Are coastal dune management actions for biodiversity restoration and conservation underpinned by internationally published scientific research?

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Abstract

Scientific research in coastal dunes, published in international journals, has mainly focussed on the understanding of processes of landscape development, vegetation succession and its interaction with animal ecology. Both fundamental and applied questions were dealt with. In theory, results of these investigations should underpin nature management practices and should give a solid foundation to monitoring. In this contribution, we review past and present, internationally published scientific research and its most important consequences for nature management and the conservation/restoration of biodiversity. Results are contrasted with contemporary management practices in order to detect management shortcomings and fields where scientific research needs to be extended and published in order to fine-tune often expensive and quite radical irreversible management practices. In general, our mini-review stresses the need for process-based research on a broad spatial scale and detailed research at a local scale for the assessment of optimal nature management actions, especially in view of potential negative feedback mechanisms.

Keywords: Nature management; Mini-review; Management actions; Ecosystem processes.

Introduction

In Europe, coastal dune habitats are listed in the CORINE biotope classification (Natura, 2000), and are considered priority habitat in the annex I of the EU Habitat Directive (Hopkins and Radley, 1998). This status implies coastal dunes deserve special conservation attention (Herrier and Killemaes, 1998). Fortunately, as far as Flanders is concerned, the coastal dunes indeed receive more than average management and nature conservation interest.

Coastal dunes are classified as semi-natural ecosystems, in which succession is initiated by fixation and driven by the complex of soil formation (humus accumulation) and

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vegetation succession. Leaching and mobilisation of CaCO₃ complicate the picture and are important in nutrient dynamics. At present, tall grass- and scrub encroachment greatly overrule these fine-scaled soil processes and cause substantial loss of regional biodiversity in Flemish coastal dunes (Provoost *et al.*, 2004). Within the coastal dune system a dynamic, stressed and unconstrained landscape phase is distinguished (Provoost and Bonte, 2004). The dynamic landscape is characterized by highest diversity of system specific species, which are often threatened at a regional and international scale. During the last decades a fast (increased) development towards an unconstrained landscape is recorded, due to *e.g.* eutrophication, disturbance of hydrology and lack of agropastoral stress. These man-driven processes lead to an apparent qualitative shift toward a less specific flora and fauna. Above that, an increased invasion of garden escapes of exotic species has been recorded (Provoost and Bonte, 2004). Illustrative is that in Belgium, typical dune butterflies have become extinct or very rare (Maes and Van Dyck, 2001) and 95% of the typical dune carabid beetles are included in the Flemish Red List (Desender *et al.*, 1995).

Due to this process towards an unconstrained landscape, scrub vegetation tends to encroach, at the expense of dynamic landscape habitats like grey dunes and dune slacks. They are now heavily fragmented and patchily distributed within a matrix of closed dune vegetation (shrubs, monospecific tall grassland), often urging species to survive in a completely different landscape than the one they are adapted to. This apparent shift in landscape structure and the decline of at least regional biodiversity urges managers to take often quite radical nature management measures on relatively short terms. Removal of scrub and woodland, mowing and grazing, are the most commonly applied measures for dune grassland restoration. Well-documented examples of management schemes are available for the Dutch dunes (e.g. Annema and Jansen, 1998) and the LIFE initiative at the Sefton coast in the UK (Houston et al., 2001). In Belgian dunes, around 15ha of scrub have been cut down and currently nearly 500ha are grazed (Herrier and Killemaes, 1998). None of these measures enable a complete regression towards a dynamic landscape, since e.g. soil processes changed the soil more or less irreversibly, into more stratified and organically enriched soils.

In this paper, we review the international peer-reviewed scientific literature on the relationship between coastal dune biodiversity and nature management actions and the processes, underlying biodiversity patterns. With this information we aim (i) to find out how management strategies and ecosystem processes determine biodiversity patterns in general, (ii) to what amount current management actions are underpinned by well designed (and internationally published) scientific research and (iii) what kind of future research is needed to understand how management actions can tackle the problem of the declining system specific biodiversity in coastal dunes.

Method

We scanned the Web of Science-database for papers dealing with the relation between coastal dune management and ecology. The following search items were used: "coastal dunes and management", "coastal dunes and diversity", "coastal dunes and

assemblage", "coastal dunes and community", "coastal dunes and ecology", "coastal dunes and population". Relevant papers were reviewed and screened for scientifically underpinned results on the relation between management actions, relevant processes within the coastal dune ecosystem and aspects of biodiversity. In order to avoid a bias towards locally available, but not widespread, papers, only results from papers recorded in the Web of Science were used. In total 72 papers were selected for further analyses. We admit that a larger quantity of internationally available literature has been published on grazing as a general process and on other management measures as well. Up to a certain and general level, these results will also be of value to underpin coastal dune management, but not as far as dune specific processes, landscape phases and taxa are concerned.

Results

General

The number of internationally available publications on the relation between coastal dune biodiversity aspects and nature management (including ecosystem functioning) clearly shows an increase during the last 15 years (r_{15} =0.80; P<0.001; Fig. 1). The majority (59 %) of the studies were conducted in European coastal dunes (incl. Israel), followed by North America (22%) and (South) Africa (9%). Studies in coastal dunes from Australia, South America and Asia are rare. Studies focused on a wide taxonomic range of model groups, but studies using vascular plants and to a lesser amount arthropods are clearly dominant (Fig. 2).

Management actions

On the Web of Science, we found 50 records on effects of nature management actions on biodiversity patterns. Studies have especially focussed on effects of trampling, stabilisation of mobile dunes by plantations, beach cleaning and grazing by domestic livestock (Table I). Although the number of records is low, some trends are clear: beach cleaning and dune stabilisation always had a negative impact on species diversity. Also, recreation disturbance, generally results in a decrease of species diversity. Only two studies in Mediterranean dunes (Kutiel *et al.*, 2000; Kutiel and Zhevelev, 2001) did not find a significant impact. Effects of grazing by domestic livestock can have positive or negative impact on diversity, depending on the scale of research: often diversity increases within the landscape (this is beta-diversity), but at very local scales (patch- or site-scale), alfa diversity can dramatically reduce. Unfortunately, at the international publication level, effects of sod cutting, shrub removal and mowing practices in coastal dunes are not documented.

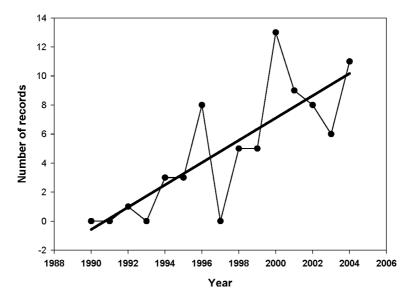


Fig. 1. The number of publications on the relation between nature management in coastal dunes and patterns of biodiversity, published between 1990 and 2004.

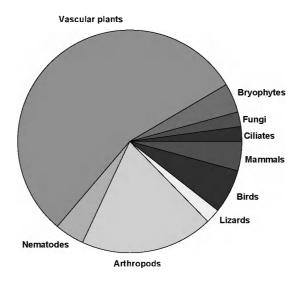


Fig. 2. Overview of used taxa within studies on the relation between coastal dune management and biodiversity.

Table I. Overview of results in literature on the effects of management actions on coastal dune biodiversity. + and – indicate positive and negative effects, respectively; Sspec: diversity of typical (=coastal dune specific) diversity; Stot: diversity of all species within taxon; HabDiv: Habitat diversity; NS: no trend in biodiversity; Refs: used references

Management action			ı .				
Management action	+Sspec	+Stot	NS	-Sspec	-Stot	+HabDiv	Refs
Grazing	4	1	4	1	1	2	Desender, 1996; Kerley et al., 1996; Kooijman and vander Meulen, 1996; Ten Harkel and vander Meulen, 1996; Garcia-Mora et al., 1999; Bonte et al., 2003; Wallis De Vries and Raemakers 2001.
Plantation/stabilisation	0	0	0	3	2	0	Lawesson and Wind, 2002; Munoz- Reinoso, 2004.
Restricting recreation	0	0	2	7	7	0	Burger, 1994; Watson et al., 1996; Kutiel et al., 1999; Kutiel et al., 2000a; Imbert and Hoele, 2001; Kutiel and Zhevelev, 2001.
Shrub removal	1	0	0	1	0	0	Kutiel et al., 2000b.
Sod cutting	1	0	0	0	0	0	Ernst et al., 1996.
Beach cleaning	0	0	0	4	2	0	Griffiths and Stenton- Dozey, 1981; Brown and McLachan, 2002; Llewellyn and Shackley 1996; Jedrzejczak, 2002a,b; Verhoeven, 2002a; Brown and McLachan 2002; Colombini and Chelazzi, 2003.

Coastal dunes processes

A total of 40 records emphasize on the interaction between environmental processes within the coastal dune ecosystem and biodiversity patterns. These studies clearly indicate a decreasing diversity with increasing patterns of fragmentation, trampling and the occurrence of invasive species. Increasing aeolian dynamics does result in decreasing diversity patterns, if all species are taken into account. However, the number of dune-specific, threatened species (Red lists), increases if dynamics remain high. Two studies confirmed the Intermediate Disturbance Hypothesis with a maximal diversity in the middle gradient of the disturbance gradient (Henriques and Hay, 1998; Gordon, 2000). The relation between diversity and eutrophication is variable, but contains a trend of increasing total species richness accompanied with a decline of the number of typical dune species.

Table II. Overview of results in literature on the effects of coastal dune processes on biodiversity. + and – indicate positive and negative effects, respectively; Sspec: diversity of typical (=coastal dune specific) diversity; Stot: diversity of all species within taxon; NS: no trend in biodiversity

Process	+Sspec	+Stot	NS	-Sspec	-Stot	References
Aeolian dynamics	7	0	1	0	3	Henriques and Hay, 1998; Garcia-Mora et al., 1999; Wilson and Sykes 1999; Gordon, 2000; Martinez et al., 2001; Franks and Peterson, 2003; Bonte et al., 2004b; Jun et al., 2004.
Eutrophication	0	4	0	5	3	De Vries et al., 1994; Gaylard et al., 1995; Desender, 1996; Pollet and Grootaert, 1996; Ten Harkel and vander Meulen, 1996; Beena et al., 2000. Verhoeven, 2001; Verhoeven 2002a,b; Wamelink et al., 2003; Bonte et al., 2004; Bossuyt et al., 2004a; Jun et al., 2004.
Acidification	0	0	0	1	1	Wamelink et al., 2003.
Fragmentation	0	0	0	4	2	Obeso and Aedo, 1992; Bonte et al., 2002; Bonte et al., 2003; Bossuyt et al., 2003; Bonte et al., 2004b; Bossuyt et al., 2004b.

Table II (cont.): Overview of results in literature on the effects of coastal dune processes on biodiversity. + and – indicate positive and negative effects, respectively; Sspec: diversity of typical (=coastal dune specific) diversity; Stot: diversity of all species within taxon; NS: no trend in biodiversity

Process	+Sspec	+Stot	SN	-Sspec	-Stot	References
Trampling	0	0	0	6	5	Andersen, 1995; Kutiel et al., 1999; Kutiel et al., 2000a; Imbert and Hoele, 2001; Kutiel and Zhevelev, 2001.
Invasive species	0	0	0	1	1	Hertling and Lubke, 2000; Webb <i>et al.</i> , 2000; Aigner, 2004.

Discussion

Although research efforts on the relation between dune management and biodiversity clearly increased during the last decade, well-documented studies remain fairly uncommon, or are not internationally available. To our opinion, this is not the result of the lack of scientific interest, but rather caused by the lack of studies beyond the local level. Dune managers are often more interested in studies dealing with local inventories of natural values and direct evaluations of management actions. Hence, these short-term studies are intrinsically focussed on local patterns, and as a result very difficult to generalize into a larger framework. Possibly, long term and well designed studies are only available within the local scientific community because of the lack of a more generally applicable framework of research.

Although information is rather scarce, it is possible to separate studies on effects of management actions from studies on underlying processes, which indirectly indicate how changes in the (a)biotic environment result in varying biodiversity patterns. Results from the first type of research do more often come to different conclusions than the latter processed aimed studies do. We believe this is partly due to often completely differing local environmental conditions, but also to the use of only a limited number of model taxa. Hence, we believe that well designed experiments on a broad regional scale with many biotic models, but focussing on a restricted number of actions in similar environmental conditions of humidity, soil productivity, vegetation typology and habitat geometry are urgently needed.

Are nature management actions underpinned by internationally published scientific research?

Nowadays, nature conservation management actions in coastal dunes mainly aim to tackle problems of shrub and tall grass encroachment and the expansion of (plantations with) non-native species. Actions taken are grazing by live stock, sod cutting, mowing and mechanical/manual removal of invasive species. With the exception of recent initiatives in *e.g.* the Netherlands and Belgium (Herrier and Killemaes 1998), actions aiming to restore aeolian processes are rare. These management actions act on different spatial scales: mowing and sod cutting are applied at very small scales in order to restore/conserve local populations of threatened ephemeral or subclimax species. Grazing actions take place at a larger spatial scale in order to change vegetation structural patterns and are assumed to be beneficial for the biotic and abiotic diversity within larger entities. Together with hydrological actions, restoration of aeolian processes is the only type of action, that aims at restoring biodiversity by interfering in the underlying deteriorating processes. It probably is one of the only possible ways to regress the landscape from its stressed or unconstrained phase back into its dynamic phase.

Evaluations of management actions are as a result dependent of the used reference framework and we need to distinguish between effect on small scales of the site and the entire dune ecosystem. The choice of different reference situations is to our opinion the reason why results of local actions are often contradictory. Only for grazing management, some results are available: at local scales, it seems to increase or at least conserve total diversity patterns because of an increasing heterogeneity of the habitat. In few cases, focussed on the effects of high-density grazing, opposite patterns are found. Clearly, information about optimal grazing efforts (type of grazers, densities) within landscapes of different vegetation composition and/or habitat composition is lacking. Whether grazing management is a valid option for the restoration of dune ecosystems remains unanswered, at least its positive impact has not unequivocally been proven. Nonetheless, grazing is widely applied in coastal dunes for nature management reasons. Inherently to the grazing process, it results in a spatial shift of nutrients within the system at the most and not in a substantial nutrient removal (only caused by animals taken out of the system). So, grazing alone cannot be responsible for a complete restoration of the dune system, especially in case of decalcified areas, where atmospheric nitrogen deposition stimulates increasing biomass production (Kooijman et al., 1998). As a result, it seems to be an important action for conserving biodiversity but, as a measure on its own, insufficient for the regression of the ecosystem towards a dynamic landscape. It retains the landscape into its stressed phase which is accompanied by a high biodiversity, but not by a typical biotic and dynamic environment, characterised by typical and specialised biota (Provoost and Bonte, 2004). The removal of invasive species and plantations, restricting beach cleaning and recreation are certainly actions of primordial importance and may be important for restoration actions. Certainly a restriction of beach cleaning and the removal of introduced sand fixators (Populusplantations) are a necessary key-action in dune ontogenesis and restoring sand dynamics.

Process-based research appears to deliver more general and straightforward results: high aeolian dynamics are beneficial for the typical dune diversity, while total diversity

decreases. As the former is inversively related to eutrophication (and soil formation), opposite diversity patterns are found for the latter. Both habitat fragmentation and trampling influence diversity patterns in a negative way. Effects of hydrological restoration and acidification in interaction with soil formation and mineralization on biodiversity remain internationally unpublished. Also, integrated research on the link between abiotic processes and biotic (cascade) interaction are lacking. Here, we think on the relation between e.g. changes in soil productivity, microclimate, nutritional value and morphology of the plant species and the presence of specific faunal elements from different functional groups (specialist and generalist herbivores, carnivores and parasites with different life histories and behaviour). Additionally, we only have limited knowledge on the underlying reason why specific species are restricted to typical dune habitats. A comparative analysis of life history characteristics between habitat specialists and habitat generalists should reveal general patterns on the underlying causes of the decline of specific biota and as a result generate general theory about underlying processes of the deteriorating biotic assemblages. As reported by Bonte et al. (2004a), limited dispersal abilities of typical grey dune species are responsible for their rarity in a fragmented coastal dune ecosystem.

Conclusion: from a descriptive to a process-based approach?

Our screening of internationally available literature suggests that understanding biotic and abiotic processes in coastal dune ecosystems, even if focussed on few model species within a narrow taxonomic range, results in conceptual ideas on the potential interaction between nature management and the conservation and restoration of biodiversity in coastal dunes. Therefore, we suggest encouraging process-based and multi-taxonomical studies on a wide geographical scale. Once patterns in ecosystem functioning (senso recent studies of Ernst et al., 1996; Imbert and Houle, 2001; Coomes et al., 2002; Beckstead et al., 2003; Bonte et al., 2003; Franks et al., 2003; Aigner, 2004; Maun, 2004) and the ecological background of species' rarity are clearly understood, more detailed action-based studies need to be performed on the fine-tuning of suggested management actions on a local scale. We especially believe that a critical evaluation of potential negative feedback mechanisms in the applied action, which induces novel stress situations, has to be performed. Bossuyt et al. (2004ab) documented for example the link between habitat isolation and a declining diversity, but smaller succession rate towards high productive vegetation. Similarly, the restoration of hydrological actions may hypothecate aeolian processes, or beneficial effects of grazing on vegetation structure may induce specific bottlenecks for threatened species due to increased grazing stress, resulting in a reduction of flowering and seed set, or because fragile vegetations with a scarce soil development become trampled and hence reduce survival chances of fossorial invertebrates.

References

Aigner PA. 2004. Ecological and genetic effects on demographic processes: pollination, clonality and seed production in *Dithyrea maritima*. Biological Conservation 116:27-34.

- Andersen U.V. 1995. Resistance of Danish coastal vegetation types to human trampling. Biological Conservation 71: 223-230.
- Annema M. and A.E.M. Janssens. 1998. Het herstel van het vroongrondgebied Middenen Oostduinen op Goeree. Stratiotes 17:20-60.
- Bar P., O. Cohen and M. Shoshany. 2004. Invasion rate of the alien species *Acacia saligna* within coastal sand dune habitats in Israel. Israel Journal of Plant Sciences 52:115-124.
- Beckstead J and I.M. Parker. 2003. Invasiveness of *Ammophila arenaria*: Release from soil-borne pathogens?. Ecology 84:2824-2831.
- Beena K.R., N.S. Raviraja, A.B. Arun and K.R. Sridhar. 2000. Diversity of arbuscular mycorrhizal fungi on the coastal sand dunes of the west coast of India. Current Science 79:1459-1466.
- Bonte D., L. Baert and J.-P. Maelfait. 2002. Spider assemblage structure and stability in a heterogeneous coastal dune system (Belgium). Journal of Arachnology 30:331-343.
- Bonte, D., L. Lens, J.-P. Maelfait, M. Hoffmann and E. Kuijken. 2003. Patch quality and connectivity influence spatial dynamics in a dune wolfspider. Oecologia 135: 227-233
- Bonte D., L. Baert, L. Lens and J.-P. Maelfait. 2004a. Effects of aerial dispersal, habitat specialisation, and landscape structure on spider distribution across fragmented grey dunes. Ecography 27:343-349.
- Bonte D., P. Criel, L. Vanhoutte, I. Van Thournout and J.-P. Maelfait. 2004b. The importance of habitat productivity, stability and heterogeneity for spider species richness in coastal grey dunes along the North Sea and its implications for conservation. Biodiversity and Conservation 13:2119-2134.
- Bossuyt B., O. Honnay, and M. Hermy. 2003.An island biogeographical view of the successional pathway in wet dune slacks. Journal of Vegetation Science 14:781-788.
- Bossuyt B. and M. Hermy. 2004a. Seed bank assembly follows vegetation succession in dune slacks. Journal of Vegetation Science 15:449-456.
- Bossuyt B., O. Honnay and M. Hermy. 2004b. Scale-dependent frequency distributions of plant species in dune slacks: Dispersal and niche limitation. Journal of vegetation Science 15: 323-330.
- Brown A.C. and A. McLachlan. 2002. Sandy shore ecosystems and threats facing them: some predictions for the year 2025. Environmental Conservation 29:62-77.
- Burger J. 1994. The effect of human disturbance on foraging behaviour and habitat use in Piping plover (*Charadrius melodus*). Estuaries 17:695-701.
- Colombini I. and L. Chelazzi. 2003. Influence of marine allochthonous input on sandy beach communities. Oceanography and Marine Biology 41:115-159.
- Coomes D.A., M. Rees, P.J. Grubb and L. Turnbull. 2002. Are differences in seed mass among species important in structuring plant communities? Evidence from analyses of spatial and temporal variation in dune-annual populations. Oikos 96:421-432.
- Desender K., D. Maes, J.-P. Maelfait and M. Van Kerckvoorde. 1995. Een gedocumenteerde Rode lijst van de zandloopkevers en loopkevers van Vlaanderen. Mededelingen van het Instituut voor Natuurbehoud 1:1-208.
- Desender K.R.C. 1996. Diversity and dynamics of coastal dune carabids. Annales Zoologici Fennici 33:65-75.
- De Vries W., J.A. Klijn and J. Kros. 1994. Simulation of the long-term impact of atmospheric deposition on dune ecosystems in the Netherlands. Journal of Applied Ecology 31:59-73.

- Durou S., A. Dejean, I. Olmsted and R.R. Snelling. 2002. Ant diversity in coastal zones of Quintana Roo, Mexico, with special reference to army ants. Sociobiology 40:385-402.
- Ernst W.H.O., Q.L. Slings and H.J.M. Nelissen. 1996. Pedogenesis in coastal wet dune slacks after sod-cutting in relation to revegetation. Plant and Soil 180:219-230.
- Ferreira S.M. and R.J. van Aarde. 2000. Maintaining diversity through intermediate disturbances: evidence from rodents colonizing rehabilitating coastal dunes. African Journal of Zoology 38:286-294.
- Franks S.J. and C.J. Peterson. 2003. Burial disturbance leads to facilitation among coastal dune plants. Plant Ecology 168:13-21.
- Garcia-Mora M.R., J.B. Gallego-Fernandez and F. Garcia-Novo. 1999. Plant functional types in coastal foredunes in relation to environmental stress and disturbance. Journal of Vegetation Science 10:27-34.
- Gaylarn A., A. McLachlan and G.I.H. Kerley. 1995. Faunal changes along a vegetation gradient in the Alexandria coastal dunefield, South Africa. African Journal of Zoology 30:23-28.
- Goralczyk K. 1998. Nematodes in a coastal dune succession: Indicators of soil properties? Applied Soil Ecology 9:465-469.
- Gordon D.M. 2000. Plants as indicators of leafcutter bee (Hymenoptera: Megachilidae) nest habitat in coastal dunes. Pan-Pacific Entomologist 76:219-233.
- Griffiths C.L. and J. Stenton-Dozey. 1981. The fauna and rate of degradation of stranded kelp. Estuarine, Coastal and Shelf Science 12:645-653.
- Henriques R.P.B. and J.D. Hay. 1998. The plant communities of a foredune in southeastern Brazil. Canadian Journal of Botany 76:1323-1330.
- Herrier J.-L. and I. Killemaes. 1998. Acquisition and protection of the coastal dunes of Flanders. Coastline 4:10-15.
- Hertling U.M. and R.A. Lubke. 1999. Use of *Ammophila arenaria* for dune stabilization in South Africa and its current distribution Perceptions and problems. Environmental Management 24:467-482.
- Hertling U.M. and R.A. Lubke. 2000. Assessing the potential for biological invasion the case of *Ammophila arenaria* in South Africa. South African Journal of Science 96:520-527.
- Hopkins J. and G. Radley. 1998. Sand dunes and the Habitat directive: preparation of the UK national list. p.283-301. In: Coastal dune management. Shared experience of European Conservation Practice. Houston J.A., S.E. Edmondson and P.J. Rooney (Eds). Liverpool University Press, Liverpool.
- Houston J.A., S.E. Edmondson and P.J. Rooney (Eds). 1998. Coastal dune management, shared experience of European conservation practice. Proceedings EUCC Symposium, Southport, September 1998. Liverpool University Press. 458p.
- Houston J.A., S.E. Edmondson and P.J. Rooney (Eds). 2001. Coastal dune management. Shared experience of European Conservation Practice. Liverpool University Press, Liverpool: 316-325.
- Kerley G.I.H., A. McLachlan and J.G. Castley. 1996. Diversity and dynamics of bushpockets in the Alexandria Coastal Dunefield, South Africa. Landscape and Urban Planning 34:255-266.

- Imbert E. and G. Houle. 2000. Persistence of colonizing plant species along an inferred successional sequence on a ubarctic coastal dune (Quebec, Canada). Ecoscience 7:370-378.
- Imbert E. and G. Houle. 2001. Spatio-temporal dynamics of root mass density in a coastal dune in subarctic Quebec, Canada. Journal of Coastal Research 17:877-884.
- Jedrzejczak M.F. 2002a. Stranded Zostera marina L. vs. wrack fauna community interactions on a Baltic sandy beach ecosystem: a short-term pilot study. Oceanologia 134:189-194.
- Jedrzejczak M.F. 2002b. Spatio-temporal decay 'hot spots' of stranded wrack in a Baltic sandy coastal system. Oceanologia 44:491-512.
- Jun R., R.B. Clement and F. Roze. 2004. Primary succession of bryophyte and lichen communities in non-forested Atlantic coastal dunes: the example of the Pointe d'Arcay (France). Nova Hedwigia 78:453-468.
- Kooijman A.M. and F. vanderMeulen. 1996. Grazing as a control against 'grass-encroachment' in dry dune grasslands in the Netherlands. Landscape and Urban Planning 34:323-333.
- Kooijman A.M., J.C.R. Dopheide, I. Takken and J.M. Verstraeten. 1998. Nutrient limitations and their implications on the effects of atmospheric deposition in coastal dunes; lime-poor and lime-rich sites in the Netherlands. Journal of Ecology 86:511-526.
- Kowalchuk G.A., F.A. De Souza and J.A. Van Veen. 2002. Community analysis of arbuscular mycorrhizal fungi associated with *Ammophila arenaria* in Dutch coastal sand dunes. Molecular Ecology 11:571-581.
- Kutiel P., O. Cohen, M. Shoshany and M. Shub. 2004. Vegetation establishment on the southern Israeli coastal sand dunes between the years 1965 and 1999. Landscape and Urban Planning 67:141-156.
- Kutiel P. and Y. Zhevelev. 2001. Recreational use impact on soil and vegetation at picnic sites in Aleppo pine forests on Mount Carmel, Israel. Israel Journal of Plant Sciences 49:49-56.
- Kutiel P., E. Eden and Y. Zhevelev. 2000a. Effect of experimental trampling and offroad motorcycle traffic on soil and vegetation of stabilized coastal dunes. Israel. Environmental Conservation 27:14-23.
- Kutiel P., Y. Peled and E. Geffen. 2000b. The effect of removing shrub cover on annual plants and small mammals in a coastal sand dune ecosystem. Biological Conservation 94:235-242.
- Kutiel P., H. Zhevelev and R. Harrison. 1999. The effect of recreational impacts on soil and vegetation of stabilised coastal dunes in the Sharon Park, Israel. Ocean and Coastal Management 42:1041-1060.
- Lawesson J.E. and P. Wind. 2002. Oak dune forests in Denmark and their ecology. Forest Ecology and Management 164:1-14.
- Llewellyn P.J. and S.E. Shackley. 1996. The effects of machinal beach-cleaning on invertebrate populations. British Wildlife 7:147-155.
- Martinez M.L., G. Vazquez and S. Sanchez Colon. 2001. Spatial and temporal variability during primary succession on tropical coastal sand dunes. Journal of Vegetation Science 12:361-372.
- Maes D. and H. Van Dyck. 2001. Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario? Biological Conservation 99:263-276.

- Maun M.A. 1998. Adaptations of plants to burial in coastal sand dunes. Canadian Journal of Botany 76:713-738.
- Munoz-Reinoso J.C. 2004. Diversity of maritime juniper woodlands. Forest Ecology and Management 192:267-276.
- Natura. 2000. Interpretation manual of European Union habitats. Eur 15/2, Nature prediction, coastal zones and tourism. European Commission and Environment. 144p.
- Obeso J.R. and C. Aedo. 1992. Plant species-richness and extinction on isolated dunes along the rocky coast of Northwestern Spain. Journal of Vegetation Science 3:129-132.
- Owen N.W., M. Kent and M.P. Dale. 2001. Spatial and temporal variability in seed dynamics of machair sand dune plant communities, the Outer Hebrides, Scotland. Journal of Biogeography 28:565-588.
- Pollet M. and P. Grootaert. 1996. An estimation of the natural value of dune habitats using Empidoidea (Diptera). Biodiversity and Conservation 5:859-880.
- Provoost S., C. Ampe, D. Bonte, E. Cosyns and E. Hoffmann. 2004. Ecology, management and monitoring of grey dunes in Flanders. J. Coastal Conservation 10 (in press).
- Provoost S. and D. Bonte. 2004. Specificiteit van soorten en hun gebruik als bioindicatoren voor schor en duin. p.366-415. In: Levende duinen. Een overzicht van de biodiversiteit in de Vlaamse kuststreek. Provoost S. and D. Bonte (red.). Mededelingen van het Instituut voor Natuurbehoud, Brussel.
- Quilichini A., M. Debussche and J.D. Thompson. 2004. Geographic differentiation of morphological traits and isozymes in the Mediterranean island endemic *Anchusa crispa*: implications for the conservation of a protected species. Biological Conservation 118:651-660.
- Ten Harkel M.J. and F. vanderMeulen. 1996. Impact of grazing and atmospheric nitrogen deposition on the vegetation of dry coastal dune grasslands. Journal of Vegetation Science 7:445-452.
- Van der Putten W.H. and C.D. Van der Stoel. 1998. Plant parasitic nematodes and spatio-temporal variation in natural vegetation. Applied Soil Ecology 10:253-262.
- Vega L.E., P.J. Bellagamba and L.A. Fitzgerald. 2000. Long-term effects of anthropogenic habitat disturbance on a lizard assemblage inhabiting coastal dunes in Argentina. Canadian Journal of Zoology 78:1653-1660.
- Verhoeven R. 2001. Response of soil microfauna to organic fertilisation in sandy virgin soils of coastal dunes. Biology and Fertility of Soils 34:390-396.
- Verhoeven R. 2002a. Ciliates in coastal dune soils of different stages of development. European Journal of Soil Biology 38:187-191.
- Verhoeven R. 2002b. The structure of the microtrophic system in a development series of dune soils. Pedobiologia 46:75-89.
- Wallis DeVries M.F. and I. Raemakers. 2001. Does extensive grazing benefit butterflies in coastal dunes? Restoration Ecology 9:179-188.
- Wamelink G.W.W., C.J.F. ter Braak and H.F. van Dobben. 2003. Changes in large-scale patterns of plant biodiversity predicted from environmental economic scenarios. Landscape Ecology 18:513-527.
- Watson J.J., G.I.H. Kerley and A. McLachlan. 1996. Human activity and potential impacts on dune breeding birds in the Alexandria Coastal Dunefield. Landscape and Urban Planning 34:315-322.

- Webb C.E., I. Oliver and A.J. Pik. 2000. Does coastal foredune stabilization with *Ammophila arenaria* restore plant and arthropod communities in southeastern Australia? Restoration Ecology 8:283-288.
- Wilson J.B. and M.T. Sykes. 1999. Is zonation on coastal sand dunes determined primarily by sand burial or by salt spray? A test in New Zealand dunes. Ecology Letters 2:233-236.