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Ecology of coastal dune fauna

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The distinguishing feature of coastal dunes is their connection to the shore. This maritime influence results in most coastal dunefields exhibiting a marked shore-normal gradient of decreasing physical stress and increasing complexity and vegetation cover landwards. Physical stresses include sand movement, salt spray, temperature variability, wind and disturbances such as storms. Increasing vegetation cover, often coupled to succession, mediates physical stress, creates stable microenvironments and is responsible for a general increase in habitat complexity landwards. Fauna respond to this gradient in a number of ways. Crustaceans of marine origin decrease in abundance landwards. Many of the special adaptations, which equip fauna for psammophilic lifestyles and allow them to cope with salt spray and temperature extremes, are only encountered near the beach. Insects, vertebrates and interstitial fauna increase in abundance landwards as vegetation cover, height and diversity increase, soil develops and greater stability is attained. Biological interactions and impacts of fauna on vegetation via grazing, seed dispersal and disturbance also increase landwards. There may be a shift from primarily *r*-strategist species near the beach to *k*-strategists inland and birds may replace small mammals as vegetation height increases. Coastal dune fauna differs from that of deserts in being more diverse and having a well developed interstitial component. Furthermore, coastal dune inhabitants are less specialised to cope with physical extremes and are seldom unique or endemic to these systems. However, this fauna has received considerably less attention than that of desert dunes and much research is warranted on subjects such as adaptations to sand movement and salt spray, endemism, trophic relations and exchanges with adjacent systems. Wind is the major factor impinging on these dune ecosystems.

Introduction

This paper examines the fauna and ecology of coastal dunes as opposed to desert dunes. What are coastal dunes and how do they differ from desert dunes? For the purpose of this review I define coastal dunes as being eolian sand systems adjacent to the littoral and mostly receiving rainfall above 250 mm per annum. Coastal dune systems are usually clearly demarcated, associated with beaches and have been considered discrete ecosystems in their own right (Ardo, 1957; Tinley, 1985). Unlike desert dunes, coastal dunes have attracted little scientific attention to their faunas and ecological processes, most work having focused on topical issues of geomorphology and vegetation where man has modified the coast.

Coastal dunes occur at all latitudes and may be tropical or temperate, wet or dry. They have been considered edaphic deserts as a consequence of well drained sands, the desiccating effects of salt spray and their low nutrient status (van Heerdt & Morzer Bruyns, 1960; Callan, 1964; Skiba & Wainwright, 1984). They are, however, relatively

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well supplied with moisture and, with their maritime climates, exhibit more predictable and moderate conditions. They are invariably long, narrow strips parallel to the coast. Desert dunes are arid and may be subject to episodic events. They usually make up large areas and have widely varying topographies and shapes. Coastal and desert dunes, both characterised by eolian sand transport, thus exhibit many similarities and differences.

Boundaries, scales and gradients

Coastal dunefields are narrow strips hugging the coast, metres to kilometres in width, with distinct boundaries determined by the sea- and landward limits of eolian sand transport. The seaward boundary may be taken as the driftline or first dune above the beach. Four main coastal dune types have been described by Hesp (1986): foredunes, blowout/parabolic dunes, transgressive dune sheets and relict foredunes. These may be subdivided into different categories or into vegetation types (Lowrie, 1948; Barnes, 1953; Doing, 1985; Tinley, 1985; Extine & Stout, 1987). Habitats within the dunes are more significant than dune form in influencing faunal distribution (Duffey, 1968; Caussanel, 1970); especially important are the structure of the vegetation and associated microclimates (Boomsma & de Vries, 1980; den Hollander & van Heerdt, 1981; Ghabbour *et al.*, 1987). The difference between surface and subsurface microclimates has also been stressed (van Heerdt & Morzer Bruyns, 1960).

Moisture levels, sand movement, salt spray and vegetation cover are the most critical elements of dunefield habitats influencing animal distribution. The depth and vertical migration of the water table exert a marked influence on coastal dunes by demarcating the baseline for deflation and the position of slacks and vegetation types. Moisture may also influence the fauna directly. The ant *Lasius niger* for example is limited by insufficient moisture at high dune elevations and possibly by vegetation at lower elevations (Boomsma *et al.*, 1982). Several authors have stressed differences between sun and shade slopes, sea-facing and inland slopes, slip- and windward faces, as well as features of habitats such as thicket, slacks, grassland, marsh, forest, etc. as being key factors determining animal distribution in coastal dunes (van Heerdt & Morzer Bruyns, 1960; Ranwell, 1972; den Hollander & van Heerdt, 1981; Wiedemann, 1984). The crest of the first dune ridge forms an important boundary between the foredunes, strongly influenced by the sea, and the more terrestrial part (van Heerdt & Morzer Bruyns, 1960). On the small scale, dunefields consist of many hummocks and these should perhaps be considered as the environmental units in coastal dunes (Hesp & McLachlan, 1989), as they may function as ecosystems or independent oases (Noy-Meir, 1980).

Crawford (1991) argues that a gradient exists in desert dunes through asymmetry in detritus distribution dependent on prevailing wind. A distinguishing feature of coastal dunes is the presence of an environmental gradient set up perpendicular to the shore by the proximity of the sea. Key elements are changes in salt spray load, sand movement rates, temperature and vegetation. Absent in inland dunes, this gradient is the most characteristic feature of coastal dunes. In coastal dunes a series of vegetation zones may usually be recognised (Cotton, 1967; Messana *et al.*, 1977; den Hollander & van Heerdt, 1981; Ronchetti *et al.*, 1986; Extine & Stout, 1987). These zones often correspond to a successional sequence (Chapman, 1964; Ranwell, 1972), especially where the shore is prograding. Faunal distribution is often closely related to these zones (Duffey, 1968; Sacchi, 1971; Extine & Stout, 1987). The sea also exerts a strong influence on climate and affects dune food chains and energetics by supplying organic materials, sometimes in huge quantities.

The most distinctive feature of coastal dunes is thus their border with the sea and the resultant physical, chemical and vegetation gradients.

Composition of the fauna

The fauna of coastal dunes is dominated by arthropods and vertebrates, particularly insects, birds and mammals. Arachnids are common (Barnes, 1953; Cooke & Cotton, 1961; Duffey, 1968; Almquist, 1969, 1970, 1971, 1973*a*,*b*) and crustaceans may be important near the beach, as the backshore and dunes represent one of the avenues of land colonisation by crustaceans, especially talitrid amphipods and oniscid isopods (Chelazzi & Ferrara, 1978; van Senus, 1984; McLachlan *et al.*, 1987; Vader & de Wolf, 1988). Molluscs (Sacchi, 1971, 1986; Sacchi & Violani, 1977) and frogs (Roberts, 1984) also occur, the former preferring lime-rich soils (Sacchi, 1986; Ranwell, 1972). However, insects are usually dominant, especially the orders Hymenoptera, Coleoptera and Diptera (Verdier & Quezel, 1951; Ardo, 1957; Cloudsley-Thompson, 1960; Callan, 1964; Caussanel, 1965; Ranwell, 1972; Desender *et al.*, 1980; den Hollander & van Heerdt, 1981; Joswig, 1984; Ronchetti *et al.*, 1986; Riemann, 1987). Most larger mammals traverse dunes temporarily for feeding or to gain access to the beach to forage among wrack or for carcasses.

Van Heerdt & Morzer Bruyns (1960) distinguished six groups of insects in their classical study of the yellow dune region of Terschelling (The Netherlands): (1) halobionts, only found in coastal areas; (2) halo-psammophiles, salt-tolerant species which also occur on sandy soils elsewhere; (3) psammophiles found everywhere on sandy soil but not tolerant of places with a high salt content; (4) ubiquists found everywhere; (5) social Formicidae; and (6) a small number of flying insects found everywhere. They distinguished two communities separated by the crest of the dune ridge, a seaward and a landward one, the former dominated by halobionts. Chelazzi & Ferrara (1978) also recognised a salt-tolerant group of isopods on the seaward side of the dune ridge and in the supralittoral region. Callan (1964) distinguished minor communities associated with driftwood and carcasses of animals cast ashore.

Dune soils, because of their often high moisture content, may support rich interstitial faunas. This neglected component consists of bacteria, fungi, actinomycetes and algae (Webley *et al.*, 1952; Forster & Nicholson, 1981) as well as meiofauna (Boomsma & van Loon, 1982; van der Merwe, 1989), which may be important in both dune vegetation succession and in the decomposition of organic material in the sand. Bacteria and fungi are the primary colonisers of supralittoral and dune sands and exhibit a landward succession (Webley *et al.*, 1952; Forster & Nicholson, 1981). Meiofauna are predominantly plant parasites and detritivores, the former associated with plant roots (van der Merwe, 1989).

Endemism and diversity

The fauna of coastal sand dunes may display high diversity but limited endemism, containing few unique elements (Callan, 1964). The beach vole *Microtus breweri* is an example of a unique dune species, having evolved over the past 3000 years on Muskeget Island (Tamarin, 1977*a*,*b*; Tamarin *et al.*, 1987). The species status of this vole is disputed, but its population is distinctive and acyclic, unlike mainland voles (Tamarin, 1977*c*). Similarly, the American beach mouse *Peromyscus polionotus* ssp. from the Gulf of Mexico coast is endemic to coastal sand dunes (Holliman, 1983) and a subspecies *P. p. leucocephalus* is unique to Santa Rosa Island (Blair, 1946). Further, damara terns *Sterna balaenarum* in South Africa breed only in coastal dunes (Randall & McLachlan, 1982) and the hairy-footed gerbil *Gerbillurus paeba exilis* is restricted to these areas (Ascaray, 1986). Coastal dune endemics are, however, few (Duffey, 1968). This is due to the small size of most coastal dunefields and their extensive sea and landward boundaries, which allow free exchange of fauna. In addition, coastal dune systems are geologically young, a consequence of changing climates and sea levels. Unlike desert dunes, which may be ancient, coastal dunes have thus had little time for the evolution of unique inhabitants.

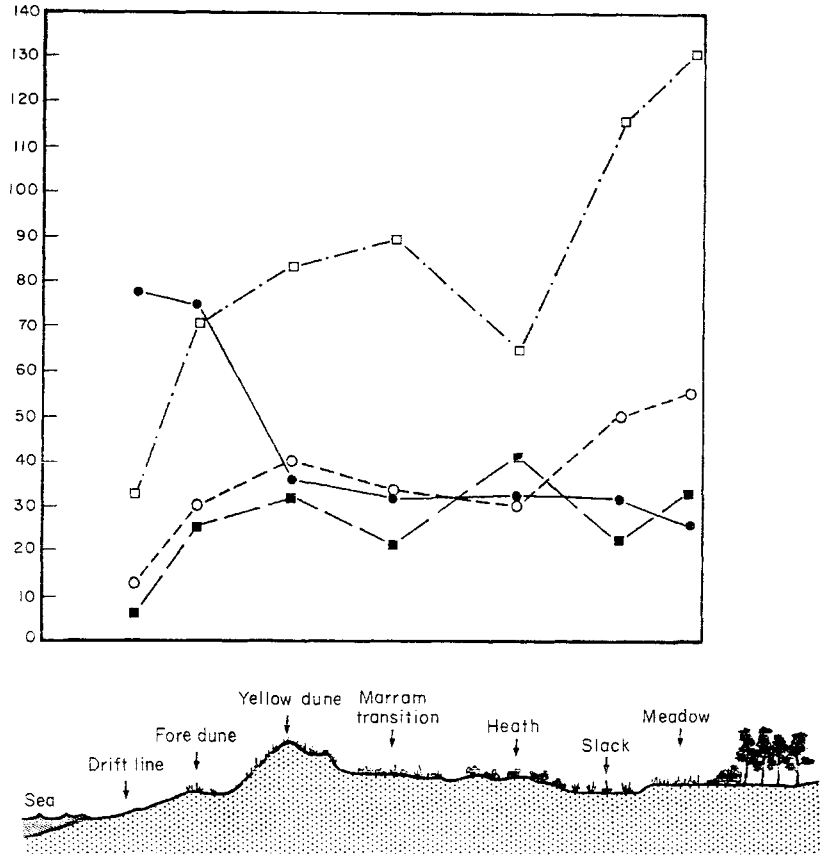

Figure 1. Changes in spider fauna across a dune gradient. Compiled from Duffey (1968). □ - · - □, Total number of species recorded; ○ – – ○, mean number of species per season; ■ – – ■, number of species per hour; ●— —●, Simpsons index of dominance diversity × 10.

Coastal dune fauna may be impoverished in arid areas (Cloudsley-Thompson, 1987), but is diverse where moisture is less limiting. Numerous accounts exist of large assemblages of invertebrate species, especially insect families and orders, collected in coastal dunes (Krogerus, 1932; Lowrie, 1948; van Heerdt & Morzer Bruyns, 1960; Mackie, 1967; Cotton, 1967; Duffey, 1968; Almquist, 1973*a*; Chelazzi & Ferrara, 1978; Gordon, 1983; Chelazzi *et al.*, 1983; Perttula, 1984; Stein & Haeseler, 1987; Riemann, 1987). The most impressive list comes from a collection of papers on the invertebrate fauna of two young (<100 years) dune islands in the North Sea (Haeseler, 1988; and 23 other papers in the same volume), including more than 1500 species of insects.

Species richness responds to changes in vegetation and habitat complexity primarily along the gradient perpendicular to the shore. Boomsma & van Loon (1982) found ant species diversity to increase with age of the dune valley away from the sea and Lowrie (1948) and Almquist (1973*a*) showed a marked increase in spider diversity landwards towards climax vegetation. Similarly, Duffey (1968) showed an increase in spider diversity moving inland from the driftline to the marram transition zone (Fig. 1). Here, there was no relation between plant species diversity and spider diversity. Instead, spider diversity increased with complexity of habitat structure. Slobodchikoff & Doyen (1977) found arthropod diversity to decrease in the presence of *Ammophila*, an introduced pioneer, and increased numbers of organisms were correlated with greater cover of other plant species. Similarly, Boomsma & van Loon (1982) noted that ant species diversity was positively related to the structural diversity of soil and vegetation. Fauna responds positively to vegetation, which usually increases in cover and diversity away from the sea (Perttula, 1984; Duffey, 1968) as salt spray and sand movement rates decline. The largest increase in diversity occurs across the first dune ridge, moving from the sea-facing slope, with its fauna of halobionts, to areas of higher vegetation cover. Thus the diversity of coastal dune fauna may largely be attributed to ecotone effects, successional sequences and vegetation complexity.

There is limited evidence for competition and consequent habitat partitioning in coastal dune systems. Atkinson & Begon (1988) could not demonstrate competitive interactions in grasshoppers, but Ronchetti *et al.* (1986) showed temporal partitioning in beetles, one dominating in the wet season and the other in the dry season. Shure (1970) speculated that competition might occur between voles and beach mice in barrier dunes in New Jersey as they exhibited inverse distribution patterns.

Geographical variations in coastal dune faunal taxonomic composition and trophic groups are unknown due to the paucity of information from most parts of the world. Microgeographic races coupled to edaphic changes have been described for a tenebrionid (Doyen & Slobodchikoff, 1984), but nothing has been examined on a larger scale. Doing (1985) has suggested a major division between coastal dune flora of tropical and temperate regions, the former divided into arid and wet regions and the latter into temperate and polar/sub-polar. As there is some coupling between fauna and flora it may be expected that similar patterns might be distinguished for the fauna of coastal dunes. Finally, many species or genera may be cosmopolitan as a consequence of ocean transport, e.g. the earwig *Labidurus riparia* (Callan, 1964).

Adaptations

Are the activities of animal populations in coastal dunes correlated with weather, as in deserts (Noy-Meir, 1980), or with population densities? The physical environment may limit growth in certain cases (Atkinson & Begon, 1987,1988), but coastal dunes lack the extremes associated with deserts. Crustaceans, for example, poorly represented in deserts, may be abundant in coastal dunes where their requirements for moist air for respiration are met. Physiological specialisations seem unlikely to be essential and the main adaptations of animals are behavioural.

A common adaptation to life in coastal dunes is rhythmic activity. Near the beach and supralittoral, tidal rhythms are evident in the form of activity during the low tide to avoid inundation. In true dune fauna, however, rhythms are primarily diel. Most species seem to be nocturnal and there may be discrete day and night faunas (Callan, 1964; Almquist, 1973*a*,*b*; Ronchetti *et al.*, 1986). Chelazzi *et al.* (1983), studying supralittoral coleopterans in the tropics, found that nocturnal activity prevailed in the dry season and diurnal activity in the wet. Chelazzi & Ferrara (1978) described a transition from nocturnal to diurnal activity in tropical isopods with increasing distance away from the supralittoral. They related this to decreasing resistance to desiccation with nocturnalism. Diel movements between beaches and dunes occur in many cases. Terrestrial hermit crabs of the genus *Coenobita*, which shelter in dunes during the day, emerge at night to forage on the beach (Vannini, 1976; Achituv & Ziskind, 1985). Some insects may move from the driftline into the dunes to overwinter (Duffey, 1968).

A distinguishing feature of many dune animals is the ability to bury or burrow rapidly (Callan, 1956; den Hollander & van Heerdt, 1981; van Wingerden *et al.*, 1981). It has been suggested that changes in sand characteristics along the coast–inland gradient may result in changes in body size in a tenebrionid beetle, possibly related to burrowing constraints (Doyen & Slobodchikoff, 1984). Cryptic coloration (psammochromy) has been described for dune insects (Callan, 1964) and mice (Blair, 1946, 1951; Reardon, 1959; Bowen, 1968; Ascaray, 1986).

Dune animals also need to tolerate or avoid flying sand, salt loads and the absence of protective litter (van Heerdt & Morzer Bruyns, 1960; Callan, 1964; Boomsma & Isaaks, 1982). Adaptations to extremes of temperature or aridity are less critical. Ardo (1957), however, found a relationship between thermal preferences, desiccation tolerances and zonation of Diptera in Swedish dunes. In a similar vein Almquist (1970, 1971, 1973*b*) concluded that temperature and humidity were important in habitat selection by spiders, although he demonstrated no cause and effect relationships. Den Hollander & van Heerdt (1981) also stressed tolerances and preferences to different temperatures and other conditions, but admitted that motility, especially in the case of flying insects, enabled animals to survive more extreme environments than would be expected. Species associated with plants, rather than the sand surface, show fewer specialisations and differ little from the fauna of plants elsewhere (Callan, 1964).

In low-lying areas, such as dune slacks and the immediate supralittoral, the ability to survive flooding, by flotation or use of air bubbles in the sand, and the ability to tolerate immersion in a range of salinities may be important (Boomsma & de Vries, 1980; van Wingerden *et al.*, 1981; Boomsma & Isaaks, 1982; Chelazzi *et al.*, 1983, Witteveen & Joosse, 1988). Conversely, for crustaceans colonising the dunes via the supralittoral, lack of moisture may be a problem. Desiccation stress has, however, not been the only factor in the evolutionary history and adaptations of talitrids; ionic regulation is also critical (Morritt, 1988).

Whereas many authors have commented on salt stress, few have examined it experimentally. Besides salt spray on the dune facing the sea and its 'halobiotic' fauna, salt load on dune vegetation must also affect herbivores. Eliminating excess salt load should not pose a problem to vertebrates or insects which can form hyperosmotic excreta, but crustaceans may face osmotic problems unless they have access to moisture.

Pulmonate snails, by virtue of their permeable bodies, may experience particular problems in dune environments where climatic and edaphic factors may be limiting (Sacchi, 1971). In warm parts of the Mediterranean with dry summers, long aestivation can force the common dune snail *Euparypha pisana* into a 2-year life cycle. On more moist Atlantic coasts aestivation is avoided; the life cycle is completed in 1 year and less energy is required as the epiphragm and shell are thinner than in the drier areas. In regions experiencing cold winters snails may hibernate. Edaphic factors are less important in coastal dunes where calcium carbonate is plentiful. Calcium plays a role in lowering permeability to mineral ions which maintain the osmotic pressure of snail body fluids high enough to retain water during inactivity.

Roberts & Bradshaw (1981), Roberts (1984) and Tyler *et al.* (1980) described the adaptations of sand frogs to life in dry Australian dunes. Pairing of males and females occurred at least 5 months before egg deposition. The entire larval development took place in the egg capsule with the young emerging during the wettest period of the year. These frogs avoided the arid summer by remaining underground in moist sand where their survival was facilitated by the predictable winter rainfall. They also experienced elevated plasma and urine urea levels during dry periods, this probably assisting the osmotic reclamation of water from the soil.

Dune fauna may include many *r*-strategists, especially in unstable areas (van Wingerden *et al.*, 1981). Tamarin (1977*a*), however, considered voles examples of *k*-strategists. These may supersede *r*-strategists in the more stable and vegetated parts of coastal dunes where diversity and abundance are greater and the need to develop competitive ability and avoid predators is more imperative.

Foodwebs and trophic relations

Dune food chains are fuelled by autochthonous primary production of the dune flora and organic inputs from the sea and land. None have been quantified for a coastal dune system.

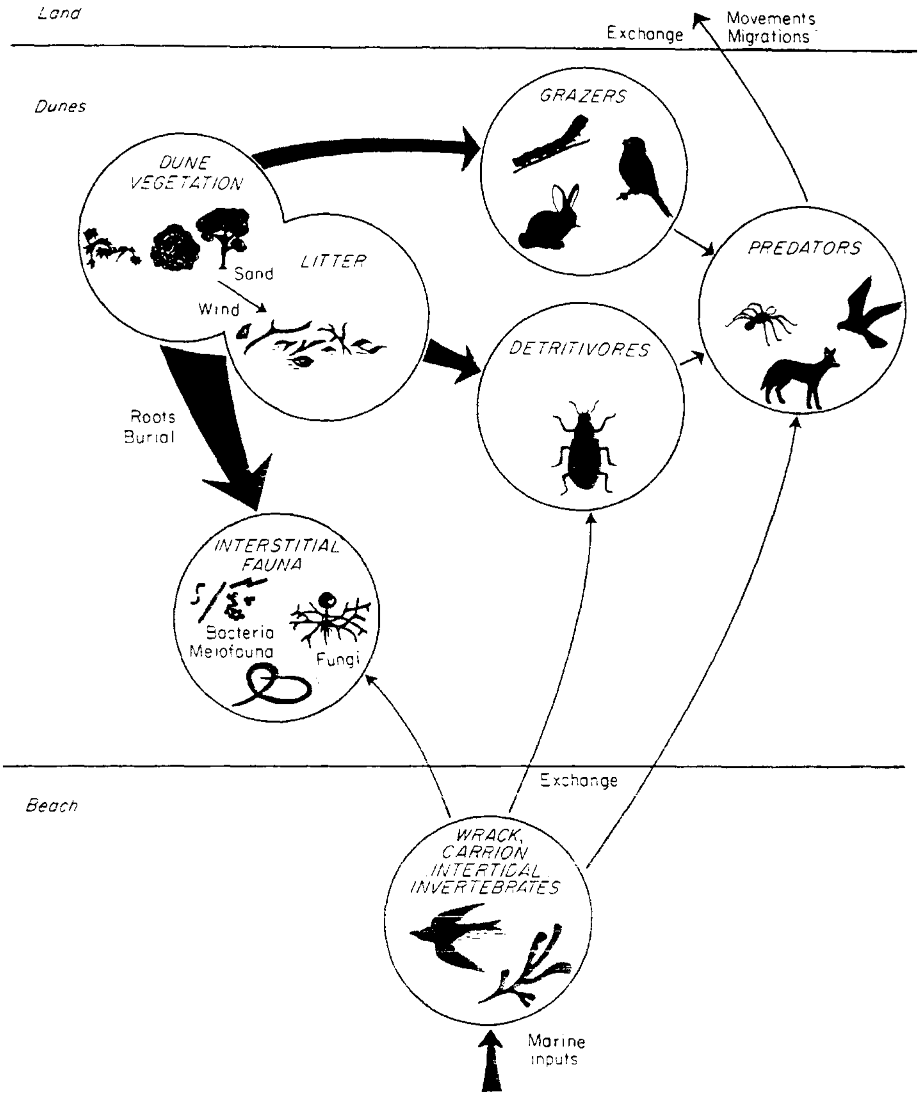

Figure 2. The trophic structure of coastal dunes including three food chains and exchanges.

Three food chains may be distinguished (Fig. 2): a grazing food chain which includes herbivorous insects, mammals and seed- and fruit-eating birds; a detrital food chain occupied by macroscopic detritivores, particularly insects; and an interstitial food chain in the sand, comprising bacteria, actinomycetes, algae, fungi and meiofauna. The former two chains may be linked by common predators. Despite some possible consumption of interstitial fauna by detritivores taking organisms associated with buried detritus, the latter is distinct and probably the most important of the three food chains generally.

A high proportion of plant biomass, both living and dead, may occur below the ground where it is available to interstitial fauna (McLachlan *et al.*, 1987). A prominent feature of coastal dunes, in contrast to desert dunes, may be the great importance of interstitial pathways, because the moist conditions and a high proportion of buried organics favour the development of a rich interstitial fauna of bacteria, fungi and meiofauna. In wet dune slacks, van der Merwe (1989) showed that the biomass of interstitial fauna far exceeded that of the macrofauna and concluded that most consumption of carbon in the slack ecosystem was via the interstitial pathway below the surface. The relative significance of interstitial and macrofauna in different types of dunefields may vary considerably, depending on soil moisture and organic levels. This warrants further study, as does the process of detritus production and decomposition rates.

Macrofauna food chains have been little studied. Van Wingerden *et al.* (1981) discussed food relations of arthropods in Dutch dunes and McLachlan *et al.* (1987) gave a broad outline of energy flow patterns in an African dune slack. Several studies have been done on feeding and foraging of mammals and birds and their impacts on the flora (Ranwell, 1972; Boorman, 1977; Rothstein & Tamarin, 1977; Boorman & Fuller, 1982; van den Berg, 1986; Ascaray, 1986; van der Merwe, 1987). It is documented that the persistence of dune grasslands is encouraged by grazing animals and in their absence scrub and woodland may develop (Boorman, 1977). The impact of seed eaters, ants, birds and rodents on dune seed reserves is unknown and may be high. Plant species occurring in later stages of dune succession rely mainly on birds for seed dispersal (Tinley, 1985). Spiders and carabid beetles are major predators of insects (van Wingerden *et al.*, 1981), but insectivorous and raptorial birds and carnivorous mammals are probably the top predators in most cases.

Because of the small scale of most coastal dunefields and the relatively great extent of their sea- and landward boundaries, much exchange occurs. Consequently animals will move across both boundaries to seek food and shelter in the dunes, on the beach or inland. Such systems are thus very 'open' and food chains may begin in the sea (e.g. with wrack cast ashore and eaten by dune animals) or end inland (e.g. by inland predators making foraging excursions into the dunes).

Are coastal dune animals opportunist generalist feeders, as are most desert animals (Noy-Meir, 1980), or are they more specialised? Generalists may dominate in physically extreme parts of dunes, whereas specialists may be more typical of the landward margins of dunefields where there is more biological structure. Perttula (1984), however, suggested that generalist spiders were more typical of complex habitats and specialists of extreme habitats such as open sand. At present there is insufficient evidence to evaluate this.

Nutrient cycles

Little is known of nutrient cycling in coastal dunes. Dune sands are generally poor in nutrients (Willis, 1963; Willis & Yemm, 1961; Hesp, 1991), but the groundwater may be an important reserve for plants with roots capable of reaching it. Boorman & Fuller (1982) added nutrients to dune grasslands grazed by rabbits and found an overall decrease in plant diversity but an increase in those species not grazed by rabbits. Willis (1963) had shown earlier that nutrient addition increased plant biomass but decreased diversity in ungrazed dune swards.

Dune soil changes as a consequence of succession, distance from the sea and/or age: calcium carbonate is leached out, sands become less alkaline and finer and organic content increases (Ranwell, 1972). Accompanying this build-up of soil are increases in the major nutrients (Boorman, 1977). Nitrogen can come from fixation at root nodules, blue-green algae (Forster & Nicholson, 1981) or input from rain. Despite much attention to nutrient–plant relations, no research has been conducted on recycling by the fauna.

Dune–beach interactions

Besides climatic interactions and moisture, four materials are exchanged across the dune/beach interface (Fig. 3): (1) sand; (2) groundwater; (3) salt spray; and (4) living and dead organic materials (McLachlan, 1988).

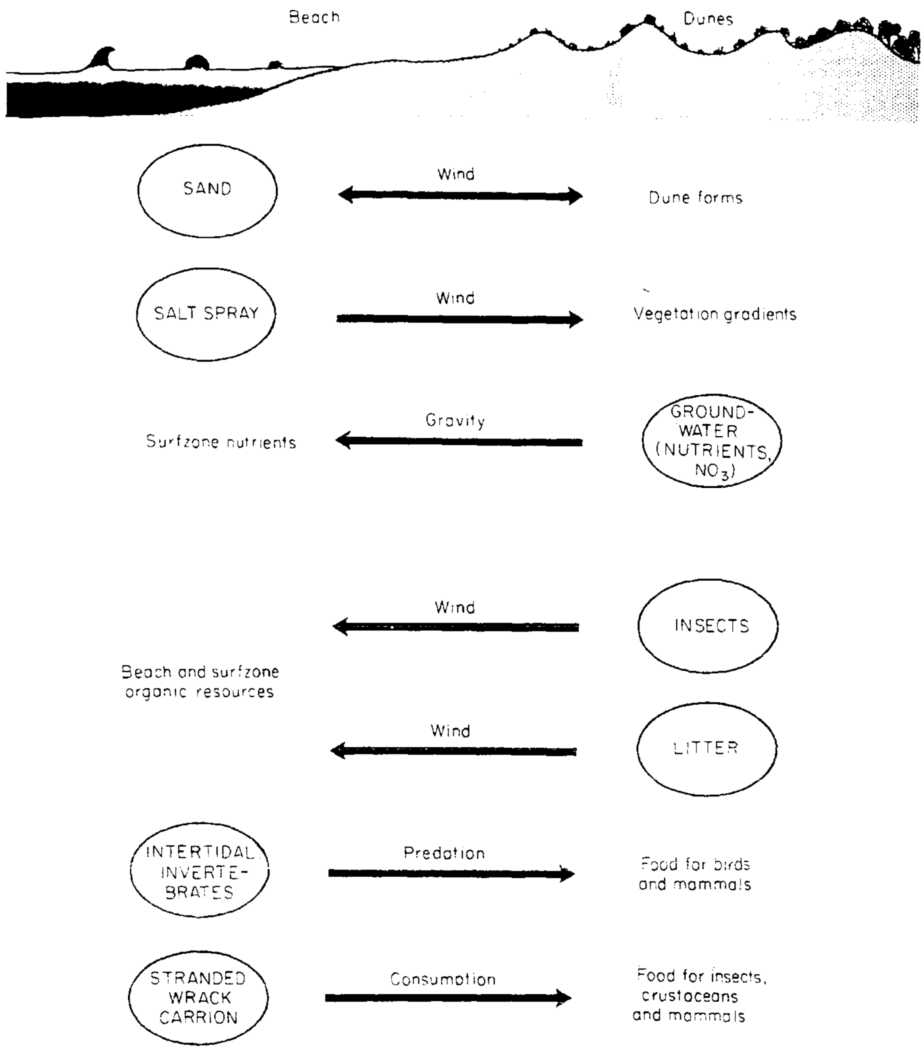

Figure 3. Exchanges of materials across the dune/beach interface. After McLachlan (1988).

Sand exchange has been discussed in an earlier paper in this issue. Groundwater flow through confined and unconfined aquifers may be an important supplier of inorganic nutrients to coastal waters as it is usually high in nitrogen (Johannes, 1980; McLachlan & Illenberger, 1986). Salt spray input comes from landward eolian transport of droplets derived from the surf. The quantities of salt transported increase with wind speed, wave height and surfzone width and decrease with distance inland (Young, 1987; Hesp, 1988). Exposed dunefields, such as transgressive dune sheets backing dissipative beaches, thus experience the greatest salt input. This has a major influence on the gradient across the dunes and especially on the vegetation (see review on coastal dune vegetation earlier in this issue).

Four groups of organic materials are exchanged across the dune/beach interface: stranded wrack and carrion available to dune fauna, insects blown into the sea during offshore winds (Romer, 1986; Quilter, 1987), intertidal fauna preyed on by dune birds and mammals and litter blown onto the beach (McLachlan, 1988). On beaches receiving large marine inputs even the dune food chains may be strongly dependent on these subsidies with much of the fauna located near the dune/beach interface.

Conclusions

What are the primary factors influencing animal ecology in coastal sand dunes? Are these systems physically controlled or do biological structure (vegetation) and interactions control the community?

Noy-Meir's (1980) 'autecological hypothesis' suggests that in physically extreme environments, such as deserts, control is primarily physical and communities are the

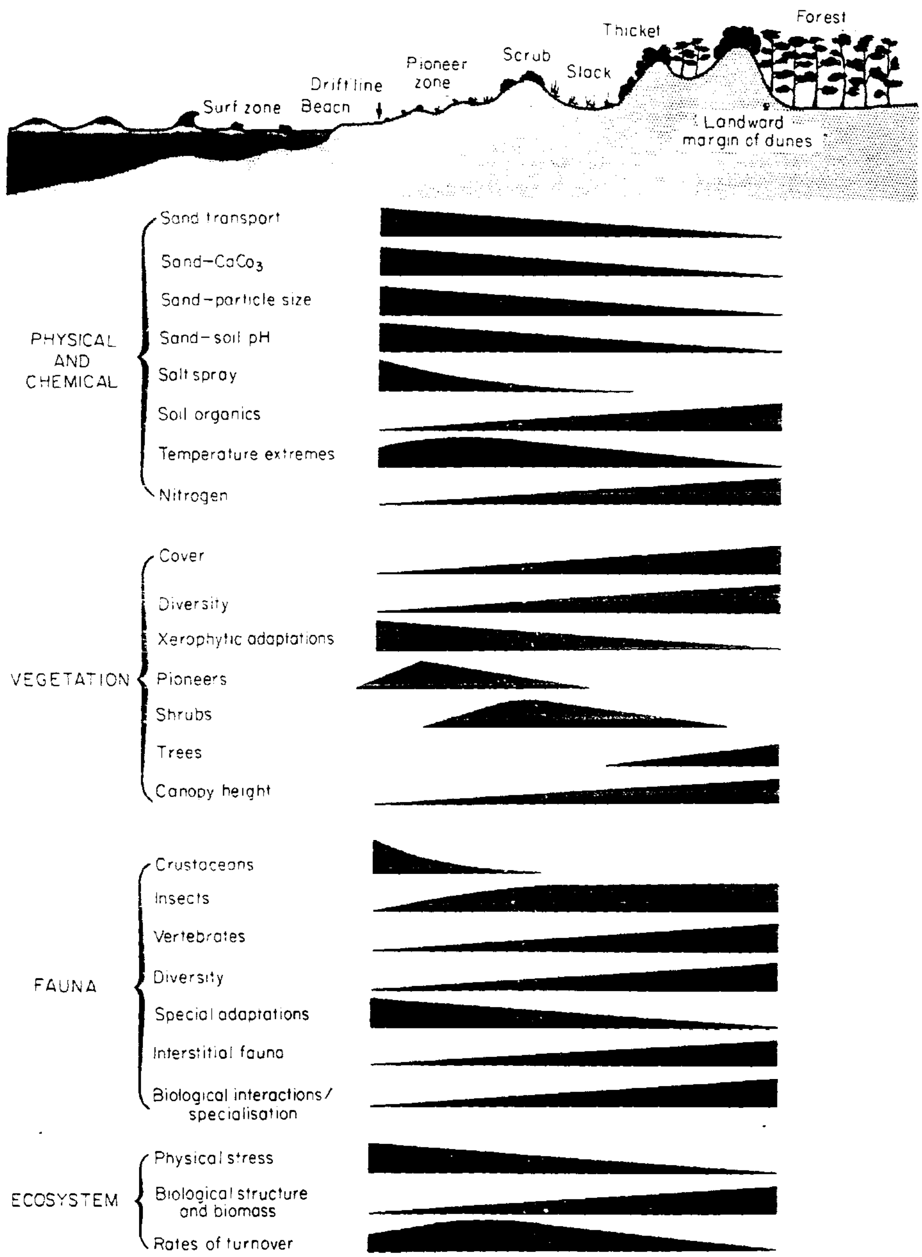

Figure 4. Conceptual model of physical, chemical and biological gradients across a coastal dunefield in a non-arid region.

result of the independent response of each population to the rigours of the environment. In coastal dunes the picture is more complex—a whole spectrum may be encountered, from physically controlled situations, such as transgressive dune sheets with high rates of sand movement, salt spray and little, if any vegetation, to systems with considerable biological structure, such as forested dunes in moist climates.

In coastal dunefields the main response is to the sea/land gradient and in a simplified sense the 'typical' sequence is a succession from a physically controlled situation, adjacent to the beach, to a biologically structured situation landward. Seldom will a single dunefield span the entire gradient, rather arid coasts will tend to display only the pioneer zones whereas stable, moist coasts might have climax (forest) zones extending almost to the beach. Most coastal dunefields may therefore be considered as representing only a part of the total potential gradient. Changes expected along the complete gradient from the beach landwards (Fig. 4) include several faunal responses:

Increasing insect diversity and abundance, vertebrate diversity and abundance, birds as vegetation height increases, interstitial fauna as soil develops and pH drops, biological interactions, faunal impact on vegetation (grazing, seed dispersal).

Decreasing crustacean abundance and diversity, rodents as trees replace ground cover, specialisation for psammophilic lifestyles, adaptations to salt spray, temperature extremes.

At the ecosystem level one might expect higher rates of turnover closer to the beach where pioneer plants are fast-growing, as opposed to the forest end of the gradient, where much energy is tied up in relatively inert woody biomass. Further, detrital pathways may be important in coastal dunes in arid areas or where vegetation cover is low, whereas herbivory may be more significant in moist or well vegetated dunes.

Apart from their sea connection, coastal dunes are not unique and have many features in common with other terrestrial ecosystems. In extreme situations and near the beach in high-energy environments they may be similar to desert dunes. However, unlike desert dunes, coastal dunes are not marked by pulses, although wrack inputs from the sea may be erratic following storms, and rainfall may be seasonal. Rather they have more constant climates and organic inputs, and often exhibit marked succession in their vegetation, a feature not found in desert dunes (Noy-Meir, 1980).

The ultimate control of the gradient across coastal dunes and the resulting vegetation succession is by wind. By its strength, frequency and prevailing direction, especially in terms of the land/sea interface, it controls (1) sand movement, (2) dune forms, (3) microclimate, (4) seed and detritus dispersal and (5) salt spray load and the form of the gradient inland from the beach, thereby influencing both vegetation and fauna.

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