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The Mediterranean Dune–Beach–Banquette Ecosystem, Its Pivotal Role in Land–Sea Coupling and the Functioning of Coastal Systems, and Some Related Management Issues

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Abstract: In the Mediterranean, the dune–beach ecosystem is characterized by the presence of thick deposits of dead leaves of the endemic seagrass *Posidonia oceanica*, called banquettes (Dune–Beach–Banquette ecosystem—DBB). This ecosystem plays an important role in the coupling between sea and land. The banquettes provide important ecosystem services: protection of beaches against erosion, contribution to the building of the dune, and a source of nitrogen for coastal vegetation. They are home to a rich and diverse invertebrate fauna that are consumed by other predatory invertebrates and seabirds. A conceptual model of the functioning of the DBB ecosystem and its relation with adjacent ecosystems has been outlined. When dead *P. oceanica* leaves return to the sea, which is the fate of most of the banquette, they constitute an important source of carbon and nutrients for coastal ecosystems and fisheries. Beach management, with the removal of banquettes and driftwood to meet the supposed requirements of beach users and tourists, is an ecological disaster, in addition to being an economic burden for coastal municipalities. Beach management methods that respect the interactions between the marine and terrestrial realms, which preserve the beaches from erosion and allow the return of the banquettes to the sea, and which take into account the real perceptions of beach users are feasible in the framework of the concept of the ‘ecological beach’.

Keywords: beach; dune; ecosystem-based approach; management; Mediterranean; *Posidonia oceanica* banquette



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1. Introduction

Dune–beach ecosystems constitute worldwide an ecotone between marine and terrestrial realms, juxtaposing predominantly marine taxa (e.g., crabs) and predominantly

terrestrial taxa (e.g., birds and flowering plants). In addition, they are essential sites for the coupling between the marine and terrestrial realms, where they exchange organic carbon and nutrients [1–5].

The sand moves perpendicular to the coast, from the sea to the dune, and parallel to the coast. During storms, the swell erodes the beach and the dune and quickly transports the sand toward the sea; during periods of good weather, which last longer, the sand slowly rises from the sea toward the beach, and then the wind carries it toward the dune [4]. The sand comes partly from the land, *via* rivers, and partly from the calcareous debris of marine organisms (e.g., molluscs, sea urchins, calcified macroalgae) living in ecosystems such as in the Mediterranean, *Posidonia oceanica* (Linnaeus) Delile meadows and Coastal Detrital bottoms, which constitute what might be described as ‘sand factories’ [6–11].

In most parts of the world’s oceans, drift marine macroalgae and wood of terrestrial origin (driftwood) are washed up on the beaches. Drift macroalgae, mainly belonging to brown algae (kingdom Stramenopiles) and red and green algae (kingdom Archaeplastida) are relatively easy to consume for beach detritus feeders; they can be totally consumed within one night to a couple of months [12–14]. In contrast, driftwood, which feeds a rich arthropod fauna, requires much more time for total re-mineralization: up to several years.

The dune–beach ecosystem of the Mediterranean Basin is almost unique in that it displays a more or less thick carpet of drift dead leaves (‘banquette’) of the seagrass *P. oceanica*: the Dune–Beach–Banquette (DBB) ecosystem (Figure 1) [15]. This banquette can be seasonal (appearing and disappearing from one storm to the next), almost permanent year-round, or permanent over many years. The thickness of the banquette can reach up to 2.5 m, as in Sicily [16]. It is made of dead *P. oceanica* leaves, rhizomes, and sea balls (aegagropiles) of *P. oceanica*. The leaves can be intact or more or less fragmented into pieces measuring as small as 2 cm [17]. The seagrass *P. oceanica* is endemic to the Mediterranean Sea. It thrives along most of its shores, with the exception of the Levantine Basin (Egypt to Lebanon), where the summer sea temperature is too high (over 30 °C), the northern Adriatic Sea, where the winter sea temperature is too low (below 10 °C), the immediate vicinity of the Strait of Gibraltar and river deltas, such as the Rhône delta (Camargue, Provence) and the Ebro delta (Catalonia), where salinity is too low [18,19]. *Posidonia oceanica* forms vast meadows from the mean sea level down to 20–40 m depth, depending upon the water transparency [18].



Figure 1. Banquette, beach, and dune. Minaccia Bay, Corsica, November 2014. Pl: *Pistacia lentiscus* thicket. Photo © Guilhan Paradis.

Similar banquettes of seagrass remains are uncommon outside the Mediterranean Sea. They occur in particular in southwestern Australia with *Posidonia australis* Hook f. [20], in the Red Sea with *Thalassodendron ciliatum* (Forsk.) Hartog and at Banc d’Arguin, Mauretania, with *Zostera noltei* Hornemann and *Cymodocea nodosa* (Ucria) Ascherson [21].

Both macroalgae and seagrass beds export not only macro-detritus (leaves, individuals, and their fragments) but also dissolved and particulate organic matter (DOM and POM) [13].

Two habitats are adjacent to the DBB ecosystem and constitute exchange interfaces with the marine and terrestrial realms. On the seaside, the surf zone may contain drifting patches of dead leaves of *P. oceanica*, more or less fragmented. This seagrass wrack is accompanied by an assemblage of detritus-feeding crustaceans and by their fish consumers, e.g., *Atherina* sp., *Diplodus sargus* (Linnaeus, 1758), *D. vulgaris* (Geoffroy Saint-Hilaire, 1817), and *Mullus surmuletus* Linnaeus, 1758 [22]. On the land side, a permanent or not permanent water body, which may or may not be open to the sea, is often present where human activities have not disrupted the DBB ecosystem [23].

Mediterranean coastal dune systems occupy 46% of the Mediterranean coasts [24], but they have suffered a dramatic decline and a severe alteration of their habitats induced by human activity linked to coastal development, tourism, and related infrastructures (e.g., [4,25–27]). These major changes have induced the local extinction of some plant populations or the strong decline in several emblematic psammophilous taxa, such as the diverse Corso-Sardinian endemic *Anchusa* plant species (Boraginaceae) [28,29] or the highly threatened *Stachys maritima* Gouan (Lamiaceae) in the western Mediterranean part of its distribution area [30–32]. The same situation also applies to many invertebrates, particularly emblematic beetles such as the predator *Nebria complanata* (Linnaeus, 1767) [33], the coprophagous *Scarabaeus sacer* Linnaeus, 1758 and *S. semipunctatus* Fabricius, 1792 [34], the root-feeder *Calicnemis latreillii* Laporte de Castelnau, 1832 [35], and several other psammophilous coleoptera which are declining, on the verge of extinction or locally extinct on the Mediterranean coast. Some less ‘popular’ groups of arthropods, such as myriapods and spiders, are also affected by this decline; this is the case of the halophilic species *Henia bicarinata* (Meinert, 1870), *Geophilus fucorum* Brölemann, 1909, *Tuoba poseidonis* (Verhoeff, 1901) (myriapods) [36] and *Chaerea maritimus* Simon, 1884 (spider) [37]; the latter has been included recently as “Endangered” (EN) in the IUCN Red List of metropolitan French spiders [38].

Here, on the basis of an extensive literature survey and the authors’ expert judgment, we propose a first conceptual model of the DBB ecosystem, and we expand on the pivotal role of this ecosystem in the coupling between the marine and terrestrial realms. We also highlight the ecosystem services it provides and the way Mediterranean beaches should be managed to save or restore these services. The conceptual model we propose is intended to serve as a basis for the future development of an ecosystem-based quality index.

2. Materials and Methods

We analyzed the available online literature (Google Scholar® and ResearchGate®) dealing with Mediterranean beach biota (accessed: May 2021). The keywords were Banquette, Beach, Bench, Driftwood, Dune, Ecosystem, Erosion, Fauna, Flora, Management, Mediterranean, Overcrowding, *Posidonia oceanica*, Seaside tourism, and Trampling. We also analyzed early scientific articles and the grey literature not included in the databases, documents archived in the MIO library (*Plateforme Macrophytes*) in Marseilles (Aix-Marseille University), one of the most comprehensive documentary collections for the Mediterranean Basin. We did not set a time range on the references taken into account: all references have been considered, whatever their date of publication. The occurrence of duplicate studies between the two databases was not a problem in the framework of expert judgment and the Delphi process (see below). All information from the literature was incorporated directly into the text as key findings.

For the design of the conceptual model of the DBB ecosystem, we relied on the above-mentioned literature and the expertise of the authors. A Delphi-like [39] process was used

for the delimitation of functional compartments and the evaluation of flows. Obviously, not every beach harbors the same DBB ecosystem; this ecosystem diversity was tackled via an average conceptual model, a difficult, risky, but essential exercise. This average conceptual model, therefore, matches biological elements that occur in different Mediterranean regions and within a region in different types of beaches, dunes, and banquettes. It is possible that no individual dune–beach–banquette system fits this average conceptual model, a risk also assumed by authors who, for other regions and other ecosystems, have attempted to conceptualize their functioning (e.g., [1,2]).

Taxonomy follows Algaebase [40] for macroalgae and Tison and Foucault [41] for vascular plants.

3. Results and Discussion

3.1. A Conceptual Model of the Dune–Beach–Banquette Ecosystem (DBB)

3.1.1. General Considerations

A conceptual model of the dune–beach ecosystem, including the surf zone (the zone between the line at which the waves break and the shore), has been established by Hedgpeth [1] for a Peruvian beach. Similarly, a conceptual model, together with a model of energy flows between compartments, has been proposed by McLachlan et al. [2] for a South African beach. The conceptual model we present here is the first attempt to represent the functioning of the Dune–Beach–Banquette ecosystem of the Mediterranean Basin.

A major difference between the dune–beach ecosystem of most areas of the world ocean and the DBB ecosystem of the Mediterranean (Figure 2) is that in the former, inputs of organic matter from the sea (both macroalgae and carrion) are intermittent, pulsed, while in the latter, the input of seagrasses is more or less permanent year-round, despite differences between beaches and seasons. Ephemeral resources, such as drift macroalgae and carrion, are characterized by a succession of species and stages associated with the decomposition and aging of the wrack [13]; in the Mediterranean, such successions are smoothed by the permanence or near permanence of the banquettes. Overall, the input of marine organic matter of vegetal origin is higher, up to two orders of magnitude, than the phytomass of land plants [42].

Other putative differences between the DBB ecosystem of the Mediterranean and most dune–beach ecosystems in other regions are, in the former, (i) the lesser role of carrion inputs, (ii) the lesser role of drift macroalgae, and (iii) the lesser role of birds.

While inputs of marine origin play an important role as a source of nitrogen for the DBB vegetation [43,44] and in subsidizing the invertebrate fauna of the beach, their contribution to the food web rapidly decreases along a sea–land axis and is very low in the back dune and more inland ecosystems [42,45]. On the basis of stable isotopes, macroinvertebrates of the DBB ecosystem exhibit three patterns: (i) A mainly marine signature, such as the coleopterans *Hypocaccus dimidiatus* (Illiger, 1807), *Isidus moreli* Mulsant & Rey, 1875 (in habitats close to the sea), *Scarites laevigatus* Fabricius, 1792, *Phaleria provincialis* Fauvel, 1901, and *Phytosus nigriventris* (Chevrolat, 1843); (ii) A relatively balanced marine and terrestrial signature, such as *Macarorchestia remyi* (Schellenberg, 1950), *Talitrus saltator* (Montagu, 1808) (amphipods), *Tylos europaeus* Arcangeli, 1938 (isopod), *Cylindera trisignata* (Dejean in Latreille & Dejean, 1822), *Isidus moreli* (in habitats far from the sea), *Nebria complanata* (Linnaeus, 1767) (coleopterans), *Pompilus cinereus* (Fabricius, 1775) (hymenopteran), *Arctosa cinerea* (Fabricius, 1777) (spider), and *Geophilus* sp. (myriapod); (iii) A mainly terrestrial signature, such as *Halammobia pellucida* (Herbst, 1799), *Pimela muricata* Olivier, 1795, *Stenostoma rostratum* (Fabricius, 1787) (coleopterans), *Lygus pratensis* (Linnaeus, 1758) (hemipteran), and *Thomisus onustus* Walckenaer, 1805 (spider) [42,45].

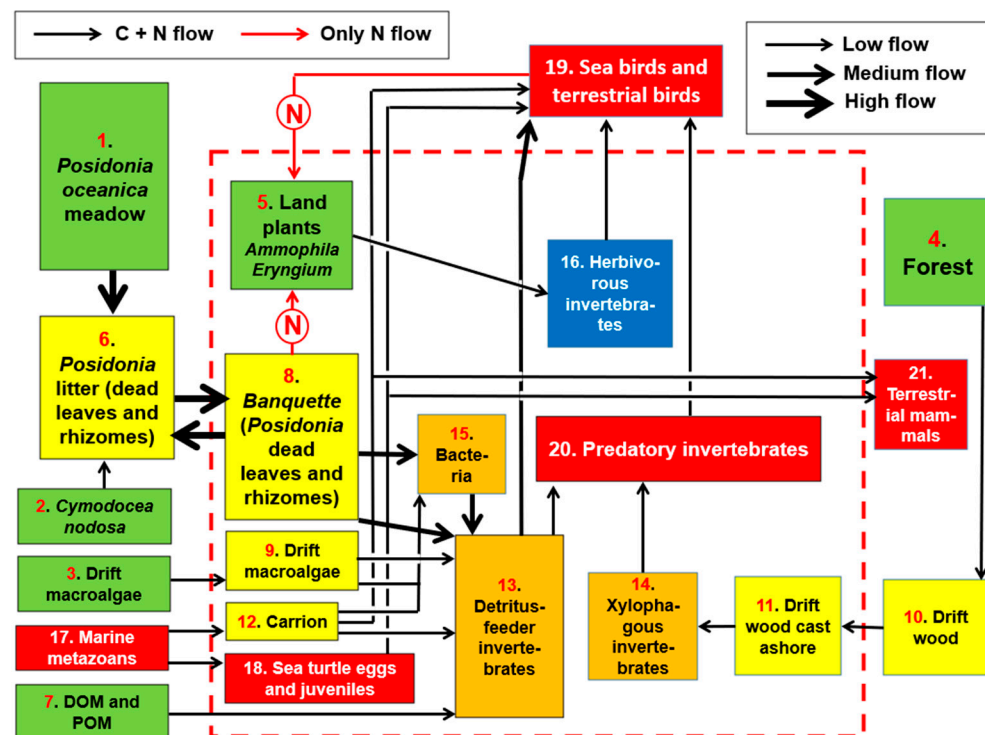


Figure 2. A conceptual model of the functioning of the Dune–Beach–Banquette ecosystem. Boxes in green: primary producers. Yellow: detritus. Ochre: detritus feeders. Blue: herbivores. Red: predators. Red rectangle: Dune–Beach–Banquette ecosystem.

Our study aims to treat all the beaches and dunes of the Mediterranean as a single ecosystem; this may seem justified at first glance. However, on reflection, it might be more appropriate to consider separately the different regions: North Africa, the Eastern Mediterranean, the Northwestern Mediterranean, and the Adriatic Sea. Island vs. mainland ecosystems also probably differ. In addition, the impact of human activities (e.g., urbanization, tourism, pollution) and the resulting fragmentation of habitats should be taken into account. These caveats will be the subject of recommendations for future research (see the section ‘Conclusions’).

3.1.2. Primary Producers

Relatively few species of flowering plants occur in the harsh environment of the beach and dune (Box 5, Figure 2). Dead leaves of *P. oceanica*, carried by the wind from the banquette, are a significant source of nitrogen for vegetation [43,44] (Figure 3). On the sites not damaged by human activities, in the Western Mediterranean, just inland from the banquette of *P. oceanica* dead leaves, five vegetation belts can generally be observed [46–48] (Figure 4): (i) On the seaward part of the beach, on organic debris deposited by the sea, an area with annual species, mostly summer flowering [*Cakile maritima* Scop (Brassicaceae), *Kali australis* (R.Br.) Akhani & Roalson (Amaranthaceae), and *Euphorbia peplis* Linnaeus (Euphorbiaceae)]; (ii) Higher up on the beach, an embryonic dune area, with several perennial species [*Polygonum maritimum* Linnaeus (Polygonaceae), *Sporobolus pungens* (Schreb.) Kunth, *Elytrigia juncea* (Linnaeus) Nevski (Poaceae), *Achillea maritima* (Linnaeus) Ehrend. & Y.P. Guo (Asteraceae), *Eryngium maritimum* Linnaeus, *Echinophora spinosa* Linnaeus (Apiaceae), *Euphorbia paralias* Linnaeus (Euphorbiaceae), *Medicago marina* Linnaeus (Fabaceae), and *Pancreatium maritimum* Linnaeus (Amaryllidaceae)]; (iii) The dune itself, characterized by tufts of *Ammophila arenaria* (Linnaeus) Link subsp. *arundinacea* (Poaceae) (Figure 5); (iv) The back dune area, where the sand is fixed, presents some

shrubby species [*Crucianella maritima* Linnaeus (Rubiaceae), *Ephedra distachya* Linnaeus (Ephedraceae), *Genista* spp. (Fabaceae), *Scrophularia canina* Linnaeus subsp. *ramosissima* (Loisel.) P. Fourn. (Scrophulariaceae)], and some herbaceous species [*Armeria pungens* (Link) Hoffmanns. & Link (Plumbaginaceae), *Lomelosia rutifolia* (Vahl) Avino & P. Caputo (Caprifoliaceae), etc.]; (v) Finally, furthest away from the beach, a thicket whose floristic composition varies according to the geomorphology. Where, behind a sandy rim, there extends a wetland, the thicket consists mainly of *Tamarix africana* Poir. (Tamaricaceae) when the wetland is brackish (lagoon), and of *Salix* spp. (Salicaceae) and *Alnus glutinosa* (Linnaeus) Gaertn. (Betulaceae) in freshwater wetlands (pond or marsh). Where the sand is in contact with rocky hills, the thicket, often anemomorphic, presents various shrubs or trees, notably the maritime juniper [*Juniperus oxycedrus* Linnaeus subsp. *macrocarpa* (Sm.) Ball], which forms a remarkable and highly threatened community [49], associated with some thermophilous species such as *Juniperus phoenicea* Linnaeus subsp. *turbinata* (Guss.) Archang. (Cupressaceae), *Myrtus communis* Linnaeus (Myrtaceae), *Olea europaea* Linnaeus (Oleaceae), *Pistacia lentiscus* Linnaeus (Anacardiaceae), *Rhamnus alaternus* Linnaeus (Rhamnaceae), etc. and lianoid plants such as *Clematis flammula* Linnaeus (Ranunculaceae) and *Smilax aspera* Linnaeus (Smilacaceae).



Figure 3. Dead leaves of *Posidonia oceanica* carried by the wind to the dune, a significant source of nitrogen for vegetation. Plage d'Argent, Porquerolles Island, eastern Provence, France. Photo © Sandrine Ruitton, courtesy of the author.

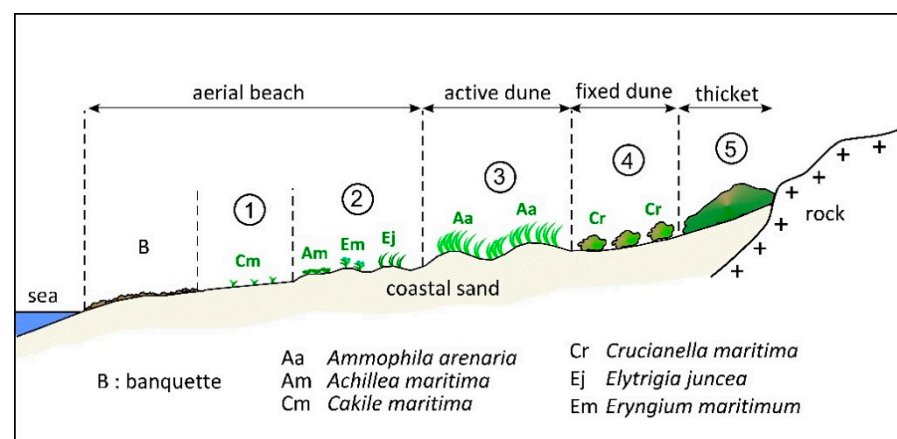


Figure 4. Schematic zonation of vegetation on coastal sand in contact with a rocky hill along Mediterranean shores. Original drawing © Guilhan Paradis and Carole Piazza.



Figure 5. Vegetation of the dune, Pinarellu Beach, Corsica, May 2019. Aa: *Ammophila arenaria* subsp. *arundinacea*. Ej: *Elytrigia juncea*. Em: *Eryngium maritimum*. Pm: *Pancratium maritimum*. Photo © Guilhan Paradis.

All of these species have a wide geographical distribution. However, on the coastal sand, some endemic plants can also occur, such as, in Corsica and Sardinia, *Silene succulenta* Forssk. subsp. *corsica* (D.C.) Nyman (Caryophyllaceae), quite common, and *Anchusa crispa* Viv. (Boraginaceae), with a sporadic distribution and considered endangered (EN) by the IUCN [47,48,50,51]. In Israel, the 190 km of coastal sand dunes shelter 173 vascular plants, including 26% of endemic species [52]. In fact, if vegetation of the embryonic or active dunes is very similar all around the Mediterranean, that of the fixed dunes is often more site-specific: the plant communities are here enriched by endemic plants or taxa with restricted distribution. This is the case of the dune complexes of the island of Djerba (southern Tunisia), which are characterized by two Fabaceae, *Lotus polyphyllus* E.D. Clarke (Figure 6 top) and *Ononis angustissima* Lam. (Figure 6 bottom) [53,54].

In Tuscany (Italy), the mean biomass of the terrestrial plants of the foredune and dune was 210 g DM (dry mass)/m² [42,45].

3.1.3. Herbivorous Invertebrates

Herbivorous invertebrates (Box 16, Figure 2) can eat above-ground (phytophagous) or underground (rhizophagous) parts of the plants.

The caterpillar of the moth *Brithys crini pancratii* (Cyrillo, 1787) is strictly associated with the sea daffodil *Pancratium maritimum*, consuming its leaves at night. Among the Heteroptera, *Lygus maritimus* Wagner, 1949 sometimes thrives on *Cakile maritima*. This plant is also home to many phytophagous beetles, such as the flea beetles *Psylliodes marcida* (Illiger, 1807) and *Psylliodes pallidipennis* Rosenhauer, 1856. Another species of flea beetle, *Psylliodes puncticollis* Rosenhauer, 1856, is associated with the Poaceae of the dune, in particular *Ammophila arenaria*. Among the weevils, *Otiorhynchus juvencus* Gyllenhal, 1834 and *Philopodon plagiatus* (Schaller, 1783) are strictly psammophilous species that live on dune plants, various *Anthemis* in the case of *O. juvencus* and *Ammophila arenaria* in the case of *P. plagiatus*. Another weevil, *Charagmus variegatus* (Fåhraeus, 1840), is associated with *Medicago marina*. *Bruchidius cinerascens* (Gyllenhal, 1833) is thought to develop in the dry stems of *Eryngium maritimum*.



Figure 6. Two shrubs of the Fabaceae family, *Lotus polyphyllus* (**top**) and *Ononis angustissima* (**bottom**) that are characteristic of particular plant communities present on the large fixed dunes of the Island of Djerba (southern Tunisia), April 2015. Photos © Frédéric Médail.

Among the beetles that are rhizophagous during the larval stages is the Oedemeridae *Stenostoma rostratum*: ‘*Stenostoma rostratum* is restricted to undamaged littoral dunes with a good cover of herbaceous halophytes and psammophytes’ [55]. The larvae develop in the roots and lower stems of *Eryngium maritimum* and *Achillea maritima* (= *Otanthus maritimus*), while the adults are found on various flowers. The Elateridae *Cardiophorus exaratus* Erichson, 1840 also has a radicicolous larva, similar to several Scarabaeidae and Dynastidae of the genus *Anoxia*, *Calicnemis latreillii* Laporte de Castelnau, 1832 [35], and the weevil *Leucomigus candidatus tessellatus* (Fairmaire, 1849), whose larvae produce galls on the roots of *Artemisia caerulescens* Linnaeus subsp. *gallica* (Willd.) K.Perss.

A third trophic category of phytophagous psammophilous insects is associated with plant debris produced by dune plants and accumulated on the dune surface or buried in the sand. These are essentially saprophagous beetles belonging to the Tenebrionidae and Scarabaeidae families and represented by a large number of species, including *Ammobius rufus* (Lucas, 1846), *Trachyscelis aphodioides* Latreille, 1809, *Brindalus porricollis* (Illiger, 1803), *Psammodyus basalis* Mulsant & Rey, 1870 among the species that spend most of their lives buried in the sand, and *Pimelia muricata* Olivier, 1795, *Tentyria mucronata* Steven, 1829,

Leichenium pulchellum (Lucas, 1846) among the species that are active in broad daylight on the surface of the sand and are much more polyphagous.

The Gastropoda *Theba pisana* (O.F. Müller, 1774) is also phytophagous [56].

3.1.4. The Banquette

The seagrass *P. oceanica* is a flowering plant (Magnoliophyta) that forms dense meadows in the infralittoral zone (*sensu* Pérès and Picard [57]) in most of the Mediterranean Sea (Box 1, Figure 2). Together with the Coastal Detrital bottom ecosystem of the circalittoral zone, it is the most extensive ecosystem of the Mediterranean photic system. The total surface area is not accurately known, but some regional data highlight its overwhelming dominance (Table 1). The primary production of *P. oceanica* is conspicuously high (e.g., [58,59]). The leaves are usually poorly consumed by herbivores; they shed year-round but mainly in fall, and most of the leaf primary production ends in the litter (necromass) (Box 6, Figure 2) (e.g., [60–63]; but see [64]). Main leaf consumers are the sea urchin *Paracentrotus lividus* (Lamarck, 1816) and the teleost *Sarpa salpa* (Linnaeus, 1758) in the Western Mediterranean, together with the introduced teleosts *Siganus luridus* (Rüppel, 1829) and *S. rivulatus* Forsskal & Niebuhr, 1775, native to the Red Sea, in the eastern basin [64–67]. Rhizomes, with living shoots of leaves, are often broken during storms and are found with dead leaves within the litter. This litter not only occurs in the *P. oceanica* meadow but is also widely exported to adjacent ecosystems of the infralittoral zone, such as sand ecosystems and rocky reefs with *Cystoseira sensu lato* forests or barren grounds, together with ecosystems of the circalittoral and the bathyal zones [63,68–70]; finally, the litter is also exported toward beaches (see below). Overall, on average, 50% of the litter is exported to other ecosystems [71]. Dead *P. oceanica* leaves of the litter, more or less fragmented, are a significant source of organic carbon in these marine ecosystems [72]; they are consumed by a variety of invertebrates: *Holothuria* spp. [73], Amphipoda such as *Nototropis guttatus* (A. Costa in Hope, 1851), *N. swammerdami* (H. Milne Edwards, 1830), *Gammarus aequicauda* (Martynov, 1931), *G. subtypicus* Stock, 1966, *G. crinicornis* Stock, 1966, *Melita hergensis* Reid, 1939, the Isopoda *Synischia hectica* (Pallas, 1772), harpacticoid Copepoda such as *Sarsamphiacus tenuiremis* (Brady & Robertson, 1876), and Nematoda [74–77]. The litter, via detritus feeders, is the basis of a food chain, with omnivores such as the decapods *Liocarcinus navigator* (Herbst, 1794) and *Hippolyte leptocerus* (Heller, 1863) and carnivores such as the decapod *Palaemon xiphias* Risso, 1816 and the teleosts *Gobius* spp. [77].

Table 1. Surface area of *Posidonia oceanica* meadows in some Mediterranean regions (from west to east). Alternative estimates (where available) are not mentioned.

Region or Country	Surface Area	Reference
Mainland Spain	~600 km ²	Extrapolated from Telesca et al., 2015 [78]
Balearic Islands	1200 km ²	Garcias-Bonet et al., 2011 [79]
Provence and French Riviera	267 km ²	Andromede Oceanologie, 2014 [80]
Corsica	537 km ²	Pergent-Martini et al., 2017 [81]
Sardinia	1534 km ²	In Pergent et al., 2019 [82]
Sicily	760 km ²	Calvo et al., 2010 [83]
Tunisia (Gulf of Gabès—Libyan border to Kerkennah Islands)	11,530 km ²	Hattour and Ben Mustapha, 2013 [84]
Greece	2510 km ²	Traganos et al., 2018 [85]
Cyprus	90 km ²	Kletou et al., 2020 [86]

In the infralittoral zone, the litter of dead leaves of *P. oceanica* is displaced by currents and storms from one site to another, from one ecosystem to another. During storms, especially in fall and winter, huge amounts of litter are thrown onto most of the Mediterranean beaches, where they form banquettes (Box 8, Figure 2). The banquettes are more developed in exposed conditions; their volume fluctuates from one year to the next and is greater in stormy years [87]. Over the course of a year, the banquettes are frequently reshaped, gaining or losing thickness and volume and even appearing or disappearing, depending on the strength and direction of the wind, the height of the waves, and the availability of litter in the infralittoral [88–91] (Figure 7). Here, we distinguish three types of banquettes: (i) non-permanent banquettes, e.g., naturally absent in summer, as at Cala di Tarna (Sardinia) [88]; (ii) banquettes present year-round but frequently reshaped, without a compacted, hard basal layer, as at U Barcaghju (Capicorsu, Corsica); (iii) permanent banquettes whose accretion is continuous over decades, resulting in their stratification, with a basal stratum of compacted, stone-hard, layers or leaf remains, capped with more recent, loose litter; dead *P. oceanica* leaves are there still recognizable (Figure 8) [15].

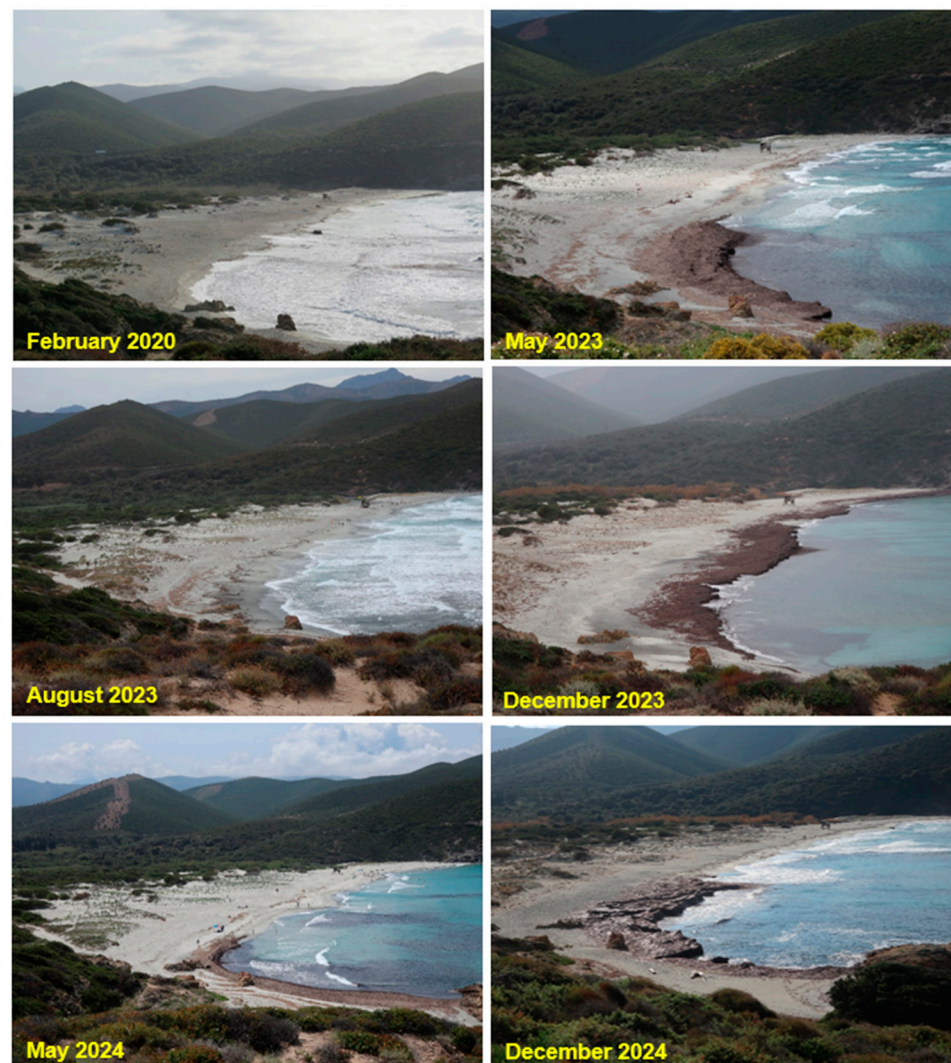


Figure 7. Changes over time in the shape and extension of the banquette at L'Ostriconi beach (L'Agriate, northern Corsica). In February 2020 and August 2023, it is almost absent, while in December 2023, it extends over the entire beach. Photos © Charles-François Boudouresque.

The volume and mass of the banquettes can be considerable (Table 2). In Calvi Bay (western Corsica), the 826-ha *P. oceanica* meadow produces 4509 t DM of litter, 53% of which (2411 t DM) is exported towards beaches [92]. The banquette contains sand, sometimes in great abundance (Table 3) [93], e.g., an average of 82% of the banquette volume in the Balearic Islands [91].

Table 2. Volume, dry mass (DM), or wet mass (WM) of some *Posidonia oceanica* banquettes.

Beach (Region)	Length of the Beach (m)	Volume or DM of the Banquette	Volume or DM per Metre of Shoreline	Reference
Nueva Tabarca (Alicante, Spain)	357	-	500 kg	Mateo et al., 2003 [94]
Four à Chaux (Giens, Provence, France)	65	126 m ³ (June)	1.9 m ³	Authors' unpublished data
Petit Lequin (Porquerolles Island, Provence, France)	45	143 m ³ (June)	3.1 m ³	Authors' unpublished data
Macinaggio (Corsica)	620	4355 m ³	7.0 m ³	Fontaine et al., 2020 [95]
Pietracorbara (Corsica)	550	1133 m ³	2.1 m ³	Fontaine et al., 2020 [95]
Olzu (Patrimonio, Corsica)	200	727 m ³	3.6 m ³	Fontaine et al., 2020 [95]
Olzu (Patrimonio, Corsica)	200	1348 m ³ (June)	9.6 m ³	Authors' unpublished data
Stentino (Asinara, Sardinia)	2100	255 t	121 kg	Vitale and Chessa, 1998 [96]
Calabria (Italy)	-	-	18 to 500 kg	Cantasano, 2011 [97]

Table 3. Amount of sand within some *Posidonia oceanica* banquettes.

Beach	Region	Dry Mass of Sand (kg DM/m ³)	Reference
Padulu-Macinaggio	Corsica	2–15	Fontaine et al., 2020 [95]
Pietracorbara	Corsica	1–294	Fontaine et al., 2020 [95]
Calvi	Corsica	2–3 *	Pergent-Martini et al., 2006 [92]
Region of Bonifacio	Corsica	6–160	Cancemi and Buron, 2008 [88]
Olzu	Corsica	8–72	Fontaine et al., 2020 [95]
44 beaches	Sardinia	93	De Falco et al., 2008 [98]
Punta d'Elice	Sardinia	43	Chessa et al., 2000 [17]
Punta Negra	Sardinia	43	Chessa et al., 2000 [17]
Punta Trabuccato	Sardinia	7	Chessa et al., 2000 [17]
San Giovanni	Sardinia	1	Chessa et al., 2000 [17]

* Estimated from the authors' data.

In the southern and eastern Mediterranean, dead leaves of *Cymodocea nodosa*, another seagrass (Box 2, Figure 2), can occur within the *P. oceanica* banquette [87,99]. Locally (e.g., Grosseto, Tuscany, Italy), *C. nodosa* can be the main stranding seagrass, with an input of 458 g DM per meter of shoreline and per year [42,45].



Figure 8. (Top left) A banquette that generally occurs year-round, frequently reshaped by waves and storms. Note the *Posidonia oceanica* leaves thrown into the air by the splash. L'Ostriconi beach, Corsica, December. Photo © Charles-François Boudouresque. (Top right) A permanent banquette showing the stratification of compacted, stone-hard, ancient litter, capped with recent, loose litter (dead *P. oceanica* leaves are still recognizable). Les Chevaliers beach, Giens Peninsula, eastern Provence. Photo © Charles-François Boudouresque. (Bottom left) A permanent banquette with a compacted base (L'Olzu Beach, Capicorsu, Corsica). Photo © Bruno Belloni. (Bottom right) Detail of the compacted base. Photo © Bruno Belloni.

It is worth emphasizing that the fate of a dead leaf of *P. oceanica* is to be transported, depending on currents and storms, from one habitat to another throughout the coastal zone (beaches, infralittoral, circalittoral, and bathyal zone). In each of these habitats, it is consumed partially or totally by detritus feeders (Figure 9). With regard to the banquettes, the majority of the dead leaves that constitute them are destined to return to the sea, less the moderate quantities that are consumed on the beach or that are carried by the wind toward the dune [63]. In total, the enormous mass of dead leaves of *P. oceanica*, coming from very extensive infralittoral meadows, represents a nitrogen and carbon stock of paramount importance that feeds all coastal ecosystems, including fish exploited by artisanal fisheries [100].

3.1.5. Drift Macroalgae

Some macroalgae dwelling in the algae-dominated infralittoral rocky reef ecosystem [101–103] are torn off during storms and can join the *P. oceanica* dead leaf litter. They can be cast ashore and, therefore, contribute to the banquette [94] (Box 9, Figure 2). Cast ashore macroalgae, where seagrass dead leaves are absent, as along the Atlantic shore, have been shown to be a nutrient supply in the interstitial water of the beach [104]. Such a process probably also occurs in the Mediterranean.

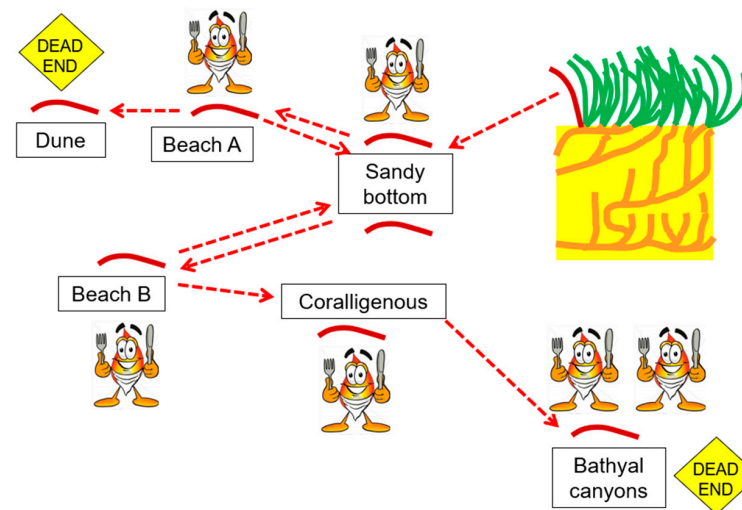


Figure 9. The possible fate of a dead *Posidonia oceanica* leaf after it has been shed (top right). Its consumption (partial or not) is symbolized by a detritus-feeder crustacean. “Dead end” means a possible end of the journey for the leaf. Many other routes, passing through other ecosystems, are possible. Original drawing © Charles-François Boudouresque.

The macroalgae most commonly found in the banquettes are *Padina* cf *pavonica* (Linnaeus) Thivy, *Sargassum* spp. and *Cystoseira sensu lato* (brown algae, kingdom Stramenopiles), *Codium bursa* (Linnaeus) C. Agardh and *C. fragile* (Suringar) Hariot (green algae, Archaeplastida), and *Sphaerococcus coronopifolius* Stackhouse (red algae, Archaeplastida) (Figure 10). Several species of the genus *Padina* occur in the Mediterranean: *P. boergesenii* Allender & Kraft, *P. pavonica*, and the more recently described *P. ditristomatica* Ni-Ni-Win & H. Kawai, and *P. pavonicoides* Ni-Ni-Win & H. Kawai [105,106]. *P. pavonica* is the most common species, but other species could occur in the banquette. The genus *Cystoseira* (*sensu lato*) has been split into three genera: *Cystoseira* (*sensu stricto*), *Ericaria*, and *Gongolaria* [107,108]. Here, we consider *Cystoseira sensu lato*, as specimens cast ashore are often fragments that are not identifiable at the level of these new genera. From a formal point of view, drift macroalgae are detritus, and their consumers are, therefore, detritus feeders (Box 13, Figure 2). Yet, given their state of freshness, this interpretation could be challenged, and their consumers could be considered herbivores.



Figure 10. Banquette, Minaccia beach, Corsica, September 2020. Note a drift of *Codium bursa* (bottom center) and the occurrence of some green *Posidonia oceanica* leaves (left). Photo © Guilhan Paradis.

3.1.6. Carrion

Drift carrion is mainly represented by jellyfish, siphonophores, bivalves, tunicates, fishes, turtles, seabirds, and marine mammals (Box 12, Figure 2) [13]. In contrast with *P. oceanica* dead leaves of the banquet, carrion constitutes an intermittent food resource that could be sporadically important (e.g., jellyfish stranding). It supports land detritus feeders, scavengers, and predators. The yellow-legged gull *Larus michahellis* Naumann, 1840, is an important scavenger [109]. In contrast with some areas of the world ocean where carcasses of marine mammals are not uncommon and subsidize land mammals such as foxes and hyenas [13], carrion probably plays a lesser role in the Mediterranean (but see [110]).

The communities of carrion consumers present worldwide a succession over time of dominant taxa: (i) rapid colonization by dipterans and ants, (ii) which facilitate through their combined tunneling and feeding actions the access of necrophagous taxa, such as trogid and dermestid beetles, to internal tissues, and (iii) the arrival of burying beetles (Silphidae). Dipteran larvae attract coleopteran predators, mainly Staphylinidae (*Cafius*) and Histeridae (*Saprinus*). A similar succession was observed on a dolphin carcass stranded on a beach in southern Italy [13].

The Mediterranean coleopteran *Scarites laevigatus* is an active predator of isopods and amphipods, but it also feeds on the remains of stranded marine animals when available [111].

3.1.7. Driftwood and Xylophagous Invertebrates

Driftwood is inhabited by several saproxylophagous organisms, e.g., the larvae of *Anomala ausonia* Erichson, 1847, *Styphloderes exsculptus* (Boheman, 1843), and several weevils such as *Mesites pallidipennis* Boheman, 1838, *Rhyncolus filum* (Chevrolat, 1880), and *Amaurorhinus sardous* Folwaczny (Coleoptera) [56,112]. *Isidus moreli* is also a coleopteran, the larvae of which dwell in driftwood, with possible excursions in the sand [113]. This species is usually rare and on the verge of extinction in mainland France but may be observed in large numbers in favorable conditions, e.g., in July 1995 at the mouth of the river Tavignani in Corsica, where huge quantities of driftwood carried by the river and deposited by the waves were available.

3.1.8. Bacteria

Bacteria, as well as fungi, play a major role in all ecosystems, terrestrial and marine, although precise data are lacking for some ecosystems, such as the DBB ecosystem (Box 15, Figure 2). Generally speaking, leaf fragmentation increases the surface/volume ratio and, therefore, the activity of microorganisms. In addition, bacteria mobilize nitrogen from the surrounding environment, which enriches the detritus with nitrogen (e.g., [114,115]).

Most detritus feeders also cause fragmentation of the debris and actually consume the bacteria and fungi located within and around the debris (e.g., [116–118]).

3.1.9. Detritus-Feeder Invertebrates

The litter constitutes a habitat for invertebrate metazoans [15], which are proven or suspected detritivores (Box 13, Figure 2). (i) A number of coleopterans, such as *Cercyon arenarius* Rey, 1885, *Ptenidium punctatum* (Gyllenhal, 1827), *Actinopteryx fucicola* (Allibert, 1844), *Phaleria bimaculata* (Linnaeus, 1767), and *P. provincialis* Fauvel, 1901 [42,45,119–123]. (ii) Dipterans, e.g., *Chersodromia anisopyga* Plant, 1995, *C. suda* Plant, 1995, *Rachispoda caudatula* Rohacek, 2001, *Thoracochaeta brachystoma* (Stenhammar, 1854) [121,124], and *Fucellia maritima* (Haliday, 1838) [125]. (iii) Dictyopterans: *Lobopectera decipiens* (Germar, 1817) [120]. (iv) The orthopteran cricket *Pseudomogoplistes squamiger* (Fischer, 1853) [124,126,127] and

the maritime earwig *Anisolabis maritima* (Bonelli, 1832) [128]. (v) A dozen species of Acari including *Arthrodamaeus* sp., *Hermannia minuta* Woas, 1980, *Indotritia krakatauensis* (Sellnick, 1923), *Pelops hirtus* Berlese, 1916, *Pergalumna altera* (Oudemans, 1915), *Phthiracarus* spp., *Pseudotectoribates* sp., *Rhyzotritia ardua* (C.L.C. Koch, 1836), *Scheloribates* sp., and *Zygoribatula frisiae* (Oudemans, 1900) [129]. (vi) At least 13 species of crustaceans including *Armadilloniscus candidus* Budde-Lund, 1885, *A. ellipticus* (Harger, 1878), *Buchnerillo litoralis* Verhoeff, 1942, *Chaetophiloscia elongata* (Dollfus, 1884), *Halophiloscia couchii* (Kinahan, 1858), *H. tyrrhena* Verhoeff, 1928, *Hybleoniscus vallettai* (Caruso, 1975), *Speziorchestia stephensi* (Cecchini, 1928), *Steoniscus pleonalis* Aubert & Dollfus, 1890, *Talitrus saltator*, *Trichoniscus fragilis* Racovitza, 1908, *Trichorhina buchnerorum* (Verhoeff, 1941), and *Tylos europaeus* [42,121,124,130]. (vii) Annelids such as *Ophelia bicornis* Savigny in Lamarck, 1818 and *Anchitraeus albidus* Henle, 1837, and gastropods such as *Gibbula adansonii* (Payraudeau, 1826), *Myosotella myosotis* (Draparnaud, 1801), and *Truncatella subcylindrica* (Linnaeus, 1767) [124].

The invertebrate fauna of the beach, including the banquette where present, and of the dune are conspicuously different [131]. Granulometry is also a key factor for species occurrence: e.g., *Truncatella subcylindrica* is a characteristic species found on pebble and gravel ridges [132].

On a Tyrrhenian sandy shore (Italy) covered with drift material mainly of fluvial origin and with scattered *P. oceanica* detritus, the most abundant invertebrate species were *Talitrus saltator* (Amphipoda, crustaceans; 53% of individuals), dipterans [mainly *Thoracocheata brachystoma* (Stenhammar, 1854); 14%], and *Tylos europaeus* (Isopoda, crustaceans; 9%). Isotopic analysis established the absence of any direct dietary link between *P. oceanica* debris and these invertebrates; particulate organic matter (POM—Box 7, Figure 2) was the most plausible carbon and nitrogen source [121]. It is worth noting that in the absence of a true banquette, this result cannot be generalized to beaches with banquettes. In contrast, in the well-developed banquettes of Calvi Bay (Corsica), litter bag experiments evidence the extensive consumption of *P. oceanica* debris by detritus feeders; after 4 weeks, 56% of the necromass had disappeared from the litter bags [92].

3.1.10. Sea Turtle Eggs and Juveniles

Sea turtles lay eggs on the beaches. The eggs, as well as the juveniles, when they descend towards the sea (Box 18, Figure 2), constitute prey for terrestrial mammals, seabirds, and crabs living on the beach (e.g., [133,134]).

In the Mediterranean Sea, six species have been reported, but only three species definitely frequent this sea: the leatherback turtle *Dermochelys coriacea* (Vandellius, 1761), the green turtle *Chelonia mydas* (Linnaeus, 1758) and the loggerhead turtle *Caretta caretta* (Linnaeus, 1758) [135,136]. As in other regions of the world, they are considered to have declined because of human pressures: seaside tourism, light pollution on beaches, bycatch by fishing gear, and deliberate capture for human consumption or the sale of the shell to tourists [135,137].

In the recent past, i.e., after the cold episode of the Little Ice Age (LIA), nesting of *C. caretta* and *C. mydas* was mainly limited to the Levantine Basin. Nowadays, nesting areas of both species are on the increase, and *C. caretta* regularly lays in the western basin, including its northwestern beaches [136,138–142].

3.1.11. Predatory Invertebrates

Predatory and putatively predatory species (Box 20, Figure 2) belong to (i) coleopterans: the Staphylinidae [e.g., *Cafius xantholoma* (Gravenhorst, 1806), *Carpelimus pusillus* (Gravenhorst, 1802), *Myrmecopora* spp., *Phytosus nigriventris*, *Remus filum* (Kiesenwetter, 1849), *R. pruinosis* (Erichson, 1840), *R. sericeus* Holme, 1837, *Aleochara albopila* (Mulsant

& Rey, 1852), *Brachygluta globulicollis* (Mulsant & Rey, 1861)], and the Histeridae [several species including the common *Hypocaccus dimidiatus*], and the Carabidae [e.g., *Cylindera trisignata*, *Dicheirotichus obsoletus* (Dejean, 1829), *Distichus planus* (Bonelli, 1813), *Harpalus attenuatus* Stephens, 1828, *Nebria complanata*, *Scarites buparius* (J.R. Forster, 1771), and *S. laevigatus*] [42,121,124,131,143]. The relatively rare, large Carabidae *Scarites buparius* lives on sand and feeds on insects, large coleoptera, such as *Anoxia* and *Anomala*, and gastropods, such as *Theba pisana* and *Eobania vermiculata* (O.F. Müller, 1774) [144]. *Scarites laevigatus* is a predator of amphipods and isopods [111]. *Nebria complanata* is a predator of the crustacean *Talitrus saltator* [143]. (ii) Spiders [e.g., *Arctosa cinerea*, *Aulonia albimana* (Walckenaer, 1805), *Chaerea maritimus* Simon, 1884, *Drassodes* sp., *Gnathonarium dentatum* (Wider, 1834), *Oecobius annulipes* Lucas, 1846, *Oedothorax paludigenus* Simon, 1926, *Primerigone vagan*, and *Thomisus onustus*] [37,42,121,124,145,146]. (iii) Chilopoda, such as the centipede species *Geophilus fucorum*, *Tuoba poseidonis*, *Henia bicarinata* [42,147], and *Scutigera coleoptrata* (Linnaeus, 1758)] [124]. (iv) Crustaceans e.g., *Armadillidium vulgare* (Latreille, 1804) and *Porcellio laevis* Latreille, 1804. Some of these species (Carabidae, crustaceans, and spiders) are not residents of the banquette and invade it at night to prey on amphipods and isopods [124].

3.1.12. Sea Birds and Terrestrial Birds

The birds that frequent the Mediterranean coast are not the same throughout the year. Migration governs the presence of these birds, which use the DBB ecosystem differently according to their needs (Box 19, Figure 2). This habitat has a particularly important role during migration as a stopover site for feeding and resting. This results in occasional higher densities of passerines and shorebirds. Mediterranean DBB systems are rich in marine invertebrates, insects, and various seeds, which provide essential food for migratory birds. The diversity of size and shape of the beaks of shorebirds is adapted to this richness and allows them to exploit a wide range of resources offered by this coastal environment (marine worms, shellfish, crabs, mollusks, etc.) [148,149]. In addition to the variety of resources consumed, the quantity consumed is also important. Birds, especially migratory ones, need a lot of energy for flight [150,151] making them important predators in the food chain of this ecosystem.

These birds can cover thousands of kilometers in one or more stopovers and are, therefore, potential dispersal vectors for terrestrial and aquatic plants, invertebrates, and even pathogens [152–154]. As a result, they have a real dispersal role on a more or less large scale, either by exozoochory (adhesion to feathers, beaks, and legs) or by endozoochory (ingestion and survival in the digestive tract). They, therefore, enable the colonization of new habitats and the maintenance of gene flow [155–157].

Seabirds, mainly gulls, and passerines such as the water pipit [*Anthus spinoletta* (Linnaeus, 1758)] or the starling [*Sturnus vulgaris* Linnaeus, 1758] also feed in the banquette. Gulls will, for example, find an important calcium resource in the cuttlebones of sepia cuttlefish [158]. They feed on a wide variety of prey and can also be scavengers when fish or cetaceans wash up on the beaches.

This environment is also a breeding ground for some birds. The Kentish plover (*Charadrius alexandrinus* Linnaeus, 1758), the little plover (*Charadrius dubius* Scopoli, 1786), and the little tern [*Sternula albifrons* (Pallas, 1764)] nest in the sand, simply forming a small cavity in which they lay their eggs. Mediterranean warblers such as the Sardinian warbler [*Sylvia melanocephala* (Gmelin, 1789)], the western subalpine warbler [*Currucula iberiae* (Svensson, 2013)], or the spectacled warbler (*Currucula conspicillata* Temminck, 1820) use the back dune for their nests.

Birds, therefore, play an important ecological role in these environments because of the diversity of species they represent and the diversity of resources on which they rely,

especially as they are at the top of the food chain. Moreover, at certain sites, their high abundance during limited periods of the year puts pressure on the environment, as they are essential to these species. Threats of habitat loss, pollution, or overexploitation of prey can, therefore, have a direct negative effect on bird populations.

3.1.13. Terrestrial Mammals

In coastal areas, the red fox *Vulpes vulpes* (Linnaeus, 1758) makes foraging excursions in the DBB ecosystem, as evidenced by the analysis of its feces (Box 21, Figure 2); it feeds in particular on carrion, large beetles, such as *Scarites buparius* and orthopterans [13,110]. On several dunes in Corsica, European rabbits *Oryctolagus cuniculus* (Linnaeus, 1758) dig burrows, and hares *Lepus timidus* Linnaeus, 1758 have also been observed.

In some areas, such as Corsica, cattle can be found in the DBB, resting on the drift leaves, foraging in the dune, and providing organic matter through feces (Figure 11).



Figure 11. Cattle on the beach of Barcaghju (Capicorsu, Corsica), alone (right) and together with beachgoers (left), green circle, in July 2020. Note that the banquette of *Posidonia oceanica* has not been removed. Photos © Charles-François Boudouresque.

3.2. Ecosystem Services

Ecological goods and ecosystem services can be divided into four categories: ecological functions for other species and ecosystems (e.g., exportation of organic matter, shelter, nursery, spawning area, and primary and secondary production), provisioning services (e.g., fisheries), cultural services (e.g., recreational activities, attractive landscapes, education, and research), and regulating services (e.g., coastal protection and climate regulation) [159–162].

The DBB ecosystem provides important services distributed among these different categories [4,163,164].

The one that is least well taken into account by managers, although it is of major importance for coastal ecosystems, is the return to the sea of dead leaves from the banquette [165] (Figure 9); they form the base of food webs and constitute an ecological function and, when food webs lead to fish of commercial interest, a provisioning service (fisheries) [165]. The dead *P. oceanica* leaves of the banquette when blown inland by the wind to the foredune, trap the sand and increase the seaward accretion of the dune [166]. In addition, they are a major source of nitrogen for vegetation on the dune and the back dune [43,90].

The best-known cultural service provided by the DBB ecosystem is seaside tourism. The remarkable biodiversity (species diversity and organizational diversity) of the DBB ecosystem should also be considered [164].

Finally, erosion regulation of the beaches is a regulating service of major importance. Inland protection from wind, aerosols, and carbon sinks have also been highlighted [4,164].

An assessment of the non-market value of the ecosystem services provided by the habitats of the Spanish Catalonia coastal zone highlights the value of the DBB ecosystem: it is four and twenty-seven times higher than that of seagrass beds and temperate forests, respectively [167].

These ecosystem services are particularly important in a region, the Mediterranean, which hosts a third of world tourism, while the Mediterranean Sea itself represents only 0.8% of the surface area of the world ocean (e.g., [168–170]). Of course, seaside tourism in the Mediterranean is not limited to beaches; diving, sailing, the rich and diversified cultural heritage, and even gastronomy also play an important role. The SSS trilogy (Sea, Sun, and Sand) sometimes gives way to that of RRR (Rupture, Reunion, and Resourcing) [171–174]. Nevertheless, beaches retain major economic importance in the Mediterranean.

3.3. Threats to Ecosystem Services, Conservation and Management

Dunes and beaches are worldwide a fragile system, based upon the constant movement of sand between the fore beach, the beach, and the dune, either landwards or seawards, depending upon storms and wind [2,7,175–179]. At the same time, this system is adapted to disturbances since it has experienced them throughout its evolutionary history; natural disturbance may even be necessary to maintain its diversity and ‘health’ [180].

Human activities, which modify or interrupt the natural movements of sand, perpendicular (between the dune and the beach) or parallel to the coast, have worldwide negative consequences on the sedimentary balance of the dune–beach system and result in dune destruction and beach erosion: trampling, off-road vehicles, litter (manufactured solid waste such as plastic material), sand mining, roads, construction, together with sediment nourishment and hard structure engineering to combat erosion such as groynes and riprap [1,4,13,175,176,180–183]. Overall, human pressure decreases the point diversity of plants and causes a simplification in the dune spatial pattern [184].

Drift macroalgae are widely consumed by beach invertebrates, whatever their origin (native or non-native species); the only criterion for consumption is their content in deterrent compounds, such as phenolic compounds [185].

In the Mediterranean, a further human impact on the dune and beach system is the removal, often referred to as grooming, of the banquettes by local authorities [24,91,95,163,186–192]. This removal is justified by authorities as being requested by users (beachgoers, tourists, coastal tourism professionals). In fact, these banquettes have characterized Mediterranean beaches for millions of years, and until the last decades of the 20th century, bathers had no difficulty coping with the banquettes [15]. In fact, all surveys of the perception of beachgoers show that people’s dislike of the banquettes is much less widespread than might be expected. A majority of beachgoers are not strongly opposed to beaches with banquettes, do not consider banquettes to be a nuisance, and are aware of the importance of banquettes for the protection of beaches against erosion. Once beachgoers are duly informed, this majority becomes overwhelming. By removing the banquettes of *P. oceanica*, the local authorities could, therefore, be acting on the basis of their own perception rather than that of the actual users [24,165,193–195].

The removal of the banquettes, for the supposed comfort of bathers, causes the erosion of the beach, which is no longer protected; in addition, it removes large amounts of sand (Table 3), which accentuates the erosion of the beach [15,17,88,91]. The removal of the banquettes also causes important changes in the DBB ecosystem functioning. In Malta, Deidun et al. [99] showed that the invertebrate fauna of groomed beaches is greatly impoverished when compared with ungroomed beaches: some taxa, e.g., Staphylinidae and the gastropod *Truncatella subcylindrica* do not occur in the former.

Several techniques are used for the removal of the banquettes [15,24]. The worst is sending them to landfills. Another technique consists of piling up the banquette, using heavy machines, on one side of the beach. The so-called *millefeuille* technique is practiced by some municipalities; it consists of interposing layers of leaves and layers of sand [15]; as a result, the banquette is spread out on the beach but not definitely removed. The effectiveness of this technique in protecting beaches against erosion is still poorly known, but interestingly, the process occurs naturally on some non-managed beaches (Figure 12). The least damaging technique for the coastal environment is to load the banquettes onto barges and deposit them offshore; the fate of the majority of dead leaves of the banquette is, in fact, to return to the sea and to contribute (carbon and nitrogen) to the functioning of coastal ecosystems, so this technique imitates the natural process [15,63,165].



Figure 12. A natural *millefeuille*: a thin layer of sand has covered the layer of dead *Posidonia oceanica* leaves, of which only the edge remains visible at the top of the slope. Palu Beach (Ventiseri, Corsica), December 2024. Photo © Charles-François Boudouresque.

In fact, the best solution, both for the sustainability of the beach and the DBB ecosystem, is not to remove the banquettes. This is the principle of ‘ecological beaches’, a nature-based solution [196–202]. This, of course, assumes that users are informed of the reasons for this management strategy [15,196] (Figure 13). In the framework of an EU Interreg program (POSBEMED2), innovative communication and awareness-raising tools with an appealing tone, at once humorous and instructive, have been developed [203,204] (Figure 14).

The removal of marine mammal carcasses deprives the ecosystem of carrion. It is justified for reasons of hygiene and the truly unpleasant odor. However, the impact on the ecosystem is limited by the rare and very localized nature of these strandings.

Non-indigenous species (NIS) are common on beaches and dunes. The ice plants *Carpobrotus* spp. [*C. edulis* (Linnaeus) N.E. Br. and *C. aff. acinaciformis* (Linnaeus) L. Bolus], originating from South Africa, occupy vast areas on the rocky and sandy Mediterranean coast (map in Médail et al. [205]). These are the exotic species that pose the most widespread ecological problems because of their high covering power, linked to their significant capacity for sexual and asexual reproduction. Each individual produces very numerous seeds (1000 to 1800 seeds per fruit in *C. edulis*), while fragmentation of the leafy stems increases the areas occupied. In addition, *Carpobrotus* spp. disperse easily by zoochory; the animals involved are rats, rabbits, ants, and, to a lesser extent, seabirds. Finally, the growth of the aerial leafy stems is rapid: they elongate by more than one meter per year and can cover an area of 20 m² in 10 years (in [205]). The only way to limit their surface area is to uproot them, which has a high cost because uprooting campaigns must be repeated

every year until the seed stock within the soil is exhausted [51]. Few other NIS species are observed on the sandy Mediterranean coastline. We can mention a few individuals of *Atriplex halimus* Linnaeus, *Cortaderia selloana* (Schult. & Schult f.) Asch. & Graebn., *Gazania rigens* (Linnaeus) Gaertn., *Imperata cylindrica* (Linnaeus) P. Beauv., *Spartina patens* (Aiton) Muhl., *Symphytotrichum squamatum* (Spreng.) G.L. Nesom, and *Xanthium orientale* Linnaeus subsp. *italicum* (Moretti) Greuter on a few rare beaches and dunes in Corsica [48,51].



Figure 13. Public information board on Is Traias beach, Sardinia, Italy. Photo © Charles-François Boudouresque.

A Mediterranean dune vulnerability index (MDVI) has been proposed by Ciccarelli et al. [188]; it is based on fifty-one variables grouped within five groups of factors: geomorphological conditions of the dune system, marine influence, aeolian effect, vegetation condition, and human effect (including beach cleaning). An index of dune health has been proposed by Comor et al. [186]; it takes into consideration three groups of factors: dune structure (e.g., height, width, and vegetation cover), landscape composition (e.g., roads, car parks, and buildings, trees), and disturbances (e.g., urbanization, beach use intensity, trampling, and cleaning). The conceptual model of the functioning of the DBB ecosystem we propose (Figure 2) could constitute the basis for the construction of an ecosystem-based quality index (EBQI) based on the model of the EBQIs already available [206] for the *P. oceanica* ecosystem [62], the algae-dominated rocky reefs [103], undersea caves [207] and Coastal Detrital bottoms [208].

The sea level has been constantly on the rise since the Last Glacial Maximum (LGM), 21,000 years ago, when it was 120–130 m below the current level [209–215]. As the sea level rose, most ecosystems followed this rise, shifting towards the land. This is the case of the *P. oceanica* meadow [216] and, only when the rise was very slow, of the *Lithophyllum byssoides* (Lamarck) Foslie midlittoral algal rim [213,217]. Concerning the DBB ecosystem, this shift is no longer possible in many Mediterranean regions because of developments that have been constructed on land, such as roads, houses, and marinas. The responses of

the DBB ecosystem to other consequences of climate change, such as an increase in extreme climatic events (see, e.g., [218,219]), have been the subject of only a few targeted studies in the Mediterranean.



Figure 14. First page of a leaflet edited by the French *Région Sud*, in the framework of the EU POSBEMED2 program [203,204]. The sea ball says: ‘I’m ugly and I stink. Maybe, but without me, no beach!’ And it adds: ‘So there, and that’s that’—I am *Posidonia* in person’. At the bottom, note the chosen slogan: ‘*Nos plages ont du caractère*’ (our beaches have class).

The restoration of dunes is possible when the causes of their degradation have been eliminated, which is impossible when a road, a wall, or constructions have encroached on the area. Active techniques to rebuild the dune with added sand using machines are performed, followed by plantations. Passive techniques help the reconstitution of the dune through natural processes; they are slow but inexpensive; they mainly involve the installation of wooden fences to prevent trampling and footbridges for people to cross the dune [4].

4. Conclusions

Dune–beach ecosystems occur along most shores worldwide. In the Mediterranean Sea, the ecosystem is characterized by the paramount role of *Posidonia oceanica* dead leaves cast ashore, which form a layer up to 2.5 m thick, named *banquette*, on the part of the beach closest to the sea. We call ‘Dune–Beach–Banquette’ (DBB) the dune–beach ecosystem specific to the Mediterranean. The *banquette* protects the beach against erosion; dead leaves help to feed a very diverse fauna, provide nitrogen to vegetation, and participate in the formation of the dune. The fate of most of the *banquette* is to return to the sea, and to contribute to coastal food webs, including fish exploited by artisanal fisheries.

Similar to all dune–beach ecosystems worldwide, the Mediterranean DBB ecosystem is threatened by trampling, off-road vehicles, sand mining, road construction, and urban-

ization. In the Mediterranean, an additional threat is the removal of the banquettes by local authorities.

Until the 1980s, at a time when seaside tourism was already developed, banquettes were perceived by beach users as a natural element of the Mediterranean landscape and as a tolerable nuisance with regard to the comfort of bathers. However, at that time, their role in the functioning of the ecosystem and in protecting beaches against erosion was not known. Subsequently, tour operators and local authorities wanted to respond to users' demands, or what they thought were users' demands: pristine white sand beaches conforming to a universal model. The beaches were then cleaned, generally using heavy equipment, to remove the banquettes and driftwood. At the same time as the banquettes, large quantities of sand were incidentally removed. In addition to the ecological consequences, the result has been beach erosion, both because of the removal of their protection (the banquette) and the unintentional removal of large amounts of sand.

To counteract beach erosion, local authorities have resorted to sand-replenishment operations. However, this solution has often proven not only expensive but also ineffective. The sand brought by convoys of trucks is quickly carried into the sea, where it buries and kills the meadows of *P. oceanica*; as seagrass meadows also contribute to the protection of beaches, this results in an acceleration of beach retreat. The concept of an ecological beach, which is beginning to be tested in the Mediterranean, is based on the non-removal of banquettes and public information in order to increase the social acceptance of natural beaches.

The conceptual model of functioning of the DBB ecosystem, which we present here, can serve as a basis for establishing an ecosystem-based quality index (EBQI) along the lines of those that have already been proposed for other ecosystems (see, e.g., [62,103,206–208]). In addition, by explaining the functioning of the DBB ecosystem and highlighting the richness of its flora and fauna, it will allow managers to improve their practices and will improve the social acceptability of not removing the banquettes of dead leaves of *P. oceanica* along the Mediterranean beaches. Finally, an ecosystem-based quality index will be not only a communication tool for managers but also a decision-making tool for defining areas of conservation concern.

In addition to the development of a DBB ecosystem-specific EBQI, research avenues could include: (i) A spatialized and quantified analysis of beaches by major region (North Africa, Eastern Mediterranean, Adriatic, etc.); (ii) An analysis of human-induced fragmentation of the DBB ecosystem; (iii) Comparison of DBB ecosystems between islands and mainland areas; (iv) A diachronic study, based on snapshot photographs, of the use of Mediterranean beaches (with their banquettes) by fishermen and beachgoers; (v) Integrate eco-engineering solutions, such as dune revegetation and reinforcement of sand dunes, to sustain or improve the functioning of the DBB ecosystem.

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