves, S.C.; Marques, J.C. Sandy beach macrofaunal assemblages as indicators of anthropogenic impacts on coastal dunes. *Ecol. Indic.* **2013**, *30*, 196–204. [CrossRef]
47. Innocenti Degli, E.; Defeo, O.; Scapini, F. Arthropodofauna richness and abundance across beach–dune systems with contrasting morphodynamics. *Reg. Stud. Mar. Sci.* **2021**, *44*, 101722. [CrossRef]
48. Mourglia, V.; González-Vainer, P.; Defeo, O. Distributional patterns in an insect community inhabiting a sandy beach of Uruguay. *Estuar. Coast. Shelf Sci.* **2015**, *166*, 65–73. [CrossRef]
49. Gonçalves, S.C.; Anastácio, P.M.; Pardal, M.A.; Cardoso, P.G.; Ferreira, S.M.; Marques, J.C. Sandy beach macrofaunal communities on the western coast of Portugal—Is there a steady structure under similar exposed conditions? *Estuar. Coast. Shelf Sci.* **2009**, *81*, 555–568. [CrossRef]
50. Zanella, L.; Uliana, M.; Scarton, F.; Barbieri, F.; Ratti, E. Valutazione ambientale di alcuni arenili veneti con formazioni a dune mediante lo studio della coleotterofauna specializzata (Insecta, Coleoptera). *Boll. Mus. Civ. Stor. Nat. Venezia* **2009**, *60*, 41–88.
51. Conti, E.; Costa, G.; Petralia, A.; Petralia, E.; Russo, C. Eco-ethology of *Parallelomorphus laevigatus* (Coleoptera, Carabidae): A species to protect. *Atti Fauna Sicil.* **2012**, *11*, 41–49.
52. Colombini, I.; Chelazzi, L. Environmental factors influencing the surface activity of *Eurynebia complanata* (Coleoptera, Carabidae). *Rev. Chil. Hist. Nat.* **1996**, *69*, 511–537.

53. Mouna, M.; Bensusan, K.; Pérez, C.; Cortes, J. A review of entomological research on sandy beaches in Morocco, with an emphasis on Coleoptera. In *The Sandy Beaches and Coastal Zone Management, Proceedings of the Fifth International Symposium on Sandy Beaches, Rabat, Morocco, 19–23 October 2009*; Bayed, A., Ed.; série générale; Travaux de l'Institut Scientifique: Rabat, Morocco, 2011; Volume 6, pp. 73–80.
54. Thomas, H. Etude des Relevés d'Arthropodes Indicateurs sur 93 Plages de la Côte Aquitaine (Gironde et Landes, 2e Campagne, 2016). *Nebria-Expertises Entomologiques*. 2016, pp. 1–47. Available online: https://www.researchgate.net/publication/344380481_Etude_des_releves_d'arthropodes_indicateurs_sur_93_plages_de_la_cote_aquitaine_Gironde_et_Landes_2e_campagne_2016_Nebria_-Expertises_entomologiques_Herve_THOMAS (accessed on 8 December 2024).
55. Arndt, E.; Aydin, N.; Aydin, G. Tourism impairs tiger beetle (Cicindelidae) populations—A case study in a Mediterranean beach habitat. *J. Insect Conserv.* **2005**, *9*, 201–206. [CrossRef]
56. Jaulin, S.; Soldati, F. *Les Dunes Littorales du Languedoc-Roussillon. Guide Méthodologique d'Évaluation de leur état de Conservation à Travers l'Étude des Cortèges Spécialisés de Coléoptères*; OPIE LR (Office Pour les Insectes et leur Environnement du Languedoc Roussillon): Millas, France, 2005; p. 58; ISBN 978-2-9523901-0-1.
57. Hodge, S.; Williams, A. Coleoptera found in wrack beds and strandlines around the Kent coast. *Br. J. Entomol. Nat. Hist.* **2007**, *20*, 61–70.
58. Egglishow, H.J. Observations on the fauna of the wrack beds. *Trans. Soc. Br. Entomol.* **1965**, *16*, 189–216.
59. Coiffait, H. *Coleopteres Staphylinidae de La Region Palearctique Occidentale II. Sous-Famille Staphylininae, Tribus Philonthini et Staphylinini*; La Nouvelle Revue d'Entomologie: Toulouse, France, 1974; Volume 2, p. 593.
60. Colombini, I.; Brilli, M.; Fallaci, M.; Gagnarli, E.; Chelazzi, L. Habitat partitioning and trophic levels of terrestrial macroinvertebrates of a Tyrrhenian coastal ecosystem (Grosseto, Italy). In *The Sandy Beaches and Coastal Zone Management, Proceedings of the Fifth International Symposium on Sandy Beaches, Rabat, Morocco, 19–23 October 2009*; Bayed, A., Ed.; série générale; Travaux de l'Institut Scientifique: Rabat, Morocco, 2011; Volume 6, pp. 25–35.
61. Colombini, I.; Bouslama, M.F.; Elgtari, M.; Fallaci, M.; Scapini, F.; Chelazzi, L. Study of the community structure of terrestrial arthropods of a Mediterranean sandy beach ecosystem of Morocco. In Proceedings of the Ecosystèmes Côtiers Sensibles de la Méditerranée: Cas Du Littoral de Smir; Bayed, A., Scapini, F., Eds.; série générale. Travaux de l'Institut Scientifique: Rabat, Morocco, 2005; Volume 4, pp. 43–54.
62. Labatut, S.; Thomas, H.; Dauphin, P. Données entomologiques sur la Réserve Naturelle Nationale du Banc d'Arguin (commune de La Teste-de-Buch, Gironde). *Bull. Soc. Linn. Bordeaux* **2017**, *152*, 227–254.
63. Garrido, J.; Olabarria, C.; Lastra, M. Colonization of wrack by beetles (Insecta, Coleoptera) on a sandy beach of the Atlantic coast. *Vie et Milieu* **2008**, *58*, 223–232.
64. Caussanel, C. Recherches préliminaires sur le peuplement de Coléoptères d'une plage sableuse atlantique. *Ann. Société Entomol. Fr. (NS)* **1965**, *1*, 197–248.
65. Lastra, M.; López, J.; Neves, G. Algal decay, temperature and body size influencing trophic behaviour of wrack consumers in sandy beaches. *Mar. Biol.* **2015**, *162*, 221–233. [CrossRef]
66. Olabarria, C.; Lastra, M.; Garrido, J. Succession of macrofauna on macroalgal wrack of an exposed sandy beach: Effects of patch size and site. *Mar. Environ. Res.* **2007**, *63*, 19–40. [CrossRef] [PubMed]
67. Ruiz-Delgado, M.C.; Vieira, J.V.; Veloso, V.G.; Reyes-Martínez, M.J.; Sallorenzo, I.A.; Borzone, C.A.; Sánchez-Moyano, J.E.; García García, F.J. The role of wrack deposits for supralittoral arthropods: An example using Atlantic sandy beaches of Brazil and Spain. *Estuar. Coast. Shelf Sci.* **2014**, *136*, 61–71. [CrossRef]
68. Nourisson, D.H.; Scapini, F.; Milstein, A. Small-scale changes of an arthropod beach community after hard-engineering interventions on a Mediterranean beach. *Reg. Stud. Mar. Sci.* **2018**, *22*, 21–30. [CrossRef]
69. Carpaneto, G.M.; Fattorini, S. Spatial and seasonal organisation of a darkling beetle (Coleoptera, Tenebrionidae) community inhabiting a Mediterranean coastal dune system. *Ital. J. Zool.* **2001**, *68*, 207–214. [CrossRef]
70. Fattorini, S.; Carpaneto, G.M. Tenebrionid density in Mediotyrrhenian coastal dunes: Habitat and temporal variations (Coleoptera, Tenebrionidae). *Fragm. Entomol.* **2001**, *33*, 97–118.
71. Fanini, L.; Martín-Cantarino, C.; Felicita, S. Relationship between the dynamics of two *Talitrus saltator* populations and the impacts of activities linked to tourism. *Oceanologia* **2005**, *47*, 93–112.
72. Majka, C.G.; Shaffer, F. Beetles (Coleoptera) in the diet of Piping Plovers in the Iles de la Madeleine, Québec, Canada. *Wader Study Group Bull.* **2008**, *115*, 77–83.
73. Kirkman, H.; Kendrick, G.A. Ecological significance and commercial harvesting of drifting and beach-cast macro-algae and seagrasses in Australia: A review. *J. Appl. Phycol.* **1997**, *9*, 311–326. [CrossRef]
74. McLachlan, A.; Erasmus, T.; Dye, A.H.; Wooldridge, T.; Van der Horst, G.; Rossouw, G.; Lasiak, T.A.; McGwynne, L. Sand beach energetics: An ecosystem approach towards a high energy interface. *Estuar. Coast. Shelf Sci.* **1981**, *13*, 11–25. [CrossRef]
75. Barreiro, F.; Gómez, M.; Lastra, M.; López, J.; Huz, R. De la annual cycle of wrack supply to sandy beaches: Effect of the physical environment. *Mar. Ecol. Prog. Ser.* **2011**, *433*, 65–74. [CrossRef]

76. Jedrzejczak, M.F. Stranded Zostera marina L. vs wrack fauna community interactions on a Baltic sandy beach (Hel, Poland): A short-term pilot study. Part II. Driftline effects of succession changes and colonisation of beach fauna. *Oceanologia* **2002**, *44*, 367–387.
77. Lastra, M.; Page, H.M.; Dugan, J.E.; Hubbard, D.M.; Rodil, I.F. Processing of allochthonous macrophyte subsidies by sandy beach consumers: Estimates of feeding rates and impacts on food resources. *Mar. Biol.* **2008**, *154*, 163–174. [CrossRef]
78. Lopez, G.R.; Levinton, J.S. 6.02–Particulate organic detritus and detritus feeders in coastal food webs. In *Treatise on Estuarine and Coastal Science*; Wolanski, E., McLusky, D., Eds.; Academic Press: Waltham, MA, USA, 2011; pp. 5–21.
79. Rodil, I.F.; Fernandes, J.P.; Mucha, A.P. Disentangling the effects of solar radiation, wrack macroalgae and beach macrofauna on associated bacterial assemblages. *Mar. Environ. Res.* **2015**, *112*, 104–112. [CrossRef]
80. Catenazzi, A.; Donnelly, M. Role of supratidal invertebrates in the decomposition of beach-cast green algae Ulva sp. *Mar. Ecol. Prog. Ser.* **2007**, *349*, 33–42. [CrossRef]
81. Gómez, M.; Barreiro, F.; López, J.; Lastra, M. Evaluation of phenolic content of wrack debris on estuarine beaches: The effect on upper beach macrofauna. *Mar. Ecol.* **2022**, *43*, 40–53. [CrossRef]
82. Pennings, S.C.; Carefoot, T.H.; Zimmer, M.; Danko, J.P.; Ziegler, A. Feeding preferences of supralittoral isopods and amphipods. *Can. J. Zool.* **2000**, *78*, 1918–1929. [CrossRef]
83. Jaramillo, E.; Huz, R.D.L.; Duarte, C.; Contreras, H. Depósitos de algas varadas y artrópodos macroinfaunales en playas de arena de la costa de Chile. *Rev. Chil. De Hist. Nat.* **2006**, *79*, 337–351. [CrossRef]
84. Hodge, S.; Jessop, L. Notes on Coleoptera found in wrack beds on the north-east coast of England. *Coleopterist* **1996**, *5*, 7–12.
85. Egglishaw, H.J. *The Fauna of Wrack Beds*; Newcastle University: Newcastle, UK, 1958; p. 258.
86. Phillips, D.S.; Arthur, W. Observations on the distribution of seaweed fly larvae and other invertebrates within a wrack-bed. *Entomologist* **1994**, *113*, 154–163.
87. Spungis, V. Invertebrates of the sandy coastal habitats in Latvia. *Latv. Entomol.* **2002**, *39*, 10–19.
88. Orth, R.E.; Moore, I. A revision of the species of Cafius Curtis from the west coast of North America with notes of the east coast species (Coleoptera: Staphylinidae). *Trans. San Diego Soc. Nat. Hist.* **1980**, *19*, 181–211.
89. Walls, G. *Where water meets land: Ecological values and conservation management of driftwood*; Conservation Advisory Science Notes; Department of Conservation: Wellington, New Zealand, 1997; pp. 1–9.
90. Grilliot, M.J. The role of large woody debris on sandy beach-dune morphodynamics. Ph.D. Thesis, University of Victoria, Sydney, Australia, 2019; p. 155.
91. Contarini, E. Eco-profili d'ambiente della coleotterofauna di Romagna: 4-arenile, duna e retroduna della costa adriatica. *Boll. Mus. Civ. Stor. Nat. Venezia* **1992**, *41*, 131–182.
92. Soldati, F.; Jaulin, S.; Louboutin, B.; Noblecourt, T.; Barnouin, T. *Measures Compensatoires au Parc Logistique Potuaire de Port-La-Nouvelle: Mise en Place d'un Suivi del l'État de Conservation des Melieux Dunaires au Travers des Coléoptères*; Office National del Foret; Laboratoire National d'Entomologie Forestiére Office pour les Insectes et leur Environnement, Antenne Languedoc-Roussillon: Quillan/Montferrier-sur-Lez, France, 2016; p. 88.
93. Thomas, H. Etude des Relevés d'Arthropodes Terrestres des Plages de la Réserve Naturelle des Marais d'Yves (Charente-Maritime); Nebria-Expertises Entomologiques. 2015, p. 50. Available online: https://www.academia.edu/33703202/Etude_des_relev%C3%A9s_darthropodes_terrestres_des_plages_de_la_R%C3%A9serve_Naturelle_des_Marais_dYves_Charente_Maritime_2015_Nebria_Expertises_entomologiques (accessed on 8 December 2024).
94. Delnatte, J. A propos d'*Isidus moreli* Mulsant & Rey, 1874, en France (Coleoptera, Elateridae, Elaterinae, Pomachiliini). *Bull. Société Entomol. Fr.* **2010**, *115*, 325–338.
95. Muscarella, C.; Costa, S.; Faraone, F.P.; Mascarello, G.; Salemi, A.; Sechi, D.; Giacalone, G. *Isidus moreli* Mulsant et Rey, 1874 in Sicily (Elateridae Pomachiliini): Regional distribution and threat factors. *Biodivers. J.* **2024**, *15*, 399–405. [CrossRef]
96. Zanella, L.; Uliana, M.; Barbieri, F.; Scarton, F. I coleotteri delle spiagge con dune alle bocche di porto della laguna di Venezia. In *Il Controllo Ambientale della Costruzione del MOSE. 10 Anni di Monitoraggi tra Mare e Laguna di Venezia 2004–2015*; Campostrini, P., Dabalà, C., Del Negro, P., Tosi, L., Eds.; CORILA: Padova, Italy, 2017; pp. 163–197.
97. Ponel, P.; Andrieu-Ponel, V. Un Coléoptère "marin" mythique redécouvert sur l'aire d'adhésion du Parc national de Port-Cros: *Brachemys brevipennis* (Laporte de Castelnau, 1838) (Coleoptera, Malachiidae) sur la presqu'île de Giens (Hyères, Var) | Parc national de Port-Cros et Porquerolles. *Sci. Rep. Port-Cros Natl. Park* **2024**, *31*, 325–329.
98. Liberti, G.; Franzini, G.; Poggi, R. A contribution to the knowledge of genus *Brachemys* Abeille de Perrin, 1890 (Coleoptera, Melyridae, Malachiinae). *Ann. Mus. Civ. Stor. Nat. Genova* **2023**, *116*, 403–446.
99. Ben Aba, W.; Bouragaoui, Z. Confirmation of the presence of the vulnerable species *Calicnemis obesa obesa* Erichson, 1841 (Coleoptera: Scarabaeidae: Dynastinae), in Tunisia. *Munis Entomol. Zool. J.* **2021**, *16*, 381–384.
100. Leo, P. Una nuova specie di Dynastidae della Sardegna: *Calicnemis sardiniensis* n. sp. (Coleoptera Scarabaeoidea). *Boll. Mus. Reg. Sci. Nat. Torino* **1985**, *3*, 421–426.

101. Ballerio, A.; Rey, A.; Uliana, M.; Rastelli, M.; Romano, M.; Colacurcio, L. Scarabeoidea d'Italia, Società Entomologica Italiana. 2014. Available online: https://www.societaentomologicaitaliana.it/Coleotteri%20Scarabeoidea%20d'Italia%202014/scarabeidi/home.htm (accessed on 13 November 2024).
102. Acosta, A.; Carranza, M.L.; Izzi, C.F. Are there habitats that contribute best to plant species diversity in coastal dunes? *Biodivers. Conserv.* **2009**, *18*, 1087–1098. [CrossRef]
103. Acosta, A.; Ercole, S.; Stanisci, A.; Pillar, V.D.P.; Blasi, C. Coastal vegetation zonation and dune morphology in some Mediterranean ecosystems. *J. Coast. Res.* **2007**, *2007*, 1518–1524. [CrossRef]
104. Ciccarelli, D. Mediterranean coastal sand dune vegetation: Influence of natural and anthropogenic factors. *Environ. Manag.* **2014**, *54*, 194–204. [CrossRef] [PubMed]
105. Gadgil, R.L. Marram grass (*Ammophila arenaria*) and coastal sand stability in New Zealand. *N. Z. J. For. Sci.* **2002**, *32*, 165–180.
106. Fattorini, S. Adaptations of tenebrionid beetles to Mediterranean sand dune environments and the impact of climate change (Coleoptera: Tenebrionidae). *Fragm. Entomol.* **2023**, *55*, 1–20. [CrossRef]
107. Fallaci, M.; Colombini, I.; Chelazzi, L. An analysis of the Coleoptera living along a Tyrrhenian beach-dune system: Abundances, zonation and ecological indices. *Vie et Milieu/Life Environ.* **1994**, *44*, 243–256.
108. Mifsud, D. Tenebrionids associated with sandy shores in the Maltese islands (Coleoptera, Tenebrionidae). *Centr. Med. Naturalist* **1999**, *3*, 23–26.
109. Bonometto, L.; Canzoneri, S. I Tenebrionidae delle spiagge e dune del litorale di Venezia. *Boll. Mus. Civ. St. Nat. Venezia* **1970**, *1970*, 223–231.
110. Fattorini, S.; Romiti, F.; Carpaneto, G.M.; Poeta, G.; Bergamaschi, D. I coleotteri Tenebrionidi del sito d'importanza comunitaria "Foce Saccione—Bonifica Ramitelli" (Molise) (Coleoptera Tenebrionidae). *Boll. Soc. Entomol. Ital.* **2016**, *148*, 57–62. [CrossRef]
111. Canzoneri, S. I Tenebrionidae della laguna di Venezia. XIV Contributo allo studio dei Tenebrionidi. *Boll. Mus. Civ. Stor. Nat. Venezia* **1966**, *17*, 57–68.
112. Caussanel, C. Contribution à l'étude du peuplement d'une plage et d'une dune landaise. *Vie et Milieu* **1970**, *21*, 59–104.
113. Ferrer, J.; Whitehead, P.F. The genus *Xanthomus* Mulsant, 1854 (Coleoptera: Tenebrionidae), its evolutionary history and conservation significance. *Ann. Zool. Warszawa* **2002**, *52*, 383–401.
114. Lagar, M.C.; Pazzagli, L.; Cappugi, G.; Giusfredi, G.; Colombini, I.; Fallaci, M.; Chelazzi, L.; Scapini, F. Enzyme activity and trophic links of macroarthropods living on an exposed Mediterranean beach–dune system. *Ital. J. Zool.* **2016**, *83*, 221–232. [CrossRef]
115. Colombini, I.; Chelazzi, L.; Fallaci, M.; Palesse, L. Zonation and surface activity of some Tenebrionid beetles living on a mediterranean sandy beach. *J. Arid Environ.* **1994**, *28*, 215–230. [CrossRef]
116. Siepel, H.; Nijssen, M. Role and development of soil faunal communities in drift sands. In *Inland Drift Sand Landscapes*; Fanta, J., Siepel, H., Eds.; KNNV Publishing: Zeist, The Netherland, 2010; pp. 157–172.
117. Lobo, J.M. Decline of roller dung beetle (Scarabaeinae) populations in the Iberian peninsula during the 20th century. *Biol. Conserv.* **2001**, *97*, 43–50. [CrossRef]
118. Carpaneto, G.M.; Mazziotta, A.; Valerio, L. Inferring species decline from collection records: Roller dung beetles in Italy (Coleoptera, Scarabaeidae). *Divers. Distrib.* **2007**, *13*, 903–919. [CrossRef]
119. Megías, A.G.; Sánchez-Piñero, F.; Hódar, J.A. Trophic interactions in an arid ecosystem: From decomposers to top-predators. *J. Arid Environ.* **2011**, *75*, 1333–1341. [CrossRef]
120. Koske, R.E.; Gemma, J.N.; Corkidi, L.; Sigüenza, C.; Rincón, E. Arbuscular Mycorrhizas in Coastal Dunes. In *Coastal Dunes*; Ecological Studies; Martínez, M.L., Psuty, N.P., Eds.; Springer: Berlin/Heidelberg, Germany, 2008; Volume 171, pp. 173–187; ISBN 978-3-540-74001-8.
121. Brecciaroli, B.; Onori, L. Il sistema delle aree protette e la difesa delle coste. In *Il ripristino degli ecosistemi marino-costieri e la difesa delle coste sabbiose nelle aree protette*; Rapporto 100/2009; ISPRA: Roma, Italy, 2009; pp. 1–19.
122. Garcia-Lozano, C.; Pintó, J. Current status and future restoration of coastal dune systems on the Catalan shoreline (Spain, NW Mediterranean Sea). *J. Coast. Conserv.* **2018**, *22*, 519–532. [CrossRef]
123. Augusto, M.; Abude, R.R.S.; Cardoso, R.S.; Cabrini, T.M.B. Local urbanization impacts sandy beach macrofauna communities over time. *Front. Mar. Sci.* **2023**, *10*, 1158413. [CrossRef]
124. Park, S.; Kim, M.; Joo, S.; Seo, H.; Jo, K.; Lee, Y.; Kim, T.W. Assessment of the impacts of human trampling on locally endangered crab behavior and its implications for coastal ecosystem conservation. *Ocean Coast. Manag.* **2024**, *256*, 107295. [CrossRef]
125. Cornelisse, T.M.; Hafernik, J.E. Effects of soil characteristics and human disturbance on tiger beetle oviposition. *Ecol. Entomol.* **2009**, *34*, 495–503. [CrossRef]
126. Schlacher, T.A.; Thompson, L.M.C. Exposure of fauna to off-road vehicle (ORV) traffic on sandy beaches. *Coast. Manag.* **2007**, *35*, 567–583. [CrossRef]
127. Schlacher, T.A.; Weston, M.A.; Orchard, S.; Kelaher, B.P.; Maslo, B.; Dugan, J.E.; Hubbard, D.M.; Costa, L.; Bishop, M.J.; Kostoglu, K.N.; et al. Adverse impacts of off-road vehicles on coastal dune vegetation are widespread, substantial, and long-lasting: Evidence from a global meta-analysis of sandy beach-dune systems. *Estuar. Coast. Shelf Sci.* **2025**, *312*, 109038. [CrossRef]

128. Quintanilla-Ahumada, D.; Quijón, P.A.; Jahnsen-Guzmán, N.; Lynn, K.D.; Pulgar, J.; Palma, J.; Manríquez, P.H.; Duarte, C. Splitting light pollution: Wavelength effects on the activity of two sandy beach species. *Environ. Pollut.* **2024**, *356*, 124317. [CrossRef] [PubMed]
129. Deidun, A. Beaches—More than just sand and fun. *Biologist* **2009**, *56*, 92–97.
130. Valle, R.; Scarton, F. Habitat selection and nesting association in four species of Charadriiformes in the Po delta (Italy). *Ardeola* **1999**, *46*, 1–12.
131. Scarton, F. Long-term trend of the waterbird community breeding in a heavily man-modified coastal lagoon: The case of the important bird area "Lagoon of Venice". *J. Coast. Conserv.* **2017**, *21*, 35–45. [CrossRef]
132. Wolender, M.; Zych, A. Beetles (Coleoptera) from seaside beach and dunes in the regions of Swinoujscie, Miedzyzdroje and Wiselka (Poland) located along the southern coast of the Baltic Sea. *Balt. J. Coleopterol.* **2007**, *7*, 61–71.
133. Min, H.-K.; Kim, D.S.; Cho, Y.-B. The monitoring of sand dune insects using pitfall trap in Goraebul beach, Yeongdeok-gun, South Korea. *J. Asia-Pac. Biodivers.* **2018**, *11*, 32–38. [CrossRef]
134. Hodge, S.; Marris, J.; Brown, S.D.J.; Emberson, R. Coleoptera found in marine strandlines on New Zealand beaches: Species diversity, seasonal trends and the effect of beach substrate. *N. Z. Entomol.* **2019**, *42*, 47–66. [CrossRef]
135. Bigot, L.; Legier, P.; Musso, J.J. Les biocénoses des substrats meubles d'un haut de plage (Camargue). *Ecol. Mediterr.* **1997**, *3*, 13–31. [CrossRef]
136. Audisio, P.; Muscio, G.; Pignatti, S.; Solari, M. *Dune e Spiagge sSabbiose. Ambienti fra Terra e Mare*; Quaderni Habitat; Museo Friulano di Storia Naturale: Udine, Italy, 2002; Volume 4.
137. Colombini, I.; Brilli, M.; Fallaci, M.; Gagnarli, E.; Chelazzi, L. Food webs of a sandy beach macroinvertebrate community using stable isotopes analysis. *Acta Oecologica* **2011**, *37*, 422–432. [CrossRef]
138. van der Sluijs, J.P. Insect decline, an emerging global environmental risk. *Curr. Opin. Environ. Sustain.* **2020**, *46*, 39–42. [CrossRef]
139. Wagner, D.L.; Grames, E.M.; Forister, M.L.; Berenbaum, M.R.; Stopak, D. Insect decline in the Anthropocene: Death by a thousand cuts. *Proc. Natl. Acad. Sci. USA* **2021**, *118*, e2023989118. [CrossRef] [PubMed]
140. Caussanel, C. Observations écologiques et éthologiques sur une Cicindèle littorale: *Cylindera trisignata* Lat. et Dej., race *Atlantica* Barthe (Coéoptére Cicindelidae). *Procès-Verbaux Société Linnéenne Bordx.* **1962**, *99*, 126–132.
141. Stewart, B. *The status and distribution of the strandline beetle Eurynebria complanata on Whiteford Burrows, Cefn Sidan, Laugharne & Pendine Burrows and Frainslake Sands, Castlemartin in 2016*; NRW Evidence Report N. 189; Natural Resources Wales: Bangor, UK, 2017; p. 80.
142. Comor, V.; Orgeas, J.; Ponel, P.; Rolando, C.; Delettre, Y.R. Impact of anthropogenic disturbances on beetle communities of French Mediterranean coastal dunes. *Biodivers. Conserv.* **2008**, *17*, 1837–1852. [CrossRef]
143. Williams, J.A. Burrow-zone distribution of the supralittoral amphipod *Talitrus saltator* on Derbyhaven Beach, Isle of Man—A possible mechanism for regulating desiccation stress? *J. Crustac. Biol.* **1995**, *15*, 466–475. [CrossRef]
144. Del Vecchio, S.; Jucker, T.; Carboni, M.; Acosta, A.T. Linking plant communities on land and at sea: The effects of *Posidonia oceanica* wrack on the structure of dune vegetation. *Estuar. Coast. Shelf Sci.* **2017**, *184*, 30–36. [CrossRef]
145. Menicagli, V.; Balestri, E.; Bernardini, G.; Barsotti, F.; Fulignati, S.; Raspolli Galletti, A.M.; Lardicci, C. Beach-cast seagrass wrack: A natural marine resource improving the establishment of dune plant communities under a changing climate. *Mar. Pollut. Bull.* **2024**, *201*, 116270. [CrossRef]
146. González, S.A.; Yáñez-Navea, K.; Muñoz, M. Effect of coastal urbanization on sandy beach coleoptera *Phaleria maculata* (Kulzer, 1959) in northern Chile. *Mar. Pollut. Bull.* **2014**, *83*, 265–274. [CrossRef]
147. Colombini, I.; Fallaci, M.; Chelazzi, L. Terrestrial macroinvertebrates as key elements for sustainable beach management. *J. Coast. Res.* **2011**, *2011*, 24–35. [CrossRef]
148. Fattorini, S.; Vigna Taglianti, A. Use of taxonomic and chorological diversity to highlight the conservation value of insect communities in a Mediterranean coastal area: The carabid beetles (Coleoptera, Carabidae) of Castelporziano (Central Italy). *Rend. Fis. Acc. Lincei* **2015**, *26*, 625–641. [CrossRef]
149. Ponel, P. Coléoptères du Massif des Maures et de la dépression permienne périphérique. *Faune De Provence* **1993**, *14*, 5–23.
150. Zanella, L. Biodiversity of the endangered coastal beetle *Scarites laevigatus*: Is the northern Adriatic population a geographical subspecies or a case of introgressive hybridisation? (Coleoptera: Carabidae). *Fragm. Entomol.* **2018**, *50*, 149–160. [CrossRef]
151. Cassola, F.; Pearson, D.L. Global patterns of tiger beetle species richness (Coleoptera: Cicindelidae): Their use in conservation planning. *Biol. Conserv.* **2000**, *95*, 197–208. [CrossRef]
152. Costa, L.L.; Zalmon, I.R. Sensitivity of macroinvertebrates to human impacts on sandy beaches: A case study with tiger beetles (Insecta, Cicindelidae). *Estuar. Coast. Shelf Sci.* **2019**, *220*, 142–151. [CrossRef]
153. Knisley, C.B. Anthropogenic disturbances and rare tiger beetle habitats: Benefits, risks, and implications for conservation. *Terr. Arthropod Rev.* **2011**, *4*, 41–61. [CrossRef]
154. Jaskuła, R. The Maghreb—One more important biodiversity hot spot for tiger beetle fauna (Coleoptera, Carabidae, Cicindelinae) in the Mediterranean region. *Zookeys* **2015**, *482*, 35–53. [CrossRef]

155. Pearson, D.L.; Wiesner, J. The use of tiger beetles (Coleoptera: Cicindelidae) in adapting hotspot conservation to global, regional, and local scales. *J. Insect Conserv.* **2023**, *27*, 19–48. [CrossRef]
156. Cassola, F. Le cicindele e le coste: Biogeografia e conservazione (Studi sui Cicindelidi, CXIX). *Biogeographia* **2002**, *23*, 55–69. [CrossRef]
157. Jaskuła, R.; Płóciennik, M.; Schwerk, A. From climate zone to microhabitat—Environmental factors affecting the coastal distribution of tiger beetles (Coleoptera: Cicindelidae) in the south-eastern European biodiversity hotspot. *PeerJ* **2019**, *7*, e6676. [CrossRef] [PubMed]
158. Putchkov, A.V.; Matalin, A.V. subfamily Cicindelinae Latreille, 1802. In *Catalogue of Palaearctic Coleoptera. Archostemata-Myxophaga-Adephaga*; Löbl, I., Löbl, D., Eds.; Brill: Leiden, The Netherland, 2017; Volume 1, pp. 217–249.
159. Assmann, T.; Boutaud, E.; Buse, J.; Gebert, J.; Drees, C.; Friedman, A.-L.-L.; Khoury, F.; Marcus, T.; Orbach, E.; Renan, I.; et al. The tiger beetles (Coleoptera, Cicindelidae) of the southern Levant and adjacent territories: From cybertaxonomy to conservation biology. *Zookeys* **2018**, *734*, 43–103. [CrossRef] [PubMed]
160. Irmler, U. Population size and mobility of *Cicindela maritima* Dejean, 1822 (Coleoptera: Carabidae). *Angew. Carabidol.* **2010**, *9*, 1–6.
161. Putchkov, A.; Markina, T.; Nitochko, M. Larvae of *Cylindera* (*Eugrapha*) *contorta* (Fleutiaux) (Coleoptera: Cicindelidae) and general review of larval features in the subgenus *Eugrapha*. *Zootaxa* **2019**, *4664*, 412–422. [CrossRef] [PubMed]
162. Aydın, G.; Şekeroğlu, E.; Arndt, E. Tiger beetles as bioindicators of habitat degradation in the Çukurova Delta, southern Turkey. *Zool. Middle East* **2005**, *36*, 51–58. [CrossRef]
163. Sparacio, I.; Muscarella, C.; Falci, A.; Surdo, S. Tiger beetles of Sicily (Coleoptera Cicindelidae). *Biodivers. J.* **2024**, *14*, 791–849. [CrossRef]
164. Texier, E. Atlas des Cicindèles en Loire-Atlantique et Vendée—Biohistoire et conservation. *Lett. De L'atlas Entomol. Régional* **2005**, *18*, 1–38.
165. Knisley, C.B.; Gwiazdowski, R. Conservation strategies for protecting tiger beetles and their habitats in the United States: Studies with listed species (Coleoptera: Carabidae: Cicindelidae). *Ann. Entomol. Soc. Am.* **2021**, *114*, 293–301. [CrossRef]
166. Knisley, C.B.; Drummond, M.; McCann, J. Population trends of the northeastern beach tiger beetle, *Cicindela dorsalis dorsalis* Say (Coleoptera: Carabidae: Cicindelinae) in Virginia and Maryland, 1980s through 2014. *Coleopt. Bull.* **2016**, *70*, 255–271. [CrossRef]
167. Smith, J.A.M.; Rossner, K.J.; Duran, D.P. New opportunities for conservation of a rare tiger beetle on developed barrier island beaches. *J. Insect Conserv.* **2021**, *25*, 733–745. [CrossRef]
168. Bousquet, Y. Catalogue of Geadephaga (Coleoptera: Adephaga) of America, north of Mexico. *ZooKeys* **2012**, *245*, 1–1722. [CrossRef]
169. Panella, M. Ghost tiger beetle (*Cicindela lepida*): Species conservation assessment. In *Digital Commons*; University of Nebraska: Lincoln, NE, USA, 2012; pp. 1–10.
170. Knisley, C.B.; Kippenhan, M.; Brzoska, D. Conservation status of United States tiger beetles. *Terr. Arthropod Rev.* **2014**, *7*, 93–145. [CrossRef]
171. Mawdsley, J.R.; Schlesinger, M.D.; Simmons, T.; Blanchard, O.J. Status of the tiger beetle *Cicindela hirticollis* Say (Coleoptera: Cicindelidae) in New York City and on Long Island, New York, USA. *Insecta Mundi* **2013**, *0317*, 1–7.
172. Cassola, F.; Pearson, D.L. Neotropical tiger beetles (Coleoptera: Cicindelidae): Checklist and biogeography. *Biota Colomb.* **2001**, *2*, 3–24.
173. McLachlan, A.; Defeo, O.; Jaramillo, E.; Short, A.D. Sandy beach conservation and recreation: Guidelines for optimising management strategies for multi-purpose use. *Ocean Coast. Manag.* **2013**, *71*, 256–268. [CrossRef]
174. Schlacher, T.A.; Schoeman, D.S.; Dugan, J.; Lastra, M.; Jones, A.; Scapini, F.; McLachlan, A. Sandy beach ecosystems: Key features, sampling issues, management challenges and climate change impacts. *Mar. Ecol.* **2008**, *29*, 70–90. [CrossRef]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.