References

Abreu, Z., L. D. Llambì, and L. Sarmiento. 2009. Sensitivity of Soil Restoration Indicators during Páramo Succession in the High Tropical Andes: Chronosequence and Permanent Plot Approaches. Restoration Ecology **17:**619-627.

Acosta, A., C. Blasi, and A. Stanisci. 2000. Spatial connectivity and boundary patterns in coastal dune vegetation in the Circeo National Park, Central Italy. Journal of Vegetation Science **11:**149-154.

Acosta, A., S. Ercole, A. Stanisci, V. De Patta Pillar, and C. Blasi. 2007. Coastal vegetation zonation and dune morphology in some Mediterranean ecosystems. Journal of Coastal Research **23:**1518-1524.

Ashwini KM, Sridhar KR (2008) Distribution of Pill Millipedes (Arthrosphaera) and

Arbel, Y., A. Yair, and S. Oz. 2005. Effect of topography and water repellent layer on the non-uniform development of planted trees in a sandy arid area. Journal of Arid Environments **60:**67-81.

Arellano, L., J. L. León-Cortés, and G. Halffter. 2008. Response of dung beetle assemblages to landscape structure in remnant natural and modified habitats in southern Mexico. Insect Conservation and Diversity **1:**253-262.

Arroyo-Mora, J. P., G. A. Sánchez-Azofeifa, B. Rivard, J. C. Calvo, and D. H. Janzen. 2005. Dynamics in landscape structure and composition for the Chorotega region, Costa Rica from 1960 to 2000. Agriculture, Ecosystems and Environment **106:**27-39.

Ashwini, K. M., and K. R. Sridhar. 2008. Distribution of Pill Millipedes (Arthrosphaera) and Associated Soil Fauna in the Western Ghats and West Coast of India. Pedosphere **18:**749-757.

Atauri, J. A., and J. V. de Lucio. 2001. The role of landscape structure in species richness distribution of birds,amphibians, reptiles and lepidopterans in Mediterranean landscapes. Landscape Ecology **16:**147-159.

Baguette, M., G. Mennechez, S. Petit, and N. Schtickzelle. 2003. Effect of habitat fragmentation on dispersal in the butterfly *Proclossiana eunomia*. Comptes Rendes Biologies **326:**200-209.

Barbaro, L., J.-P. Rossi, F. Vetillard, J. Nezan, and H. Jactel. 2007. The spatial distribution of birds and carabid beetles in pine plantation forests: the role of landscape composition and structure. Journal of Biogeography **34:**652-664.

Bell, S. S., M. S. Fonseca, and L. B. Motten. 1997. Linking restoration and landscape ecology. Restoration Ecology **5:**318-323.

Bender, D. J., and L. Fahrig. 2005. Matrix structure obscures the relationship between interpatch movement and patch size and isolation. Ecology **86:**1023-1033.

Bennie, J., B. Huntley, A. Wiltshire, M. O. Hill, and R. Baxter. 2008. Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. Ecological Modeling **216:**47-59.

Berg, M.P. and L. Hemerik. 2004. Secondary succession of terrestrial isopod, centipede, and millipede communities in grasslands under restoration. Biology of Fertile Soils **40:** 163-170.

Berliner, D. D. 2005. Systematic conservation planning for the forest biome of South Africa: Approach, methods and results of the selection of priority forests for conservation action. Department of Water Affairs and Forestry.

Bjørnstad, O. N., H. P. Andreassen, and R. A. Ims. 1998. Effects of habitat patchiness and connectivity on the spatial ecology of the root vole *Microtus oeconomus*. Journal of Applied Ecology **67:**127-140.

Bohlman, S. A., W. F. Laurance, S. G. Laurance, H. E. M. Nascimento, P. M. Fearnside, and A. Andrade. 2008. Importance of soils, topography and geographic distance in structuring central Amazonian tree communties. Journal of Vegetation Science **19:**863-874.

Botha, G., and N. Porat. 2007. Soil chronosequence develoment in dunes on the southeast African coastal plain, Maputaland, South Africa. Quaternary International **163:**111-132.

Bourquin, O., G. R. Hughes, and T. Sandwith. 2000. Biodiversity Loss in KwaZulu-Natal: The Role of the Natal Parks Board. IUCN. 156-174

Bowen, M. E., C. A. McAlpine, L. M. Seabrook, A. P. N. House, and G. C. Smith. 2009. The age and amount of regrowth forest in fragmented brigalow landscapes are both important for woodland dependent birds. Biological Conservation **142:**3051-3059.

Boyes, L.J., M.E. Griffiths, A.D. Manson, M.J. Lawes. 2010. Soil nutrients are not responsible for arrested succession in disturbed coastal dune forest. Plant Ecology **208**: 293-305.

Boyes, L.J., R.M. Gunton, M.E. Griffiths, A.D. Manson, M.J. Lawes. 2011. Causes of arrested succession in coastal dune forest. Plant Ecology **212**, 21-32.

Bradshaw, A. 1984. Ecological Principles and Land Reclamation Practice. Landscape Planning **11:**35-48.

Bradshaw, A. D. 1990a. Restoration: an acid test for ecology. Pages 23-29 in W. R. Jordan, M. E. Gilpin, and J. D. Aber, editors. Restoration ecology: A synthetic approach to ecological research. Cambridge University Press, Cambridge.

Bradshaw, A. D. 1990b. The reclamation of derelict land and ecology of ecosystems. Pages 53-74 in W. R. Jordan, M. E. Gilpin, and J. D. Aber, editors. Restoration Ecology: a synthetic approach to ecological research. Cambridge University Press, Cambridge.

Bradshaw, A. D. 1997. Restoration of mined lands—using natural processes. Ecological Engineering **8:**255-269.

Bredenkamp, G. J., J. E. Granger, and N. van Rooyen. 1996. Coastal Forest. in A. B. Low and A. G. Rebelo, editors. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.

Bridge, S. R. J., and E. A. Johnson. 2000. Geomorphic principles of terrain organization and vegetation gradients. Journal of Vegetation Science **11:**57-70.

Brudvig, L. A. 2011. The restoration of biodiversity: Where has research been and where does it need to go? American Journal of Botany **98:**549-558.

Bruton, M. N., and K. H. Cooper. 1980. Studies on the ecology of Maputaland, Rhodes University & The Natal Branch of the Wildlife Society of Southern Africa, Durban.

Burke, I. C., W. K. Lauenroth, R. Riggle, P. Brannen, B. Madigan, and S. Beard. 1999. Spatial variability of soil properties in the shortgrass steppe: The relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. Ecosystems **2:**422-438.

Burnett, M. R., P. V. August, J. H. Brown, Jr., and K. T. Killingbeck. 1998. The Influence of Geomorphological Heterogeneity on Biodiversity -I. A Patch-Scale Perspective. Conservation Biology **12:**363-370.

Caughley, G., D. Grice, R. Barker, and B. Brown. 1988. The Edge of the Range. Journal of Animal Ecology **57:**771-785.

Chave, J. 2001. Spatial patterns and persistence of woody plant species in ecological communities. The American Naturalist **157:**51-65.

Chazdon, R. L. 2008. Beyond Deforestation: Restoring Forests and Ecosystem Services on Degraded Lands. Science **320:**1458-1460.

Chen, T. H., C. Y. Chiu, and G. Tian. 2005. Seasonal dynamics of soil microbial biomass in coastal sand dune forest. Pedobiologia **49:**645-653.

Chen, Z. S., C. F. Hsieh, F. Y. Jiang, T. H. Hsieh, and I. F. Sun. 1997. Relations of soil properties to topography and vegetation in a sub-tropical rain forest in Southern Taiwan. Plant Ecology **132:**229-241.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology **18:**117-143.

Coppedge, B. R., D. M. Engle, R. E. Masters, and M. S. Gregory. 2001. Avian response to landscape change in fragmented southern great plains grasslands. Ecological Applications **11:**41-59.

Cristofoli, S., A. Monty, and G. Mahy. 2010. Historical landscape structure affects plant species richness in wet heathlands with complex landscape dynamics. Landscape and Urban Planning **98:**92-98.

Crk, T., M. Uriarte, F. Corsi, and D. Flynn. 2009. Forest recovery in a tropical landscape: what is the relative importance of biophysical, socioeconomic, and landscape variables? Landscape Ecology **24:**629-642.

Crooks, S., J. Schutten, G. D. Sheern, K. Pye, and A. J. Davy. 2002. Drainage and Elevation as Factors in the Restoration of Salt Marsh in Britain. Restoration Ecology **10:**591-602.

Cueto, V. R., and J. L. de Casenave. 1999. Determinants of bird species richness: role of climate and vegetation structure at a regional scale. Journal of Biogeography **26:**487-492.

Cushman, S. A., and K. McGarigal. 2004. Patterns in the species-environment relationship depend on both scale and choice of response variables. Oikos **105:**117-124.

Cushman, S. A., K. McKelvey, B. R. Noon, and K. McGarigal. 2010. Use of Abundance of One Species as a Surrogate for Abundance of Others. Conservation Biology **24:**830-840.

Cutler, N. A., L. R. Belyea, and A. J. Dugmore. 2008. The spatiotemporal dynamics of primary succession. Journal of Ecology **96:**231-246.

da Silva, W. G., J. P. Metzger, L. C. Bernacci, E. L. M. Catharino, G. Durigan, and S. Simoes. 2008. Relief influence on tree species richness in secondary forest fragments of Atlantic Forest, SE, Brazil. Acta Botanica Brasilica **22:**589-598.

Damschen, E. I., L. A. Brudvig, N. M. Haddad, D. J. Levey, J. L. Orrock, and J. J. Tewksbury. 2008. The movement ecology and dynamics of plant communities in fragmented landscapes. Proceedings of the National Academy of Sciences **105:**19078-19083.

Dangerfield, J. M., and S. R. Telford. 1991. Seasonal Activity Patterns of Julid Millipedes in Zimbabwe. Journal of Tropical Ecology **7:**281-285.

David, J. F., and D. Gillon. 2009. Combined effects of elevated temperatures and reduced leaf litter quality on the life-history parameters of a saprophagous macroarthropod. Global Change Biology **15:**156-165.

David, J.-F. 2009. Ecology of millipedes (Diplopoda) in the context of global change. Soil Organisms **81:**719-733.

Davis, A. L. V., R. J. van Aarde, C. H. Scholtz, and J. H. Delport. 2002. Increasing representation of localised dung beetles across a chronosequence of regenerating vegetation and natural dune forest in South Africa. Global Ecology & Biogeography **11:**191-209.

Davis, A. L. V., R. J. van Aarde, C. H. Scholtz, and J. H. Delport. 2003. Convergence between dung beetle assemblages of a post-mining vegetational chronosequence and unmined dune forest. Restoration Ecology **11:**29-42.

Davis, A. L. V., R. J. van Aarde, C. H. Scholtz, R. A. R. Guldemond, J. Fourie, and C. M. Deschodt. 2012. Changes in dung beetle assemblage structure across a successional sere of coastal vegetation are driven by floral physiognomy and its effect on microclimate. Restoration Ecology. In review.

Department of Water and Environmental Affairs. 2011. National List of Ecosystems that are threatened and in need of Protection, National Environmental Management: Biodiversity Act, 2004. 34809 (Act No. 10 of 2004).

Dobson, A. P., A. D. Bradshaw, and A. J. M. Baker. 1997. Hopes for the Future: Restoration Ecology and Conservation Biology. Science **277:**515-522.

Dorner, B., K. Lertzman, and J. Fall. 2002. Landscape pattern in topographically complex landscapes: issues and techniques for analysis. Landscape Ecology **17:**729-743.

Dzwonko, Z., and S. Gawronski. 1994. The role of woodland fragments, soil types, and dominant species in secondary succession on the western Carpathian foothills. Vegetatio **111:**149-160.

Eeley, H. A. C., M. J. Lawes, and S. E. Piper. 1999. The influence of climate change on the distribution of indigenous forest in Kwazulu-Natal, South Africa. Journal of Biogeography **26:**595-617.

Ehrenfeld, J. G. 2000. Defining the limits of restoration: The need for realistic goals. Restoration Ecology **8:**2-9.

Ehrenfeld, J. G., and L. A. Toth. 1997. Restoration ecology and the ecosystem perspective. Restoration Ecology **5:**307-317.

Emlen, J. M. 1966. The Role of Time, Energy and Food Preference. The American Naturalist **100:**611-617.

Endress, B. A., and J. D. Chinea. 2001. Landscape patterns of tropical forest recovery in the Republic of Palau. Biotropica **33:**555-565.

Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Review **81:**117-142.

Fernández-Juricic, E. 2004. Spatial and temporal analysis of the distribution of forest specialists in an urban-fragmented landscape (Madrid, Spain) Implications for local and regional bird conservation. Landscape and Urban Planning **69:**17-32.

Ferreira, S. M., and R. J. van Aarde. 1997. The chronosequence of rehabilitating stands of coastal dune forests: do small mammals confirm it? South African Journal of Science **93:**211-214.

Finch, J. M., and T. R. Hill. 2008. A late Quaternary pollen sequence from Mfabeni Peatland, South Africa: Reconstructing forest history in Maputaland. Quaternary Research **70:**442-450.

Fincher, G. T., T. B. Stewart, and R. Davis. 1970. Attraction of coprophagous beetles to feces of various animals. The Journal of Parasitology **56:**378-383.

Fourcade, H.G. 1889. Report on the Natal Forests, 1 edn. Watson, Pietermaritzburg.

Forman, R. T. T. 1995. Land Mosaics: The Ecology of Landscapes and Regions, Cambridge University Press, Cambridge.

Forman, R. T. T., and M. Godron. 1981. Patches and Structural Components for a Landscape Ecology. Bioscience **31:**733-740.

Fortin, M. J., and A. A. Agrawal. 2005. Landscape Ecology Comes of Age. Ecology **86:**1965-1966.

Fukami, T. 2010. Community assembly dynamics in space. Pages 45-54 in H.A. Verhoef & P.J. Morin, editors. Community Ecology: Processes, Models, and Applications, Oxford University Press, Oxford.

Furley, P. A., and W. W. Newey. 1979. Variations in Plant Communities With Topography Over Tropical Limestone Soils. Journal of Biogeography **6:**1-15.

Geldenhuys, C. J. 1994. Bergwind Fires and the Location Pattern of Forest Patches in the Southern Cape Landscape, South Africa. Journal of Biogeography **21:**49-62.

Gittings, T., and P. S. Giller. 1998. Resource Quality and the Colonisation and Succession of Coprophagous Dung Beetles. Ecography **21:**581-592.

Godfray, H. C. J. 2011. Food and Biodiversity. Science **333:**1231-1232.

Golet, G. H., T. Gardali, J. W. Hunt, D. A. Koenig, and N. M. Williams. 2009. Temporal and taxonomic variability in response of fauna to riparian restoration. Restoration Ecology **19:**126-135.

Grainger, M. J. 2012. An evaluation of coastal dune forest rehabilitation through ecological succession. PhD Dissertation. University of Pretoria.

Grainger, M. J., and R. J. van Aarde. 2012a. Does succession drive the restoration of a coastal dune forest. Restoration Ecology. In review.

Grainger, M. J., and R. J. van Aarde. 2012b. The role of canopy gaps in the regeneration of coastal dune forest. African Journal of Ecology. doi: 10.1111/j.1365-2028.2012.01348.x

Grainger, M. J., R. J. van Aarde, and T. D. Wassenaar. 2011. Landscape composition influences the restoration of subtropical coastal dune forest. Restoration Ecology **19:**111-120.

Grand, J., and M. J. Mello. 2004. A multi-scale analysis of species-environment relationships: rare moths in a pitch pine-scrub oak (*Pinus rigida-Quercus ilicifolia*) community. Biological Conservation **119:**495-506.

Gregory, R. D., A. van Strien, P. Vorisek, A. W. G. Meyling, D. G. Noble, R. P. B. Foppen, and D. W. Gibbons. 2005. Developing indicators for European birds. Philosophical Transactions of the Royal Society of London, series B **360:**269-288.

Greyling, M. D., R. J. van Aarde, and S. M. Ferreira. 2001. Seasonal changes in habitat preferences of two closely related millipede species. African Journal of Ecology **39:**51-58.

Guldemond, R., and R. J. van Aarde. 2009. Monitoring of ecological development in dune forest rehabilitation sites at RBM: Report on the results of the 2008-2009 summer field survey. Conservation Ecology Research Unit Technical Report 42. University of Pretoria.

Guldemond, R. A. R., and R. J. van Aarde. 2010. Forest patch size and isolation as drivers of bird species richness in Maputaland, Mozambique. Journal of Biogeography. **37**: 1884–1893.

Gunton, R.M., L.J. Boyes, M.E. Griffiths, M.J. Lawes. 2010. Regeneration niches and functional traits of three common species in sub-tropical dune forest. Forest Ecology and Management. **260**: 1490-1497.

Gustafson, E. J. 1998. Quantifying Landcape Spatial Pattern: What Is the State of the Art? Ecosystems **1:**143-156.

Gustafson, E. J., and R. H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology **77:**94-107.

Harper, J. L. 1990. The heuristic value of ecological restoration. Pages 35-52 in W. R. Jordan, M. E. Gilpin, and J. D. Aber, editors. Restoration Ecology: A synthetic approach to ecological research. Cambridge University Press.

Harrison, S., S. J. Ross, and J. H. Lawton. 1992. Beta Diversity on Geographic Gradients in Britain. Journal of Animal Ecology **61:**151-158.

Hartter, J., and J. Southworth. 2009. Dwindling resources and fragmentation of landscapes around parks: wetlands and forest patches around Kibale National Park, Uganda. Landscape Ecology **24:**643-656.

Hãttenschwiler, S., P. Gasser, and C. B. Field. 2005. Soil Animals Alter Plant Litter Diversity Effects on Decomposition. Proceedings of the National Academy of Sciences of the United States of America **102:**1519-1524.

Hayes, D. J., and S. A. Sader. 2001. Comparison of Change-Detection Techniques for Monitoring Tropical Forest Clearing and Vegetation Regrowth in a Time Series. Photogrammetic Engineering & Remote Sensing **67:**1067-1075.

Hendrickx, F., J. P. Maelfait, W. van Wingerden, O. Schweiger, M. Speelmans, S. Aviron, I. Augenstein, R. Billeter, D. Bailey, R. Bukacek, F. Burel, T. Diekötter, J. Dirksen, F. Herzog, J. Liira, M. Roubalova, V. Vandomme, and R. Bugter. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. Journal of Applied Ecology **44:**340-351.

Hilderbrand, R. H., A. C. Watts, and A. M. Randle. 2005. The Myths of Restoration Ecology. Ecology and Society **10:**19.

Hobbs, R. 1997. Future landscapes and the future of landscape ecology. Landscape and Urban Planning **37:**1-9.

Hobbs, R. J., E. Higgs, and J. A. Harris. 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology & Evolution **24:**599-605.

Holl, K. D., L. Pejchar, and S. G. Whisenant. 2007. Overcoming Physical and Biological Obstacles to Restoring Natural Capital. Pages 249-255 in J. Aronson, S. J. Milton, and J. N. Blignaut, editors. Restoring Natural Capital: Science, Business, and Practice. Island Press, Washington.

Hopkin, S. P., and H. J. Read. 1992. The biology of millipedes, Oxford Univeristy Press, New York.

Hutchens, J. J. J., J. A. Schuldt, C. Richards, L. B. Johnson, G. E. Host, and D. H. Breneman. 2009. Multi-scale mechanistic indicators of Midwestern USA stream macroinvertebrates. Ecological Indicators **9:**1138-1150.

Jacquemyn, H., J. Butaye, and M. Hermy. 2003. Influence of Environmental and Spatial Variables on Regional Distribution of Forest Plant Species in a Fragmented and Changing Landscape. Ecography **26:**768-776.

Jeanneret, P., B. Schüpbach, L. Pfiffner, and Th. Walter. 2003. Arthropod reaction to landscape and habitat features in agricultural landscapes. Landscape Ecology **18:**253-263.

Johnson, R. A., and D. W. Wichern. 2002. Applied multivariate statistical analysis, vol. v. 1, Prentice Hall.

Kappes, H., K. Jordaens, F. Hendrickx, J.-P. Maelfait, L. Lens, and T. Backeljau. 2009. Response of snails and slugs to fragmentation of lowland forests in NW Germany. Landscape Ecology **24:**685-697.

Kardol, P., N. J. Cornips, M. M. L. van Kempen, J. M. T. Bakx-Schotman, and W. van der Putten. 2007. Microbe-mediated plant-soil feedback causes historical contingency effects in plant community assembly. Ecological Monographs **77:**147-162.

Kemper, J., R. M. Cowling, D. M. Richardson, G. G. Forsyth, and D. H. McKelly. 2000. Landscape fragmentation in South Coast Renosterveld, South Africa, in relation to rainfall and topography. Austral Ecology **25:**179-186.

Kraft, N. J. B., L. S. Comita, J. M. Chase, N. J. Sanders, N. G. Swenson, T. O. Crist, J. C. Stegen, M. Vellend, B. Boyle, M. J. Anderson, H. V. Cornell, K. F. Davies, A. L. Freestone, B. D. Inouye, S. P. Harrison, and J. A. Myers. 2011. Disentangling the Drivers of β Diversity Along Latitudinal and Elevational Gradients. Science **333:**1755-1758.

Kritzinger, J. J. 1996. Avian community structure on rehabilitating coastal dune forests in northern KwaZulu-Natal, South Africa. MSc. Dissertation. University of Pretoria, Pretoria, South Africa.

Kritzinger, J. J., and R. J. van Aarde. 1998. The bird communities of rehabilitating coastal dunes at Richards Bay, KwaZulu-Natal. South African Journal of Science **94:**71-78.

Kruger, S.C. and M.J. Lawes. 1997. Edge effects at an induced forest-grassland boundary: forest birds in the Ongoye Forest Reserve, KwaZulu-Natal. South African Journal of Zoology **32**: 82-91.

Kubota, Y., H. Murata, and K. Kikuzawa. 2004. Effects of topographic heterogeneity on tree species richness and stand dynamics in a subtropical forest in Okinawa Island, southern Japan. Journal of Ecology **92:**230-240.

Kumssa, D. B., R. J. van Aarde, and T. D. Wassenaar. 2004. The regeneration of soil micro-arthropod assemblages in a rehabilitating coastal dune forest at Richards Bay. African Journal of Ecology **42:**346-354.

Kupfer, J. A., G. P. Malanson, and S. B. Franklin. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. Global Ecology and Biogeography **15:**8-20.

Larkin, D., G. Vivian-Smith, and J. B. Zedler. 2006. Topographic Heterogeneity Theory and Ecological Restoration. Pages 142-164 in D. A. Falk, M. A. Palmer, and J. B. Zedler, editors. Foundations of Restoration Ecology. Island Press.

Laurance, S. G. W., W. F. Laurance, A. Andrade, P. M. Fearnside, K. E. Harms, A. Vicentini, and R. C. C. Luizao. 2010. Influence of soils and topography on Amazonian tree diversity: a landscape-scale study. Journal of Vegetation Science **21:**96-106.

Laurance, W. F., P. M. Fearnside, S. G. Laurance, P. Delamonica, T. E. Lovejoy, J. M. Rankin-de Merona, J. Q. Chambers, and C. Gascon. 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. Forest Ecology and Management **118:**127-138.

Laurance, W. F., H. E. M. Nascimento, S. G. Laurance, A. Andrade, R. M. Ewers, K. E. Harms, R. C. C. Luizão, and J. E. Ribeiro. 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. PLoS ONE **10:**1-8.

Lawes, M. J. 1990. The distribution of the samango monkey (*Cercopithecus mitis erythrarchus* Peters, 1852 and *Cercopithecus mitis labiatus* I. Geoffrey, 1843) and forest history in southern Africa. Journal of Biogeography **17:**669-680.

Lawes, M. J., D. M. MacFarlane, and H. A. C. Eeley. 2004. Forest landscape pattern in the KwaZulu-Natal midlands, South Africa: 50 years of change or stasis? Austral Ecology **29:**613-623.

Lawes, M. J., P. E. Mealin, and S. E. Piper. 2000. Patch occupancy and potential metapopulation dynamics of three forest mammals in fragmented Afromontane forest in South Africa. Conservation Biology **14:**1088-1098.

Leopold, A. 1966. A Sand County almanac: with other essays from Round River, Oxford University Press, New York.

Lessard, J.-P., J. Belmaker, J.A. Myers, J.M. Chase, C. Rahbek. 2012. Inferring local ecological processes mid species pool influences. Trends in Ecology and Evolution, **27**: 600-607.

Leyequién, E., W. F. De Boer, and V. M. Toledo. 2010. Bird community composition in a shaded coffee agro-ecological matrix in Puela, Mexico: The effects of landscape heterogeneity at multiple spatial scales. Biotropica **42:**236-245.

Li, H., and J. F. Reynolds. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. Ecology **75:**2446-2455.

Li, H., and J. F. Reynolds. 1995. On definition and quantification of heterogeneity. Oikos **73:**280-284.

Lindborg, R., and O. Eriksson. 2004. Historical landscape connectivity affects present plant species diversity. Ecology **85:**1840-1845.

Lindenmayer, D., R. J. Hobbs, R. Montague-Drake, J. Alexandra, A. Bennett, M. Burgman, P. Cale, A. Calhoun, V. Cramer, P. Cullen, D. Driscoll, L. Fahrig, J. Fischer, J. Franklin, Y. Haila, M. Hunter, P. Gibbons, S. Lake, G. Luck, C. MacGregor, S. McIntyre, R. Mac Nally, A. Manning, J. Miller, H. Mooney, R. Noss, H. P. Possingham, D. Saunders, F. Schmiegelow, M. Scott, D. Simberloff, T. Sisk, G. Tabor, B. Walker, J. Wiens, J. Woinarski, and E. Zavaleta. 2008. A checklist for ecological management of landscapes for conservation. Ecology Letters **11:**78-91.

Lindenmayer, D. B., J. F. Franklin, and J. Fischer. 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation **131:**433-445.

Lindenmayer, D. B., M. A. McCarthy, and M. L. Pope. 1999. Arboreal Marsupial Incidence in Eucalypt Patches in South-Eastern Australia: A Test of Hanski's Incidence Function Metapopulation Model for Patch Occupancy. Oikos **84:**99-109.

Loranger-Merciris, G., D. B.-R. Imbert, P. Lavelle, and J. F. Ponge. 2008. Litter N-content influences soil millipede abundance, species richness and feeding preferences in a semi-evergreen dry forest of Guadeloupe (Lesser Antilles). Biology and Fertility of Soils **45:**93-98.

Lubke, R.A., A.M. Avis, J.B. Moll. 1996. Post-mining rehabilitation of coastal sand dunes in Zululand, South Africa. Landscape and Urban Planning **34**: 335–345.

Lubke, R.A., and A.M. Avis. 1999. A Review of the Concepts and Application of Rehabilitation following Heavy Mineral Dune Mining. Marine Pollution Bulletin **37**: 546-557.

Lutz, W., and S. KC. 2010. Dimensions of global population projections: what do we know about future population trends and structures? Philosophical Transactions of the Royal Society of London, series B **365:**2779-2791.

Mabry, C. M., L. A. Brudvig, and R. C. Atwell. 2010. The confluence of landscape context and site-level management in determining Midwestern savanna and woodland breeding bird communities. Forest Ecology and Management **260:**42-51.

MacArthur, R. H., and E. R. Pianka. 1966. On Optimal Use of a Patchy Environment. The American Naturalist **100:**603-609.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of Island Biogeography, Princeton University Press, Princeton and Oxford.

MacMahon, J. A., and K. D. Holl. 2001. Ecological restoration: a key to conservation biology's future. Pages 245-269 in M. E. Soule and G. H. Orians, editors. Conservation biology: research priorities for the next decade. Island Press, Washington, United States of America.

Marage, D., and J.-C. Gégout. 2009. Importance of soil nutrients in the distribution of forest communities on a large geographical scale. Global Ecology and Biogeography **18:**88-97.

Martinez, M. L., G. Vásquez, and S. Sánchez Colón. 2001. Spatial and temporal variability during primary succession on tropical coastal sand dunes. Journal of Vegetation Science **12:**361-372.

Matthews, J. W., A. I. Peralta, D. N. Flanagan, P. M. Baldwin, A. Soni, A. D. Kent, and A. G. Endress. 2009. Relative influence of landscape vs. local factors on plant community assembly in restored wetlands. Ecological Applications **19:**2108-2123.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial Pattern Analysis Porgram for Categorical Maps. Amherst, Computer software program produced by the authors at the University of Massachusetts.

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-Being: Biodiversity Synthesis. World Resources Institute, Washington, D.C.

Moir, M. L., K. E. C. Brennan, and M. S. Harvey. 2009. Diversity, endemism and species turnover of millipedes within the south-western Australian global biodiversity hotspot. Journal of Biogeography **36:**1958-1971.

Moll, E. J. 1978. The vegetation of Maputaland. Trees of South Africa31-58.

Motulsky, H. 2004. Fitting Models to Biological Data Using Linear and Nonlinear Regression: A Practical Guide to Curve Fitting. Oxford University Press, Oxford.

Mucina, L., and M. C. Rutherford, L. W. Powrie, M. C. Lötter, G. P. von Maltitz, D. I. W. Euston-Brown, W. S. Matthews, L. L. Dobson, and B. McKenzie. 2006. Afrotemperate, subtropical and azonal forests. Pages 584-615 in L. Mucina and M. C. Rutherford, editors. The vegetation of South Africa, Lesotho and Swaziland. SANBI, Pretoria, South Africa.

Naveh, Z. 1994. From biodiversity to ecodiversity: A landscape-ecology approach to conservation and restoration. Restoration Ecology **2:**180-189.

Nichols, E., S. Spector, J. Louzada, T. Larsen, S. Amezquita, and M. E. Favila. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation **141:**1461-1474.

Nichols, W. F., K. T. Killingbeck, and P. V. August. 1998. The Influence of Geomorphological Heterogeneity on Biodiversity II. A Landscape Perspective. Conservation Biology **12:**371-379.

Novák, J., and M. Konvicka. 2006. Proximity of valuable habitats affects succession patterns in abandoned quarries. Ecological Engineering **26:**113-122.

Nzunda E. F., M. E. Griffiths, M. J. Lawes. 2007. Resprouting versus turning up of leaning trees in a subtropical coastal dune forest in South Africa. Journal of Tropical Ecology **23**: 289-296.

Oliviera-Filho, A. T., N. Curi, E. A. Vilela, and D. A. Carvalho. 1998. Effects of canopy gaps, topography, and soil on the distribution of woody species in a central Brazilian deciduous dry forest. Biotropica **30:**362-375.

Oliviera-Filho, A. T., E. A. Vilela, D. A. Carvalho, and M. L. Gavilanes. 1994. Effects of soils and topography on the distribution of tree species in a tropical riverine forest in south-eastern Brazil. Journal of Tropical Ecology **10:**483-508.

Oosting, H. J., and W. D. Billings. 1942. Factors affecting vegetational zonation on coastal dunes. Ecology **23:**131-142.

Ottermanns, R., P. W. Hopp, M. Guschal, G. Pacheco dos Santos, S. Meyer, and M. Roß-Nickoll. 2011. Causal relationship between leaf litter beetle communities and regeneration patterns of vegetation in the Atlantic rainforest of Southern Brazil (Mata Atlântica). Ecological Complexity. doi:10.1016/j.ecocom.2011.06.001

Ozaki, K., M. Isono, T. Kawahara, S. Iida, T. Kudo, and K. Fukuyama. 2006. A mechanistic approach to evaluation of umbrella species as conservation surrogates. Conservation Biology **20:**1507-1515.

Pachepsky, Y. A., D. J. Timlin, and W. J. Rawls. 2001. Soil water retention as related to topographic variables. Soil Science Society of America Journal **65:**1787-1795.

Palik, B. J., P. C. Goebel, L. K. Kirkman, and L. West. 2000. Using landscape hierarchies to guide restoration of disturbed ecosystems. Ecological Applications **10:**189-202.

Palmer, M. A., R. F. Ambrose, and N. L. Poff. 1997. Ecological Theory and Community Restoration Ecology. Restoration Ecology **5:**291-300.

Parker, V. T. 1997. The Scale of Successional Models and Restoration Objectives. Restoration Ecology **5:**301-306.

Patterson, B. D. 1990. On the temporal development of nested subset patterns of species composition. Oikos **59:**330-342.

Phalan, B., M. Onial, A. Balmford, and R. E. Green. 2011. Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared. Science **333:**1289-1291.

Pickett, S. T. A., and M. L. Cadenasso. 1995. Landscape Ecology: Spatial heterogeneity in Ecological Systems. Science **269:**331-334.

Piqueray, J., G. T. Bottin, L. M. Delescaille, E. Bisteau, G. Colinet, and G. G. Mahy. 2011. Rapid restoration of a species-rich ecosystem assessed from soil and vegetation indicators: The case of calcareous grasslands restored from forest stands. Ecological Indicators **11:**724-733.

Porter, K., R. J. van Aarde, and T. D. Wassenaar. 2007. Millipede Identification Catalogue. Internal Report. University of Pretoria.

Poulsen, B. O. 2002. Avian richness and abundance in temperate Danish forests: tree variables important to birds and their conservation. Biodiversity and Conservation **11:**1551-1566.

Prevedello, J., and M. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. Biodiversity and Conservation **19:**1205-1223.

Purtauf, T., J. Dauber, and V. Wolters. 2004. Carabid communities in the spatio-temporal mosaic of a rural landscape. Landscape and Urban Planning **67:**185-193.

Rands, M. R. W. 2012. Biodiversity conservation: Challenges beyond 2010. Science **329:**1298-1303.

Redi, B. H., R. J. van Aarde, and T. D. Wassenaar. 2005. Coastal Dune Forest Development and the Regeneration of Millipede Communities. Restoration Ecology **13:**284-291.

Reynolds, H. L., A. Packer, J. D. Bever, and K. Clay. 2003. Grassroots Ecology: Plant-Microbe-Soil Interactions as Drivers of Plant Community Structure and Dynamics. Ecology **84:**2281-2291.

Riiters, K. H., R. V. O'Neill, C. T. Hunsaker, J. D. Wickham, D. H. Yankee, S. P. Timmins, K. B. Jones, and B. L. Jackson. 1995. A factor analysis of landscape pattern and structure metrics. Landscape Ecology **10:**23-39.

Ritter, E., L. Dalsgaard, and K. S. Einhorn. 2005. Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. Forest Ecology and Management **206:**15-33.

Robertson, J., and M. J. Lawes. 2005. User perceptions of conservation and participatory management of iGxalingenwa forest, South Africa. Environmental Conservation **32:**64-75.

Robinson, S. K., F. R. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science **267:**1987-1990.

Roslin, T., and A. Koivunen. 2001. Distribution and abundance of dung beetles in fragmented landscapes. Oecologia **127:**69-77.

Rotenberry, J. T. 1985. The role of habitat in avian community composition. Oecologia **67:**213-217.

Rozé, F., and S. Lemauviel. 2004. Sand Dune Restoration in North Brittany, France: A 10-Year Monitoring Study. Restoration Ecology **12:**29-35.

Rutledge, D. 2003. Landscape indices as measures of the effects of fragmentation: can pattern reflect process? Department of Conservation Science Internal Series 98, Wellington, New Zealand.

Saunders, D. A., R. J. Hobbs, and C. R. Marguiles. 1991. Biological consequences of ecosystem fragmentation: A review. Conservation Biology **5:**18-32.

Scheu S., M. Schaefer. 1998. Bottom-up control of the soil macrofauna community in a beechwood on limestone: manipulation of food resources. Ecology **79**: 1573-1585.

Sekercioglu, C. H., S. R. Loarie, B. F. E. D. Oviedo, P. R. Ehrlich, and G. C. Daily. 2007. Persistence of Forest Birds in the Costa Rican Agricultural Countryside. Conservation Biology **21:**482-494.

SER. 2004. The SER International Primer on Ecological Restoration.Version 2: October 2004. www.ser.org & Tucson: Society for Ecological Restoration International.

Shackleton, C. M., B. J. Scholes, C. Vogel, R. Wynberg, T. Abrahamse, S. E. Shackleton, F. Ellery, and J. Gambiza. 2011. The next decade of environmental science in South Africa. South African Geographical Journal **93:**1-14.

Shanahan, D. F., and H. P. Possingham. 2009. Predicting avian patch occupancy in a fragmented landcape: do we know more than we think? Journal of Applied Ecology **46:**1026-1035.

Simenstad, C., D. Reed, and M. Ford. 2006. When is restoration not? Incorporating landscape-scale processes to restore self-sustaining ecosystems in coastal wetland restoration. Ecological Engineering **26:**27-39.

Simpson, G. G. 1964. Species Density of North American Recent Mammals. Systematic Zoology **13:**57-73.

Smit, A. M., and R. J. van Aarde. 2001. The influence of millipedes on selected soil elements: a microcosm study on three species occurring on coastal sand dunes. Functional Ecology **15:**51-59.

Smith, D. A., and S. D. Gehrt. 2009. Bat response to woodland restoration within urban forest fragments. Restoration Ecology. doi: 10.1111/j.1526-100X.2009.00538.x

Smith, R. J., P. S. Goodman, and W. S. Matthews. 2006. Systematic conservation planning: a review of perceived limitations and an illustration of the benefits, using a case study from Maputaland, South Africa. Oryx **40:**400-410.

Southworth, J., D. Munroe, and H. Nagendra. 2004. Land cover change and landscape fragmentation—comparing the utility of continuous and discrete analyses for a western Honduras region. Agriculture, Ecosystems and Environment **101:**185-205.

Stuart, N., T. Barratt, and C. Place. 2006. Classifying the Neotropical savannas of Belize using remote sensing and ground survey. Journal of Biogeography **33:**476-490.

Suding, K. N. 2011. Toward an Era of Restoration in Ecology: Successes, Failures, and Opportunities Ahead. Annual Review of Ecology, Evolution and Systematics **42:**465-487.

Swanson, F. J., T. K. Kratz, N. Cain, and R. G. Woodmansee. 1988. Landform Effects on Ecosystem Patterns and Processes. Bioscience **38:**92-98.

Swihart, R. K., J. J. Lusk, J. E. Duchamp, C. E. Rizkalla, and J. E. Moore. 2006. The role of landscape context, niche breadth, and boundaries in predicting species responses to habitat alteration. Diversity and Distributions **12:**277-287.

Szabó, P., and R. Hédl. 2011. Advancing the Integration of History and Ecology for Conservation. Conservation Biology **25:**680-687.

Tateno, R., and H. Takeda. 2003. Forest structure and tree species distribution in relation to topography-mediated heterogeneity of soil nitrogen and light at the forest floor. Ecological Research **18:**571.

ter Braak, C. J. F., and P. Smilauer. 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide, Biometris, Wageningen.

Teuben, A., and H. A. Verhoef. 1992. Direct contribution by soil arthropods to nutrient availability through body and faecal nutrient content. Biology and Fertility of Soils **14:**71-75.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography **31:**79-92.

Theron, L. J. 2001. Distribution and abundance of rodents, millipedes and trees in coastal dune forests in northern KwaZulu-Natal. MSc. Dissertation. University of Pretoria, Pretoria.

Tinley, K. L. 1985. Coastal dunes of South Africa. South African National Scientific Programmes Report No. 109, Foundation for Research Development, Republic of South Africa.

Tong, C., M. G. Le Duc, J. Ghorbani, and R. H. Marrs. 2006. Linking restoration to the wider landscape: A study of a bracken control experiment within a upland moorland landscape mosaic in the peak district. Landscape and Urban Planning **78:**115-134.

Trimble, M. J., and R. J. van Aarde. 2011. Decline of Birds in a Human Modified Coastal Dune Forest Landscape in South Africa. PLoS ONE doi:10.1371/journal.pone.0016176

Turgeon, K., and D. L. Kramer. 2012. Compensatory immigration depends on adjacent population size and habitat quality but not on landscape connectivity. Journal of Animal Ecology. doi: 10.1111/j.1365-2656.2012.01990.x

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. Landscape Ecology in Theory and Practice: Pattern and Process, Springer Science+ Business Media, New York.

Turner, M. G., S. M. Pearson, P. Bolstad, and D. N. Wear. 2003. Effects of land-cover change on spatial pattern of forest communities in the Southern Appalachian Mountains (USA). Landscape Ecology **18:**449-464.

van Aarde, R. J., S. M. Ferreira, and J. J. Kritzinger. 1996a. Millipede communities in rehabilitating coastal dune forests in northern KwaZulu/Natal, South Africa. Journal of Zoology, London **238:**703-712.

van Aarde, R. J., S. M. Ferreira, and J. J. Kritzinger. 1996b. Successional changes in rehabilitating coastal dune communities in northern KwaZulu-Natal, South Africa. Landscape and Urban Planning **34:**277-286.

van Aarde, R. J., S. M. Ferreira, J. J. Kritzinger, P. J. van Dyk, M. Vogt, and T. D. Wassenaar. 1996c. An evaluation of habitat rehabilitation on coastal dune forests in Northern KwaZulu-Natal, South Africa. Restoration Ecology **4:**334-345.

van Aarde, R. J., R. A. R. Guldemond, and P. I. Olivier. 2012. Biodiversity status of dune forests in South Africa. in J. L. Lockwood, T. Virzi, and B. Maslo, editors. Coastal Conservation. Cambridge University Press.

van Aarde, R. J., A. M. Smit, and A. S. Claasens. 1998. Soil characteristics of rehabilitating and unmined coastal dunes at Richards Bay, Kwazulu-Natal, South Africa. Restoration Ecology **6:**102-110.

van Aarde, R. J., T. D. Wassenaar, L. Niemand, T. Knowles, and S. M. Ferreira. 2004. Coastal dune forest rehabilitation: a case study on rodent and bird assemblages in northern KwaZulu-Natal, South Africa. Pages 103-115 in M. L. Martinez and N. Psuty, editors. Coastal sand dunes: Ecology and restoration. Springer Verlag, Heidelberg.

van Andel, J., and J. Aronson. 2005. Restoration Ecology: The new frontier, Blackwell Publishing, Oxford.

van Diggelen, R. 2005. Landscape: spatial interactions. Pages 31-44 in J. van Andel and J. Aronson, editors. Restoration Ecology: The new frontier. Blackwell Publishing, Oxford.

van Dyk, P. J. 1996. The population biology of sweet thorn *Acacia karroo* in rehabilitating coastal dune forests in northern KwaZulu Natal, South Africa. MSc. Dissertation. University of Pretoria, Pretoria, South Africa.

van Wyk, A. E. 1996. Biodiversity of the Maputaland Centre. L. J. G. van der Maesen, X. M. van der Burgt, and J. M. van Medenbach de Rooy, editors. The Biodiversity of African Plants, Wageningen, The Netherlands, 22 September/1994. Kluwer Academic Publishers, Dordrecht.

van Wyk, A. E., and G. F. Smith. 2001. Floristic and succulent riches in southern Africa: a review of centres of endemism, Umdaus Press, Pretoria.

Vanbergen, A. J., A. D. Watt, R. Mitchell, A. M. Truscott, S. C. F. Palmer, E. Ivits, P. Eggleton, T. H. Jones, and J. P. Sousa. 2007. Scale-specific correlations between habitat heterogeneity and soil fauna diversity along a landscape structure gradient. Oecologia **153:**713-725.

Viña, A., S. Bearer, X. Chen, G. He, M. Linderman, L. An, H. Zhang, Z. Ouyang, and J. Liu. 2007. Temporal changes in giant panda habitat connectivity across boundaries of Wolong Nature Reserve, China. Ecological Applications **17:**1019-1030.

Vitousek, P. M., H. A. Mooney, and J. M. Melillo. 1997. Human Domination of Earth's Ecosystems. Science **277:**494-499.

von Maltitz, G. P., G. F. van Wyk, and D. A. Everard. 1996. Successional pathways in disturbed coastal dune forest on the coastal dunes in north-east KwaZulu-Natal, South Africa. South African Journal of Botany **62:**188-195.

Wallis de Vries, M. F., and S. H. Ens. 2009. Effects of habitat quality and isolation on the colonisation of restored heathlands by butterflies. Restoration Ecology. doi: 10.1111/j.1526-100X.2008.00447.x

Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setälä, W. H. Van der Putten, and D. H. Wall. 2004. Ecological Linkages Between Aboveground and Belowground Biota. Science **304:**1629-1633.

Wassenaar, T. D., S. M. Ferreira, and R. J. van Aarde. 2007. Flagging Aberrant Sites and Assemblages in Restoration Projects. Restoration Ecology **15:**68-76.

Wassenaar, T. D., R. J. van Aarde, S. L. Pimm, and S. M. Ferreira. 2005. Community convergence in disturbed subtropical dune forests. Ecology **86:**655-666.

Walker, L.R., R. del Moral. 2003. Primary Succession and Ecosystem Rehabilitation. Cambridge University Press. Cambridge.

Watkeys, M. K., T. R. Mason, and P. S. Goodman. 1993. The role of geology in the development of Maputaland, South Africa. Journal of African Earth Sciences **16:**205-221.

Watson, D. M. 2002. A conceptual framework for studying species composition in fragments, islands and other patchy ecosystems. Journal of Biogeography **29:**823-834.

Watson, J. E. M., R. J. Whittaker, and T. P. Dawson. 2004. Avifaunal responses to habitat fragmentation in the threatened littoral forests of south-eastern Madagascar. Journal of Biogeography **31:**1791-1807.

Weiermans, J., and R. J. van Aarde. 2003. Roads as Ecological Edges for Rehabilitating Coastal Dune Assemblages in Northern KwaZulu-Natal, South Africa. **11:**43-49.

Weiss, S. B., and D. D. Murphy. 1990. Thermal microenvironments and the restoration of rare butterfly habitat. Pages 50-60 in J. J. Berger, editor. Environmental restoration: Science & Strategies for Restoring the Earth. Island Press, CA, USA.

Weisser, P. J. 1980. The dune forests of Maputaland. Pages 78-90 in M. N. Bruton and K. H. Cooper, editors. Studies on the ecology of Maputaland. Cape & Transvaal Printers, Cape Town.

Weisser, P. J., and F. Marques. 1979. Gross vegetation changes in the dune area between Richards bay and the Mfolozi River, 1937 - 1974. Bothalia **12:**711-721.

Weisser, P. J., and R. Muller. 1983. Dune vegetation dynamics from 1937 to 1976 in the Mlalazi-Richards Bay area of Natal, South Africa. Bothalia **14:**661-667.

Wethered, R., and M. J. Lawes. 2003. Matrix effects on bird assemblages in fragmented Afromontane forests in South Africa. Biological Conservation **114:**327-340.

Wethered, R., and M. J. Lawes. 2005. Nestedness of bird assemblages in fragmented Afromontane forest: the effect of plantation forestry in the matrix. Biological Conservation **123**:125-137.

Whisenant, S. G. 2004. Wildland degradation and repair. Pages 1-23 Repairing Damaged Wildlands. Cambridge University Press, Cambridge.

White, P. S., and J. L. Walker. 1997. Approximating nature's variation: Selecting and using reference information in restoration ecology. Restoration Ecology **5:**338-349.

Wiens, J. A. 1995. Landscape mosaics and ecological theory. Pages 1-26 in L. Hansson, L. Fahrig, and G. Merriam, editors. Mosaic Landscapes and Ecological Processes. Chapman & Hall, London.

Wiens, J. A. 1997. Metapopulation Dynamics and Landscape Ecology. Pages 43-62 in I. Hanski and M. E. Gilpin, editors. Metapopulation Biology. Academic Press, San Diego, California.

Wiens, J. A. 2009. Landscape ecology as a foundation for sustainable conservation. Landscape Ecology **24:**1053-1065.

Woolard, J. W., and J. D. Colby. 2002. Spatial characterization, resolution, and volumetric change of coastal dunes using airborne LIDAR: Cape Hatteras, North Carolina. Geomorphology **48:**269-287.

Wright, J., A. Symstad, J. M. Bullock, K. Engelhardt, L. Jackson, and E. Bernhardt. 2009. Restoring biodiversity and ecosystem function: will an integrated approach improve results? Pages 167-177 in S. Naeem, D. E. Bunker, A. Hector, M. Loreau, and C. Perrings, editors. Biodiversity, Ecosystem Functioning, and Human Wellbeing: an ecological and economic perspective. Oxford University Press, New York.

Wu, J. 2004. Effects of changing scale on landscape pattern analysis: scaling relations. Landscape Ecology **19:**125-138.

Xiong, S., M. E. Johansson, F. M. R. Hughes, A. Hayes, K. S. Richards, and C. Nilsson. 2003. Interactive effects of soil moisture, vegetative canopy, plant litter and seed addition on plant diversity in a wetland community. Journal of Ecology **91:**976-986.

Xu, Z., S. Wan, G. Zhu, H. Ren, and X. Han. 2009. The influence of historical land use and water availability on grassland restoration. Restoration Ecology. doi: 10.1111/j.1526-100X.2009.00595.x

Yates, C. J., D. A. Norton, and R. J. Hobbs. 2000. Grazing effects on soil and microclimate in fragmented woodlands in southwestern Australia: implications for restoration. Austral Ecology **25:**36-47.

Zhao, Y., M. Tomita, K. Hara, M. Fujihara, Y. Yang, and L. Da. 2012. Effects of topography on status and changes in land cover patterns, Chongqing City, China. Landscape and Ecological Engineering. doi: 10.1007/s11355-011-0155-2

Zuo, X., X. Zhao, H. Zhao, T. Zhang, Y. Guo, Y. Li, and Y. Huang. 2009. Spatial heterogeneity of soil properties and vegetation-soil relationships following vegetation restoration of mobile dunes in Horqin Sandy Land, Northern China. Plant and Soil **318:**153-167.

Zuur, A. F., E. N. Ieno, and G. M. Smith. 2007b. Principal component analysis and redundancy analysis. Pages 193-224 Analysing Ecological Data, Springer Science + Business Media, LLC, New York, USA.

Appendix I: Images that illustrate mining and rehabilitation of coastal dunes along the northeast coast of KwaZulu-Natal, South Africa.

Plate 1. Heavy machinery is used to clear vegetation from the coastal dunes prior to the extraction minerals from the sand.

Plate 2. The mine works as an open-cast dredging system whereby dune sand is taken up by a bucket wheel and separated from the heavy minerals (~4% of the sand) by means of a cyclonic system on the mining plant. This heavy mineral concentrate is taken to the smelter site for further processing where the rutile, zircon and ilmenite are further separated and prepared.

Plate 3. Once separated from the heavy minerals, the sand is stacked into shapes that mimic the pre-mining topographic profile.

Plate 4. Topsoil collected from cleared areas ahead of the mine is brought and spread over the newly stacked dunes. This is then sown with annuals and indigenous to stabilize the dune as soon as possible with a cover crop. Shade-netting is erected to prevent wind erosion, as well as shade and protect seedlings.

Seral stage 1

Plate 5. The cover crop grows up within months and between these annuals and grasses, Acacia karroo seedlings begin to germinate (insert picture).

Plate 6. Within three years an impenetrable *Acacia karroo* shrubland has formed (at three years there are 20724±2143 trees/ha (van Dyk 1996)).

Seral stage 2

Plate 7. Within 11 years the *Acacia karroo* still dominates but has thinned to 737±35 trees/ha by the age of 14 (van Dyk 1996). Forest canopy species are beginning to emerge, although the understory is not well-developed

Plate 8. After about 20 years of age the *Acacia karroo* trees begin to senesce and fall over or die standing (inset), forming canopy gaps of varying sizes. Although *A. karroo* remain dominant, the understory has become more developed and forest canopy species are more common.

Seral stage 3

Plate 9. After 30 years gaps of all sizes have formed as *Acacia karroo* continue to fall down. The forest is multi-layered and forest canopy trees are in excess of 8m tall.

Plate 10. In these oldest stands (35 years) *Acacia karroo* has thinned to 141±11 trees/ha (van Dyk 1998), larger gaps comprise grassy patches and clumps of forest tree species. Importantly, these gaps are not recolonized by *A. karroo* (Grainger 2012).

Appendix II: List of species from three taxa recorded in the study area

Table A-1. List of woody plant species identified in the regenerating and unmined forests, third column indicates species associated with forest habitats (●).

Species	Family	Forest-associated species
Acalypha glabrata	Euphorbiaceae	
Acacia karroo	Mimosaceae	
Acacia kraussiana	Mimosaceae	
Acokanthera oppositifolia	Apocynaceae	
Albizia adianthifolia	Mimosaceae	
Allophylus africanus	Sapindaceae	
Allophylus natalensis	Sapindaceae	
Annona senegalensis	Annonaceae	
Antidesma venosum	Euphorbiaceae	
Apodytes dimidiata	Icacinaceae	
Artabotrys monteiroae	Annonaceae	
Barringtonia racemosa	Lecythidaceae	
Bauhinia tomentosa	Caesalpiniaceae	
Bersama lucens	Melianthaceae	
Brachylaena discolor	Asteraceae	
Bridelia cathartica	Euphorbiaceae	
Bridelia micrantha	Euphorbiaceae	
Canthium inerme	Rubiaceae	
Capparis sepiaria	Capparaceae	
Capparis tomentosa	Capparaceae	
Carissa bispinosa	Apocynaceae	●
Carissa macrocarpa	Apocynaceae	
Casuarina equisetifolia	Casuarinaceae	
Cassine eucleiformis	Celastraceae	
Cassipourea gummiflua	Rhizophoraceae	
Cassipourea malosana	Rhizophoraceae	
Cassine tetragona	Celastraceae	
Cassinopsis tinifolia	Icacinaceae	
Catunaregam spinosa	Rubiaceae	
Celtis africana	Ulmaceae	
Cestrum laevigatum	Solanaceae	
Chaetacme aristata	Ulmaceae	●
Chionanthus battiscombei	Oleaceae	
Chionanthus foveolatus	Oleaceae	
Chionanthus peglerae	Oleaceae	●
Chrysanthemoides monilifera	Asteraceae	
Citrus lemon	Rutaceae	
Clausena anisata	Rutaceae	

Clerodendrum glabrum	Verbenaceae	
Clerodendrum myricoides	Verbenaceae	
Cola natalensis	Sterculiaceae	
Commiphora neglecta	Burseraceae	
Cordia caffra	Boraginaceae	●
Croton sylvaticus	Euphorbiaceae	
Cussonia sphaerocephala	Araliaceae	
Dalbergia armata	Fabaceae	
Deinbollia oblongifolia	Sapindaceae	
Dichrostachys cinerea	Mimosaceae	
Diospyros inhacaensis	Ebenaceae	
Diospyros lycioides	Ebenaceae	
Diospyros natalensis	Ebenaceae	●
Dodonaea angustifolia	Sapindaceae	
Dovyalis longispina	Flacourtiaceae	●
Dovyalis rhamnoides	Flacourtiaceae	
Dracaena aletriformis	Dracaenaceae	
Drypetes natalensis	Euphorbiaceae	
Drypetes reticulata	Euphorbiaceae	
Ekebergia capensis	Meliaceae	●
Elaeodendron croceum	Celastraceae	
Englerophytum natalense	Sapotaceae	
Ephippiocarpa orientalis	Apocynaceae	
Erythrococca berberidea	Euphorbiaceae	●
Erythroxylum emarginatum	Erythroxylaceae	
Erythrina lysistemon	Fabaceae	
Euclea natalensis	Ebenaceae	
Euclea racemosa subsp. sinuata	Ebenaceae	●
Eugenia capensis	Myrtaceae	
Eugenia natalitia	Myrtaceae	●
Ficus burtt-davyi	Moraceae	
Ficus craterostoma	Moraceae	
Ficus lutea	Moraceae	
Ficus natalensis	Moraceae	
Ficus polita	Moraceae	
Ficus sur	Moraceae	
Ficus sycomorus	Moraceae	
Ficus trichopoda	Moraceae	
Garcinia livingstonei	Clusiaceae	
Gardenia thunbergia	Rubiaceae	
Grewia caffra	Tiliaceae	
Grewia occidentalis	Tiliaceae	
Halleria lucida	Scrophulariaceae	
Harpephyllum caffrum	Anacardiaceae	
Hibiscus tiliaceus	Malvaceae	

Hymenocardia ulmoides	Euphorbiaceae	
Inhambanella henriquesii	Sapotaceae	
Keetia gueinzii	Rubiaceae	
Kiggelaria africana	Flacourtiaceae	
Kraussia floribunda	Rubiaceae	
Lagynias lasiantha	Rubiaceae	
Lantana camara	Verbenaceae	
Macaranga capensis	Euphorbiaceae	
Maesa lanceolata	Myrsinaceae	
Maerua nervosa	Capparaceae	
Manilkara concolor	Sapotaceae	
Manilkara discolor	Sapotaceae	
Maytenus cordata	Celastraceae	
Maytenus heterophylla	Celastraceae	
Gymnosporia mossambicensis	Celastraceae	
Gymnosporia nemorosa	Celastraceae	
Maytenus procumbens	Celastraceae	
Gymnosporia senegalensis	Celastraceae	
Maytenus undata	Celastraceae	
Melia azedarach	Meliaceae	
Mimusops caffra	Sapotaceae	
Mimusops obovata	Sapotaceae	
Monanthotaxis caffra	Annonaceae	
Myrica serrata	Myricaceae	
Mystroxylon aethiopicum	Celastraceae	
Ochna arborea	Ochnaceae	
Ochna natalitia	Ochnaceae	
Olea capensis	Oleaceae	●
Olea woodiana	Oleaceae	
Osyris compressa	Santalaceae	
Oxyanthus speciosus	Rubiaceae	
Ozoroa obovata	Anacardiaceae	
Pancovia golungensis	Sapindaceae	●
Parinari capensis subsp. incohata	Chrysobalanaceae	
Passerina rigida	Thymelaeaceae	
Pavetta lanceolata	Rubiaceae	
Pavetta natalensis	Rubiaceae	
Pavetta revoluta	Rubiaceae	
Pavetta Sp01	Rubiaceae	
Peddiea africana	Thymelaeaceae	●
Persea americana	Lauraceae	
Phoenix reclinata	Arecaceae	
Pinus elliotti	Pinaceae	
Pisonia aculeata	Nyctaginaceae	
Protorhus longifolia	Anacardiaceae	

Psidium guajava	Myrtaceae	
Psychotria capensis	Rubiaceae	●
Psydrax obovata	Rubiaceae	
Rapanea melanophloeos	Myrsinaceae	
Rauvolfia caffra	Apocynaceae	
Rhoicissus digitata	Vitaceae	
Rhoicissus revoilii	Vitaceae	
Rhoicissus rhomboidea	Vitaceae	●
Rhoicissus tomentosa	Vitaceae	
Rhoicissus tridentata	Vitaceae	
Rhus natalensis	Anacardiaceae	
Rhus nebulosa	Anacardiaceae	
Ricinus communis	Euphorbiaceae	
Rothmannia globosa	Rubiaceae	
Salacia gerrardii	Celastraceae	
Sapium integerrimum	Euphorbiaceae	
Schinus terebinthifolius	Anacardiaceae	
Schefflera umbellifera	Araliaceae	
Sclerocarya birrea	Anacardiaceae	
Scolopia zeyheri	Flacourtiaceae	
Scutia myrtina	Rhamnaceae	
Senna pendula	Caesalpiniaceae	
Sideroxylon inerme	Sapotaceae	
Solanum mauritianum	Solanaceae	
Strychnos gerrardii	Loganiaceae	●
Strychnos henningsii	Loganiaceae	
Strychnos madagascariensis	Loganiaceae	
Strychnos mitis	Loganiaceae	
Strelitzia nicolai	Strelitziaceae	
Strychnos spinosa	Loganiaceae	
Strychnos usambarensis	Loganiaceae	
Syzygium cordatum	Myrtaceae	
Syzygium cumini	Myrtaceae	
Tarenna junodii	Rubiaceae	
Tarenna littoralis	Rubiaceae	
Tarenna pavettoides	Rubiaceae	
Tecomaria capensis	Bignoniaceae	
Teclea gerrardii	Rutaceae	●
Thespesia acutiloba	Malvaceae	
Trema orientalis	Ulmaceae	
Tricalysia delagoensis	Rubiaceae	
Trichilia dregeana	Meliaceae	
Trichilia emetica	Meliaceae	
Tricalysia lanceolata	Rubiaceae	
Tricalysia sonderiana	Rubiaceae	

Turraea floribunda	Meliaceae	●
Turraea obtusifolia	Meliaceae	
Uvaria caffra	Annonaceae	
Vangueria cyanescens	Rubiaceae	
Vangueria infausta	Rubiaceae	
Vangueria randii	Rubiaceae	
Vepris lanceolata	Rutaceae	
Voacanga thouarsii	Apocynaceae	
Xylotheca kraussiana	Flacourtiaceae	
Zanthoxylum capense	Rutaceae	
Ziziphus mucronata	Rhamnaceae	

Table A-2. List of millipede species identified in the regenerating and unmined forests, third column indicates species associated with forest habitats (●).

Species	**Family**	**Forest-associated species**
Doratogonus sp.	Spirostreptidae	
Centrobolus fulgidus	Spirobolidae	
Centrobolus richardii	Spirobolidae	
Centrobolus rugulosus	Spirobolidae	●
Gnomeskelus tuberosus	Dalodesmidae	●
*Orthroporoides sp.**	Spirostreptidae	●
Orthroporoides pyrocephalus	Spirostreptidae	●
Sphaerotherium giganteum	Sphaerotheridae	●
Sphaerotherium punctulatum	Sphaerotheridae	●
Sphaerotherium rotundatum	Sphaerotheridae	●
Sphaerotherium sp. B	Sphaerotheridae	●
Sphaerotherium sp. C	Sphaerotheridae	●
Sphaerotherium sp. D	Sphaerotheridae	●
Sphaerotherium sp. E	Sphaerotheridae	●
Sphaerotherium sp. F	Sphaerotheridae	●
Spinotarsus anguliferus	Odontopygidae	
Spirostreptidae sp. Imm.	Spirostreptidae	●
Spirostreptidae sp. Imm. 2	Spirostreptidae	●
Ulodesmus micramma zuluensis	Dalodesmidae	

Table A-3. List of dung beetle species identified in the regenerating and unmined forests, third column indicates species associated with forest habitats (●).

Species	**Forest-associated species**
Allogymnopleurus thalassinus	●
Anachalcos convexus	
Caccobius nigritulus	
Caccobius obtusus	
Caccobius sp. 1	●
Caccobius sp. 2	
Caccobius sp. 3	●
Caccobius sp. 4	
Caccobius sp. 5 = Caccobius cavatus	
Catharsius sp 1 (endemic)	
Catharsius mossambicanus	
Catharsius tricornutus	●
Cleptocaccobius viridicollis	
Copris inhalatus ssp santaluciae	
Copris puncticollis	
Copris urus	
Digitonthophagus gazella	
Drepanocerus impressicollis (now Afrodrepanus impressicollis)	
Drepanocerus kirbyi	
Euoniticellus intermedius	
Garreta azureus	●
Garreta unicolor	●
Gyronotus carinatus	
Heliocopris hamadryas	
Hyalonthophagus alcyonides	
Kheper lamarcki	●
Liatongus militaris	●
Metacatharsius sp. 1 (=zuluanus)	●
Milichus sp. 1	
Neosisyphus confrater	
Neosisyphus mirabilis	●
Neosisyphus spinipes	
Odontoloma sp.	
Oniticellus formosus	●
Oniticellus planatus	
Onthophagus aeruginosus	●
Onthophagus ambiguus (now Mimonthophagus ambiguus)	
Onthophagus bicavifrons	
Onthophagus depressus	
Onthophagus fimetarius (coastal var.) possibly new	
Onthophagus flavolimbatus	
Onthophagus lacustris	
Onthophagus nanus	
Onthophagus obtusicornis	
Onthophagus pugionatus	
Onthophagus quadrinodosus	●
Onthophagus signatus	●
Onthophagus sp 1 (=horned pullus)	
Onthophagus sp. 2 (v. small endemic)	

Onthophagus sp 3 (=sp. e George)	
Onthophagus sp 4	
Onthophagus sp nr bicavifrons	●
Onthophagus sp. nr sugillatus (coastal var.) possibly new	
Onthophagus ursinus	●
Onthophagus vinctus	●
Onthophagus stellio or variegatus gp??	
Onthophagus sp - mottled tail	
Onthophagus sp A	
Pachylomerus femoralis	
Pedaria sp. IV	●
Pedaria sp. III	
Proagoderus aciculatus	
Proagoderus aureiceps	
Proagoderus brucei (now P. chalcostolus)	
Scarabaeus bornemisszai	
Scarabaeus goryi	●
Sisyphus natalensis (cited as the syn. S. bornemisszanus)	●
Sisyphus seminulum	
Sisyphus sordidus	●
Sisyphus sp nr gazanus	●
Sisyphus sp y	
Stiptopodius sp. 1	

Table A-4. List of bird species identified in the regenerating and unmined forests, third column indicates species associated with forest habitats (●).

Species	Common Name	Forest-associated species
Acrocephalus palustris	Eurasian Marsh Warbler	
Alcedo cristata	Malachite Kingfisher	
Amblyospiza albifrons	Thick-billed Weaver	
Andropadus importunus	Sombre Greenbul	
Anthus cinnamomeus	African Pipit	
Apalis flavida	Yellow-breasted Apalis	
Apalis ruddi	Rudd's Apalis	
Apalis thoracica	Bar-throated Apalis	
Apalpderma narina	Narina Trogon	●
Aplopelia larvata	Lemon Dove	●
Ardea melanocephala	Black-headed Heron	
Batis capensis	Cape Batis	
Batis fratrum	Woodwards' Batis	●
Bostrychia hagedash	Hadeda Ibis	
Bradornis pallidus	Pale Flycatcher	
Bycanistes bucinator	Trumpeter Hornbill	●
Calendulauda sabota	Sabota Lark	
Camaroptera brachyura	Green-backed Camaroptera	
Campephaga flava	Black Cuckooshrike	
Campethera abingoni	Golden-tailed Woodpecker	
Caprimulgus europaeus	European Nightjar	
Centropus burchellii	Burchell's Coucal	
Cercotrichas leucophrys	White-browed Scrub-Robin	
Cercotrichas quadrivirgata	Bearded Scrub-Robin	
Cercotrichas signata	Brown Scrub-Robin	
Ceuthmochares aereus	Green Malkoha	●
Chalcomitra amethystina	Amethyst Sunbird	
Chalcomitra senegalensis	Scarlet-chested Sunbird	
Chlorocichla falviventris	Yellow-bellied Greenbul	
Chrysococcyx caprius	Diederik Cuckoo	
Chrysococcyx cupreus	African Emerald Cuckoo	●
Chrysococcyx klaas	Klaas's Cuckoo	
Cinnyris bifasciata	Purple-banded Sunbird	
Cisticola chinianus	Rattling Cisticola	
Cisticola cinnamomeus	Pale-crowned Cisticola	
Cisticola fulvicapilla	Neddicky	
Cisticola juncidis	Zitting Cisticola	
Cisticola natelensis	Croaking Cisticola	
Clamator jacobinus	Jacobin Cuckoo	
Coccopygia melanotis	Swee Waxbill	

Colius striatus	Speckled Mousebird	
Columba delegorguei	Eastern Bronze-naped Pigeon	●
Coracias caudata	Lilac-breasted Roller	
Coracias garrulus	Eurasian Roller	
Coracina caesia	Grey Cuckooshrike	
Corvus albus	Pied Crow	
Cossypha caffra	Cape Robin-Chat	
Cossypha dichroa	Chorister Robin-Chat	
Cossypha natalensis	Red-capped Robin-Chat	
Coturnix coturnix	Common Quail	
Cuculus canorus	Common Cuckoo	
Cuculus gularis	African Cuckoo	
Cuculus solitarius	Red-chested Cuckoo	
Cyanomitra olivacea	Eastern Olive Sunbird	●
Cyanomitra veroxii	Grey Sunbird	●
Dendropicos fuscescens	Cardinal Woodpecker	
Dendropicos griseocephalus	Olive Woodpecker	
Dicrurus adsimilis	Fork-tailed Drongo	
Dicrurus ludwigii	Square-tailed Drongo	●
Dryoscopus cubla	Black-backed Puffback	
Estrilda astrild	Common Waxbill	
Estrilda perreini	Grey Waxbill	
Euplectes axillaris	Fan-tailed Widowbird	
Euplectes orix	Southern Red Bishop	
Eurystomus glaucurus	Broad-billed Roller	
Guttera edouardi	Crested Guineafowl	
Halcyon albiventris	Brown-hooded Kingfisher	
Hedydipna collaris	Collared Sunbird	
Hippolais icterina	Icterine Warbler	
Indicator minor	Lesser Honeyguide	
Indicator variegatus	Scaly-throated Honeyguide	
Ispidina picta	African Pygmy-Kingfisher	
Lagonosticta rubricata	African Firefinch	
Lamprotornis corruscus	Black-bellied Starling	●
Laniarius ferrugineus	Southern Boubou	
Lanius collaris	Common Fiscal	
Lanius collurio	Red-backed Shrike	
Lanius minor	Lesser Grey Shrike	
Lonchura cucllata	Bronze Mannikin	
Lonchura nigriceps	Red-backed Mannikin	
Lybius torquatus	Black-collared Barbet	
Macronyx croceus	Yellow-throated Longclaw	
Malaconotus blanchoti	Grey-headed Bush-Shrike	
Mandingoa nitidula	Green Twinspot	

Megaceryle maxima	Giant Kingfisher	
Melaenornis pammelaina	Southern Black Flycatcher	
Merops pusillus	Little Bee-eater	
Mirafra africana	Rufous-naped Lark	
Monticola rupestris	Cape Rock-Thrush	
Motacilla aguimp	African Pied Wagtail	
Motacilla capensis	Cape Wagtail	
Muscicapa adusta	African Dusky Flycatcher	●
Muscicapa caerulescens	Ashy Flycatcher	●
Muscicapa striata	Spotted Flycatcher	
Musophaga porphyreolopha	Purple-crested Turaco	●
Myioparus plumbeus	Grey Tit-Flycatcher	
Nicator gularis	Eastern Nicator	
Oriolus larvatus	Black-headed Oriole	
Oriolus oriolus	Eurasian Golden Oriole	
Passer domesticus	House Sparrow	
Phyllastrephus terrestris	Terrestrial Brownbul	
Phylloscopus trochilus	Willow Warbler	
Platysteira peltata	Black-throated Wattle-eye	●
Plectropterus gambensis	Spur-winged Goose	
Ploceus	Weavers	
Ploceus bicolor	Dark-backed Weaver	●
Ploceus cucullatus	Village Weaver	
Ploceus intermedius	Lesser Masked-Weaver	
Ploceus ocularis	Spectacled Weaver	
Ploceus subaureus	Yellow Weaver	
Pogoniulus bilineatus	Yellow-rumped Tinkerbird	●
Pogoniulus pusillus	Red-fronted Tinkerbird	
Pogonocichla stellata	White-starred Robin	
Prinia subflava	Tawny-flanked Prinia	
Pycnonotus tricolor	Dark-capped Bulbul	
Rhinopomastus cyanomelas	Common Scimitarbill	
Sarothrura elegans	Buff-Spotted Flufftail	
Saxicola torquata	African Stonechat	
Serinus canicollis	Cape Canary	
Serinus mozambicus	Yellow-fronted Canary	
Serinus sulphuratus	Brimstone Canary	
Sigelus silens	Fiscal Flycatcher	
Smithornis capensis	African Broadbill	
Stactolaema leucotis	White-eared Barbet	●
Streptopelia capicola	Cape Turtle Dove	
Streptopelia semitorquata	Red-eyed Dove	
Sylvia borin	Garden Warbler	
Sylvietta rufescens	Long-billed Crombec	

Tauraco corythsix	Knysna Turaco	●
Tauraco livingstonii	Livingstone's Turaco	●
Tchagra australis	Brown-crowned Tchagra	
Tchagra senegala	Black-crowned Tchagra	
Telophorus olivaceus	Olive Bush-Shrike	
Telophorus quadricolor	Gorgeous Bush-Shrike	
Telophorus sulfureopectus	Orange-breasted Bush-Shrike	
Terpsiphone viridis	African Paradise-Flycatcher	
Tockus alboterminatus	Crowned Hornbill	●
Trachyphonus vallantii	Crested Barbet	
Treron calva	African Green-Pigeon	
Trochocercus cyanomelas	Blue-mantled Crested Flycatcher	●
Turdus libonyanus	Kurrichane Thrush	
Turtur chalcospilos	Emerald-spotted Wood-Dove	
Turtur tympanistria	Tambourine Dove	●
Uraeginthus angolensis	Blue Waxbill	
Urocolius indicus	Red-faced Mousebird	
Vidua macroura	Pin-tailed Whydah	
Zoothera guttata	Spotted Ground-Thrush	
Zosterops virens	Cape White-eye	

Appendix III: Manuscript accepted for publication at *Landscape and Ecological Engineering* (DOI: 10.1007/s11355-013-0211-1).

Journal: Landscape and Ecological Engineering

Manuscript type: Original paper

Title: Coastal dune topography as a determinant of abiotic conditions and biological community restoration in northern Kwazulu-Natal, South Africa

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Abstract

Topography is rarely considered as an independent goal of restoration. Yet, topography determines micro-environmental conditions and hence living conditions for species. Restoring topography may therefore be an important first step in ecological restoration. We aimed at establishing the relative importance of topography where coastal dunes destroyed by mining are rebuilt as part of a rehabilitation programme.

We assessed the response of 1) microclimatic and soil conditions, and 2) woody plant and millipede species richness and density, to location-specific topographic profiles. We enumerated the topographic profile using variables of dune morphology (aspect, elevation and gradient) as well as relative position on a dune (crest, slope, valley).

Temperature, relative humidity and light intensity varied with aspect, elevation, gradient and position. However, regeneration age was a better predictor of soil nutrient availability than these topographic variables. Age also interacted with topographic variables to explain tree canopy density and species richness, as well as millipede species richness. The density of keeled millipedes (forest specialists) was best explained by topographic variables alone. The transient nature of these new-growth coastal dune forests likely masks topography-related effects on communities because age-related succession (increasing structural complexity) drives the establishment and persistence of biological communities, not habitat conditions modulated by topography. However, our study has shown that the microhabitats associated with topographic variability influence specialist species more than generalists.

Introduction

Ecological restoration is widely recognised as a conservation tool and aims to re-instate natural processes that sustain biological diversity (Dobson et al. 1997; MacMahon & Holl 2001; Rands 2012). Such diversity is determined by both regional and local forces, the latter often as a function of topography due to cascadal effects on microclimatic conditions, water retention, and nutrient availability (Larkin et al. 2006). These relationships are especially well-documented in mountainous regions (Burnett et al. 1998; Nichols et al. 1998; Tateno & Takeda 2003; da Silva et al. 2008), but less often for coastal sand dune ecosystems (e.g. Martínez et al. 2001; Acosta et al. 2007). The restoration of topography may be a priority (Weiss & Murphy 1990; Palik et al. 2000; Larkin et al. 2006), but difficult or costly to achieve. However, an approximation of the original topography may be sufficient to maintain desired ecological processes. This may well be the case in our study areas where succession drives forest regeneration, but where the full complement of species has not yet been regained (van Aarde et al. 1996b; Grainger 2012). This may be due to the micro-environmental needs of specialist species not being met due to constraints imposed by topography. Justification to restore terrain requires an assessment of the relevance of topography for species and ecological processes. In this study, we assess the influence of dune topography on abiotic and biotic conditions (Table) in coastal dune forests regenerating in response to an ecological restoration program.

The aspect, elevation, and gradient of slopes are collectively referred to as dune morphology, while the relative position is described as the crest, slope, or valley. These variables of dune topography can modulate habitat conditions in various ways (Larkin et al. 2006). For example, nutrients leaching from dune crests into valleys where plant-communities are light-limited results in nutrient-limited communities on crests, but greater nutrient availability in valleys (Tateno & Takeda 2003). Canopy structure changes with gradients in soil fertility and light (Nichols et al. 1998; Tateno & Takeda 2003), even with limited altitudinal variation (da Silva et al. 2008). This may explain patterns in plant species composition, abundance, and distribution (Chen et al. 1997; Oliviera-Filho et al. 1998). The aspect and gradient of dune slopes may amplify these differences as they also influence light availability (Oliviera-Filho et al. 1998; Bennie et al. 2008) and wind exposure (Chen et al. 1997; Acosta et al. 2007). Wind sculpts tree canopies (Kubota et al. 2004), hastens canopy gap formation (Ritter et al. 2005), and contributes to seed dispersal (Furley & Newey 1979). The windward slopes of coastal dunes have higher evaporation rates than leeward slopes and are more exposed to salt spray that increases salt concentrations in the soil, in turn influencing soil pH and the availability of nutrients (Furley & Newey 1979; Chen et al. 1997; Acosta et al. 2007). We therefore hypothesized that dune morphology and position would 1) modulate microclimatic conditions (temperature, relative humidity, and light intensity) and 2) influence soil nutrient availability (C:N ratio) and soil pH (see Table). Disturbed or destroyed topographic profiles could therefore hinder the ecological restoration of plant and animal communities of new-growth forests, or simply alter heterogeneity and rearrange the distribution of resources. Thus the structure and composition of biotic communities at locations with different dune morphologies should be assessed to determine the importance of restoring the topographic profile.

Topography influences plant growth and species richness in old-growth forests (Tateno & Takeda 2003; da Silva et al. 2008), which has cascadal effects on biota through the responses of microclimatic conditions to topography (Larkin et al. 2006). Physiological trade-offs associated with the small size and ectothermy of invertebrates, such as millipedes, renders them sensitive to microclimatic conditions that dictate habitat preferences (Ashwini & Sridhar 2008; Loranger-Merciris et al. 2008; David & Gillon 2009). We therefore assessed the importance of the topographic profile in structuring millipede assemblages. We hypothesized that within a seral stage, dune morphology and position would 3) influence plant community structure and composition, and 4) millipede community structure and composition in regenerating stands of new-growth coastal dune forest (Table). If millipedes respond to topography, changes in the topographic profile should result in changes in millipede diversity. If this is not the case, topography has a limited role to play, if any, in explaining millipede community structure. Although this study is based upon coastal dune forests, it may have implications for any disturbed dune system under restoration.

Methods

Study area

The study area was located north of Richards Bay town (between 28°46' and 28°34' south) on the sub-tropical north coast of Kwazulu-Natal, South Africa (Fig. 1). The climate is humid with a mean annual rainfall of 1458 ± 493.5 mm (mean ± SD, n = 34 years between 1976 and 2009), peaking in February. The mean annual temperature was 23.79 ± 3.40°C (n = 3 years between 2006 and 2009. Winds of between 10 and 40 $km.h^{-1}$ blew from the north-east for about 20% of the time, as did those from south-south west and south-west combined (data courtesy of Richards Bay Minerals).

The establishment of forests on the coastal dunes here occurred with the return of warm interglacial conditions between 6,500 and 4,000 years ago, making them among the highest vegetated dunes in the world (Weisser & Marques 1979; Lawes 1990). These forests are therefore relatively young and harbour few endemic species (Lawes 1990; van Wyk & Smith 2001). Coastal dune forests are sensitive to disturbance but previous work has shown that they are relatively resilient and are thus able to recover (e.g. Wassenaar et al. 2005; Grainger et al. 2011).

Richards Bay Minerals (RBM) has leased this area since 1976 for the extraction of heavy metals from the coastal sands. Ahead of the dredging pond, all vegetation was cleared and the dunes were collapsed for mining. After mining, sand tailings were stacked to resemble pre-mining topography and were covered with topsoil (van Aarde et al. 1996c). A third of the mined area was set aside for the restoration of indigenous coastal dune forest and this area comprised known-aged stands that at the time of the study ranged in age from 1 year (in the northeast) to 33 years (in the southwest) (see Fig. 1). This age-range represented three seral stages based on those defined by Grainger (2012): seral stage one = 1-10 years, two = 11-25 years, and three >25 years. Adjoined by a coastal strip of unmined vegetation about 200 m wide, the stands were themselves no wider than 2 km, set in a mosaic of active mining areas, plantations, degraded woodland, and rural villages (Wassenaar et al. 2005).

Microclimatic data

Fifteen HOBO® 4-channel data loggers (Onset Computer Corporation, 470 MacArthur Blvd., Bourne, MA 02532, U.S.A.) were deployed in the 22-year old stand (see Fig. 1) on custom-made platforms placed 10 cm above the ground (five on the crest, five on a slope and five in the valley). We programmed these loggers to record ground-level temperature, relative humidity, and light intensity (see Table **2** for definitions) every 10 minutes between 08:00, 28 January and 05:00, 4 February 2011, yielding 14,850 records.

Soil surveys

An auger was used to collect soil samples to 20 cm depth at the corners and centre of each of the millipede survey transects (see below). These five samples were mixed into a single bag and consequently 65 bags were analyzed at the Department of Plant Production and Soil Science at the University of Pretoria using procedures described in van Aarde et al. (1998; see supplementary information for detailed chemical profile). We used Nitrogen and Carbon concentrations to calculate the carbon-to-nitrogen ratio (C:N, Table 2) and included the pH values of each sample in our analysis.

Woody plant surveys

All woody plants taller than 0.2 m in 106 randomly placed quadrats (16×16–m, at least 100 m apart) in six stands of known regeneration age (10, 14, 18, 22, 26, and 33 years) were sampled between July and November 2010. Each plant was identified against reference material. We calculated six variables of woody plant community structure for each quadrat (see Table 2).

Millipede surveys

Millipede species occurring on the ground up to 3 m on plants were counted between 13 January and 4 February 2011 in 65 randomly placed transects within a 10, 14, 18, 22, 26, and 33 year-old stand (see Fig. 2). Each transect was 32 × 6–m wide and comprised 48 2 × 2–m cells. Surveys were conducted by three observers per transect, each responsible for a column of 16 cells. All millipedes found in a cell during five minutes were identified based on reference images and descriptions (Porter et al. 2007), counted, and removed to avoid recounting. We calculated the number of millipede species and the density of cylindrical, keeled, and pill millipedes (see Table 2) within each location-specific transect.

Topographic data

We used classified topographic data based on eight cardinal directions (aspect), seven elevation categories, and five gradient categories that had been extracted from a topographic map (see Fig.1.) based on a Light Detection and Ranging (LIDAR) mission conducted in 2010 (post-mining). We used GIS overlay procedures to relate all of the sampling points and quadrat locations recorded in the field to location-specific variables of dune morphology based on the topographic maps.

Statistical analyses

We used stratified random sampling to extract one microclimate record (including the temperature, relative humidity, and light intensity readings) per hour, per logger for each sampling day (29 January – 3 February 2011), rendering 2,475 records to be included in analyses. We $\log_{10}$-transformed the light intensity data to meet assumptions for analyses of variance (ANOVA). To determine whether microclimatic conditions were modulated by topography, we conducted repeated measures ANOVA with hour and day as repeated measures factors, and categorized variables of dune morphology as between-groups factors.

We assessed the influence of dune morphological variables on soil C:N ratios and pH, as well as woody plant and millipede community variables in each of the three seral stages. We assessed these using generalized linear models with age as a covariate (Analyses of Covariance (ANCOVA) for all seral stages for woody plants and seral stages 2 and 3 for soil and millipedes. Millipede and soil data for seral stage 1 comprised too few cases and was therefore not assessed separately. All statistical analyses were conducted using STATISTICA 10 (Statsoft Inc., Tulsa, Oklahoma).

Woody plant and millipede species abundance data were $\log_{10}$-transformed and calculated the similarity between quadrats, with different dune morphological characteristics using the Bray-Curtis index. Cluster analyses and non-metric multi-dimensional scaling (NMDS) were used to detect community clusters based on the four characteristics of dune morphology. Analyses of similarity (ANOSIM) allowed us to assess the significance of community groupings based on dune morphology within each successional stage. To identify the distinguishing species, we conducted similarity percentage (SIMPER) analyses (SIMPER) for those community groupings that differed significantly based on dune morphological characteristics. All multivariate techniques were conducted using PRIMER 6 software (Clarke 1993).

Results

Dune topography and abiotic variables

Temperature was significantly modulated by aspect and gradient when sampling day and time of day were taken into account (repeated measures ANOVA: $F_{(575, 1035)} = 1.33$, $p < 0.001$ and $F_{(230, 1380)} = 1.27$, $p = 0.007$, respectively). Similarly, relative humidity was significantly modulated by elevation ($F_{(345, 1265)} = 1.7632$, $p < 0.001$), gradient ($F_{(230, 1380)} = 1.69$, $p < 0.001$) and position ($F_{(230, 1380)}=1.65$, $p < 0.001$), while light intensity was influenced by aspect ($F_{(575, 1035)} = 1.93$, $p < 0.001$) and position ($F_{(230, 1380)}=1.38$, $p < 0.001$). Northern slopes were hotter and lighter than other slopes, although south-facing slopes were also relatively warm. Low-lying areas were relatively humid compared to higher dunes. Slopes with mid-range steepness were generally more humid, but cooler than comparatively gentle and steep slopes. Valleys were generally more humid and darker than crests and slopes. For illustrative purposes, we presented one day's data for these significant cases (see Fig. 2).

Variability in soil pH was best explained by age in seral stage 2, and a model including aspect, elevation, and position in addition to age in seral stage 3 (ANCOVA and AIC; Table 3). However, none of the models significantly explained variability in soil C:N ratios (Table 3).

Dune topography and biotic variables

The 8,833 woody plants sampled in 106 quadrats comprised 7,122 canopy and 1,736 understory plants among 88 species. Variability in all woody plant variables was best explained by models that included age as a covariate within pooled seral stages, as was the case when seral stage 2 was treated separately (ANCOVA and AIC;

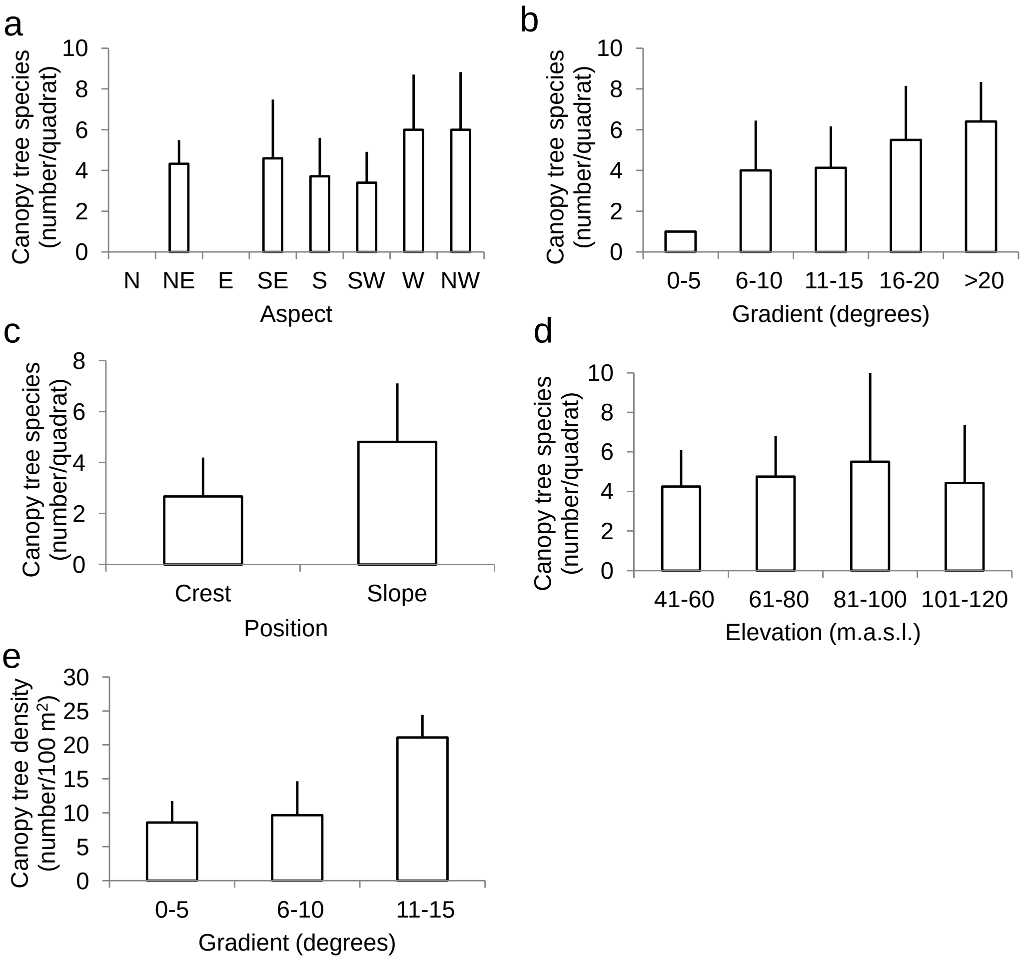

Figure 5-3. Mean ± one standard deviation of the mean of woody plant response variables presented as a function of those variables that best-explained their variability significantly despite stand age (see Table 2).

Table 5-3). The number of tree canopy species in seral stage 1 was best explained by a model including aspect, elevation, gradient, and position, but not age. There were more species on west- and northwest-facing slopes compared to south- and southwest-facing slopes (Fig. 3a), while relatively flat slopes had fewer species than other gradients (Figure 5-3b), as did crests relative to slopes (Fig. 3c). However, canopy tree species richness varied little with elevation (Fig. 3d). Tree density in seral stage 3 increased significantly with gradient (ANCOVA and AIC; Fig. 3e).

Only 11% of the variability in tree species abundances was explained by gradient in seral stage 2, although the NMDS plot was unconvincing of this separation (ANOSIM, $p < 0.05$, Fig.). Nevertheless, SIMPER analysis revealed consistent dominance by *Acacia karroo* Hayne and *Celtis africana* Burm.f. (contributing more than 80% of the community) across all gradients (Table 4). However, the number of species increased with gradient so that in addition to these two species, *Allophylus natalensis* Sond. (Dune False Currant) characterized slopes ranging from 0 to 15° and *Brachylaena discolor* DC. (Coast Silver-oak) those of 11 to 15°. Slopes of more than 15° were characterised by the addition of *Grewia occidentalis* L. (Cross-berry), *Chaetachme aristata* Planch. (Giant Pock Ironwood) and *Teclea gerrardii* I.Verd. (Zulu Cherry-orange), though all with less than a 5% contribution to tree communities on these slopes (Table 4).

Elevation explained 32% of the variability in understory species abundances in seral stage 3 (ANOSIM, $p < 0.05$, Fig.). However, this was the result of most cases representing mid-elevations of 41–60 m.a.s.l, with very few cases for other elevation categories. Nevertheless, these mid-elevations were dominated (61% contribution) by *Rhoicissus revoilii* Planch. (Bushveld grape), followed by *Scutia myrtina* Burm.F (Cat-thorn) that contributed 28%, and the invasive alien species, *Chromolaena odorata* L. (Triffid Weed), contributing 11% (Table 5). Elevations of 61–80 m.a.s.l. were dominated by *S. myrtina* alone (Table 5).

Millipede assemblages

We recorded 28,987 millipedes (28,351 cylindrical, 513 keeled, and 123 pill millipedes) from 16 species in 65 quadrats. The number of millipede species in the transects of seral stage 2 covaried with dune position (Table 3), whereby valleys had the most species, though that of slopes and crests did not differ from one another (Fig. 5). Models including age as a covariate in addition to variables of dune morphology best explained the density of cylindrical millipedes for pooled and separated seral stages. Pill millipede density was very low and also driven by rehabilitating stand age in combination with dune morphological variables for pooled as well as separate seral stages. The density of keeled millipedes for pooled seral stages was best explained by a model including aspect, elevation, gradient, and position, but not age (Table 3). These millipedes were most prolific in valleys (Fig. 5b), as well as east-facing slopes (Fig. 5c) with gradients steeper than 10° (Fig. 5d). However, we found little correlation between millipede communities and elevation (Fig. 5e), and when seral stages were separated age was included in the best-fit model (Table 3). Based on our ANOSIM analyses none of the variables of dune morphology significantly influenced species-specific millipede abundances.

Discussion

In line with our hypotheses, dune morphology modulated microclimatic conditions in a similar manner as reported for other studies (Tateno & Takeda 2003; Bennie et al. 2008). We acknowledge though, that the conditions on each dune face are likely the product of conditions ameliorated or exacerbated by surrounding dunes that have consequences for wind channelling and shading, thus cumulatively influencing microclimatic conditions. Contrary to our hypotheses, variability in soil nutrient concentrations was not explained by dune morphology, but rather by regeneration age. The processing of sand as part of the mining operation probably reshuffled soil nutrients and minerals that accumulate through natural processes. With only a few years of post-mining regeneration of biotic activity and mechanical processes (e.g. leeching) it is not surprising that soil fertility (C:N ratios) and pH levels are not yet conforming to expected spatially structured patterns induced by dune topography. Given the weak associations between topographic and abiotic variables, it is also not surprising that spatial variability in woody plant and millipede community structure could not be explained by topographic variables.

Species richness and density, as well as species-specific abundances of canopy trees and the understory varied with topography, as did millipede species richness, all in support of our formulated hypotheses, though with the caveat of an overriding influence of regeneration age. Keeled millipedes, a group of invertebrates associated with forests, also responded to topography, although cylindrical and pill millipedes did not. This suggests that forest specialists may be more sensitive to microhabitats induced by topography, but this requires further investigation.

Increasing slope steepness resulted in more dense woody plant canopies in stands older than 25 years, a finding similar to that of van Dyk (1996) for earlier stages of regeneration in the study area. Laurance et al. (1999) also described a decrease in the number of large trees with increased tree density on steep slopes. Although woody plant communities of different gradients in stands of 11-25 years were generally dominated by similar sets of forest tree species, species composition varied with the gradient of slopes. Incidentally, the majority of these dominant species were identified by Grainger (2012) as species that could colonize newly formed gaps in the woodland. This was likely due to their wide tolerance to irradiance, temperatures, and moisture that change along dune slopes with elevation and gradient (Ritter et al. 2005). Species abundances of canopy and understory communities responded to different gradients in stands of 11-25 years, and elevation in stands of >25 years, respectively. The number of canopy species, though not their abundances, was best explained by aspect, elevation, gradient, and position in stands younger than 11 years, suggesting that dune morphology may provide habitat conditions that support different species in the early stages of succession when conditions are likely to be most harsh.

Millipede variables also responded to age and dune morphology. Explanatory models for cylindrical and pill millipede density included age as a covariate. These relationships are likely the result of age-related increases in woodland complexity (Kritzinger & van Aarde 1998), moisture-retention and nutrient accumulation associated with litter accumulation (van Aarde et al. 1998) and the modulation of microclimate by topography as discussed above. As in Greyling et al. (2001), two closely related cylindrical millipedes (Centrobolidae) dominated these new-growth forests. This may have obscured patterns in species-specific abundances related to topography. However, the number of millipede species covaried with position on the dune face in stands of 11-25 years, whereby valleys supported more millipede species than slopes and crests. When considering the microclimatic data, this likely relates to the moderate temperature and light intensities but relatively humid conditions that existed in the valleys in comparison with ambient conditions such as wind and high temperatures. Keeled millipedes responded to topographic variables independent of age and this likely relates to the provision of microhabitats for this relatively small, forest-associated species and justifies further study.

Despite the idiosyncratic responses by woody plants and millipedes, position on the dune, as well as aspect, elevation and gradient of the dune face contributed to age-related changes in community structure. Our study also suggests that due to its modulation of microclimatic conditions, dune topography provides habitats conducive to forest-associated species that have narrow climatic habitat tolerances. This suggests that even though these new-growth forests are in transition, topography may influence the structure and composition of biological communities of new-growth forests, especially when acting in concert with other site-level factors. Such factors are likely to include those previously identified as determinants of community structure and composition, such as landscape composition (Grainger et al. 2011), and age (Wassenaar et al. 2005; Grainger & van Aarde 2012a).

The role of dune morphology seems more obvious in well-established ecosystems (Chen et al. 1997; Oliviera-Filho et al. 1998; Tateno & Takeda 2003; Larkin et al. 2006), than the new-growth forests that we studied, where age explained changes in assemblages better than topography. Dune topography shaped as part of the rehabilitation procedure provides for the topography that influences local conditions and therefore possibly for ecosystem patterns and processes in a set manner according to prevailing climatic conditions. Topographically, these dunes may differ from those shaped by natural forces (wind, water) which will probably affect patterns and processes. However, these differences may be negligible and therefore not be reflected in biological patterns, especially during the early stages of succession-driven forest regeneration where most community variables vary with regeneration age.

For instance, age-related increases in habitat complexity provide an increasing variety of conditions that accommodate more animal species and associated ecological processes (Kritzinger & van Aarde 1998; Wassenaar et al. 2005). For example, increased plant diversity, tree senescence and the associated development of a litter layer, increased soil water retention, and nutrient accumulation would presumably benefit millipede communities (e.g. Scheu & Schaefer 1998; Greyling et al. 2001; Berg & Hemerik 2004). In conclusion, topography matters, more so for specialists than generalists. Response to topographic variability is clearly species-specific and not necessarily reflected at the community level.

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References

Acosta A, Ercole S, Stanisci A, De Patta Pillar V, Blasi C (2007) Coastal vegetation zonation and dune morphology in some Mediterranean ecosystems. Journal of Coastal Research 23:1518-1524.

Ashwini KM, Sridhar KR (2008) Distribution of Pill Millipedes (Arthrosphaera) and Associated Soil Fauna in the Western Ghats and West Coast of India. Pedosphere 18:749-757.

Bennie J, Huntley B, Wiltshire A, Hill MO, Baxter R (2008) Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. Ecological Modeling 216:47-59.

Berg MP, Hemerik L (2004) Secondary succession of terrestrial isopod, centipede, and millipede communities in grasslands under restoration. Biology of Fertile Soils 40: 163-170.

Burnett MR, August PV, Brown JH, Jr., Killingbeck KT (1998) The Influence of Geomorphological Heterogeneity on Biodiversity -I. A Patch-Scale Perspective. Conservation Biology 12:363-370.

Chen ZS, Hsieh CF, Jiang FY, Hsieh TH, Sun IF (1997) Relations of soil properties to topography and vegetation in a sub-tropical rain forest in Southern Taiwan. Plant Ecology 132:229-241.

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117-143.

da Silva WG, Metzger JP, Bernacci LC, Catharino ELM, Durigan G, Simoes S (2008) Relief influence on tree species richness in secondary forest fragments of Atlantic Forest, SE, Brazil. Acta Botanica Brasilica 22:589-598.

David JF, Gillon D (2009) Combined effects of elevated temperatures and reduced leaf litter quality on the life-history parameters of a saprophagous macroarthropod. Global Change Biology 15:156-165.

Dobson AP, Bradshaw AD, Baker AJM (1997) Hopes for the Future: Restoration Ecology and Conservation Biology. Science 277:515-522.

Furley PA, Newey WW (1979) Variations in Plant Communities With Topography Over Tropical Limestone Soils. Journal of Biogeography 6:1-15.

Grainger,MJ (2011) An evaluation of coastal dune forest rehabilitation through ecological succession. Dissertation. University of Pretoria.

Grainger,MJ (2012) An evaluation of coastal dune forest rehabilitation through ecological succession. Dissertation. University of Pretoria.

Grainger MJ, van Aarde RJ (2011) Does succession drive the restoration of a coastal dune forest. Restoration Ecology.

Grainger MJ, van Aarde RJ, Wassenaar TD (2011) Landscape composition influences the restoration of subtropical coastal dune forest. Restoration Ecology 19:111-120.

Greyling MD, van Aarde RJ, Ferreira SM (2001) Seasonal changes in habitat preferences of two closely related millipede species. African Journal of Ecology 39:51-58.

Kritzinger JJ, van Aarde RJ (1998) The bird communities of rehabilitating coastal dunes at Richards Bay, KwaZulu-Natal. South African Journal of Science 94:71-78.

Kubota Y, Murata H, Kikuzawa K (2004) Effects of topographic heterogeneity on tree species richness and stand dynamics in a subtropical forest in Okinawa Island, southern Japan. Journal of Ecology 92:230-240.

Larkin D, Vivian-Smith G, Zedler JB (2006) Topographic Heterogeneity Theory and Ecological Restoration. Pages 142-164 In: D. A. Falk, M. A. Palmer, and J. B. Zedler, editors (ed.) Foundations of Restoration Ecology. Island Press,pp Pages 142-164

Laurance SGW, Laurance WF, Andrade A, Fearnside PM, Harms KE, Vicentini A, Luizao RCC (2010) Influence of soils and topography on Amazonian tree diversity: a landscape-scale study. Journal of Vegetation Science 21:96-106.

Laurance WF, Fearnside PM, Laurance SG, Delamonica P, Lovejoy TE, Rankin-de Merona JM, Chambers JQ, Gascon C (1999) Relationship between soils and Amazon forest biomass: a landscape-scale study. Forest Ecology and Management 118:127-138.

Lawes MJ (1990) The distribution of the samango monkey (Cercopithecus mitis erythrarchus Peters, 1852 and *Cercopithecus mitis labiatus* I, Geoffrey, 1843) and forest history in southern Africa. Journal of Biogeography 17:669-680.

Loranger-Merciris G, Imbert DB-R, Lavelle P, Ponge JF (2008) Litter N-content influences soil millipede abundance, species richness and feeding preferences in a semi-evergreen dry forest of Guadeloupe (Lesser Antilles). Biology and Fertility of Soils 45:93-98.

MacMahon JA, Holl KD (2001) Ecological restoration: a key to conservation biology's future. Pages 245-269 In: M. E. Soule and G. H. Orians, editors (ed.) Conservation biology: research priorities for the next decade. Island Press, Washington, United States of America: pp Pages 245-269

Martínez ML, Vásquez G, Sánchez CS (2001) Spatial and temporal variability during primary succession on tropical coastal sand dunes. Journal of Vegetation Science 12:361-372.

Moir ML, Brennan KEC, Harvey MS (2009) Diversity, endemism and species turnover of millipedes within the south-western Australian global biodiversity hotspot. Journal of Bioegeography 36:1958-1971.

Nichols WF, Killingbeck KT, August PV (1998) The Influence of Geomorphological Heterogeneity on Biodiversity II. A Landscape Perspective. Conservation Biology 12:371-379.

Oliviera-Filho AT, Curi N, Vilela EA, Carvalho DA (1998) Effects of canopy gaps, topography, and soil on the distribution of woody species in a central Brazilian deciduous dry forest. Biotropica 30:362-375.

Palik BJ, Goebel PC, Kirkman LK, West L (2000) Using landscape hierarchies to guide restoration of disturbed ecosystems. Ecological Applications 10:189-202.

Porter, K., R. J. van Aarde, and T. D. Wassenaar. 2007. Millipede Identification Catalogue. Unpublished Report, University of Pretoria.

Rands MRW (2012) Biodiversity conservation: Challenges beyond 2010. Science 329:1298-1303.

Ritter E, Dalsgaard L, Einhorn KS (2005) Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. Forest Ecology and Management 206:15-33.

Tateno R, Takeda H (2003) Forest structure and tree species distribution in relation to topography-mediated heterogeneity of soil nitrogen and light at the forest floor. Ecological Research 18:559-571.

Scheu S, Schaefer M (1998) Bottom-up control of the soil macrofauna community in a beechwood on limestone: manipulation of food resources. Ecology 79: 1573-1585.

van Aarde RJ, Ferreira SM, Kritzinger JJ (1996a) Millipede communities in rehabilitating coastal dune forests in northern KwaZulu-Natal, South Africa. Journal of Zoology, London 238:703-712.

van Aarde RJ, Ferreira SM, Kritzinger JJ (1996b) Successional changes in rehabilitating coastal dune communities in northern KwaZulu-Natal, South Africa. Landscape and Urban Planning 34:277-286.

van Aarde RJ, Ferreira SM, Kritzinger JJ, van Dyk PJ, Vogt M, Wassenaar TD (1996c) An evaluation of habitat rehabilitation on coastal dune forests in Northern KwaZulu-Natal, South Africa. Restoration Ecology 4:334-345.

van Aarde RJ, Smit AM, Claasens AS (1998) Soil characteristics of rehabilitating and unmined coastal dunes at Richards Bay, Kwazulu-Natal, South Africa. Restoration Ecology 6:102-110.

van Dyk PJ (1996) The population biology of sweethorn *Acacia karroo* in rehabilitating coastal dune forests in northern KwaZulu-Natal, South Africa. Dissertation. University of Pretoria, Pretoria, South Africa.

van Wyk AE, Smith GF (2001) Floristic and succulent riches in southern Africa: a review of centres of endemism, Umdaus Press, Pretoria, South Africa.

Wassenaar TD, van Aarde RJ, Pimm SL, Ferreira SM (2005) Community convergence in disturbed subtropical dune forests. Ecology 86:655-666.

Weiss SB, Murphy DD (1990) Thermal microenvironments and the restoration of rare butterfly habitat. Pages 50-60 In: J. J. Berger, editor (ed.) Environmental restoration: Science & Strategies for Restoring the Earth. Island Press, CA, USA: pp Pages 50-60

Weisser PJ, Marques F (1979) Gross vegetation changes in the dune area between Richards bay and the Mfolozi River, 1937 - 1974. Bothalia 12**:**711-721.

Tables

Table 1 Key questions and hypotheses of this study

Key question	General assumptions	Hypotheses	Examples from the literature
1. Does dune topography influence abiotic conditions?	Dune topography modulates microclimatic conditions	Irradiation, temperature and humidity may increase or decrease, depending exposure to wind and sun that is facilitated or eased by dune aspect, elevation, and position	(Tateno & Takeda 2003; Bennie et al. 2008)
	Dune topography influences soil nutrient availability	Soil carbon-to-nitrogen ratio and soil pH will be greater in valleys and at low elevations	(Chen et al. 1997; Tateno & Takeda 2003)
2. Does dune topography influence biotic conditions?	Dune topography influences woody plant community structure and distribution	• Woody plant richness will depend on aspect, elevation and position depending on their exposure to wind • Woody plant canopy structure will depend on gradient and position • Species-specific woody plant abundances will differ based on dune morphology and position	(van Dyk 1996; Oliviera-Filho et al. 1998; da Silva et al. 2008; Laurance et al. 2010)
	Dune topography influences millipede community structure and distribution	• Millipede richness, as well as taxon-specific density may be influenced by aspect, elevation, and position depending on their exposure to wind and sunlight • Species-specific millipede abundances will differ based on dune morphology and position	(Weiss & Murphy 1990; Moir et al. 2009)

Table 2 Definitions of response variables

Variable			Definition and units
Response variables	Microclimate	Temperature	Ambient temperature measured in degrees Celsius (°C)
		Relative humidity	The partial pressure of water vapor measured as a percentage (%) of the saturated vapor pressure
		Light intensity	Incident sunlight, measured as luminous power per area (illuminance) in lumens (lux)
	Soil	Soil pH	Soil acidity
		Soil C:N	Carbon and nitrogen percentage content in soil samples presented as a ratio of carbon-to-nitrogen
	Woody plants	Canopy tree species	Total number of species forming the canopy (height class 2-5, referred to as trees) per quadrat
		TH	Mean tree height (TH) class (2 [>2–4 m], 3 [>4–6 m], 4 [>6–8 m], and 5[>8 m]) of each quadrat
		CBH	Per-quadrat mean circumference at breast height (CBH), measurement carried out on all trees (height class 2-5) at ~1.4 m above ground
		Canopy tree density	Number of trees per100 m^2, calculated for each quadrat
		Understory species	Total number of species making up the understory (height class 1 [0-2m], referred to as understory plants) per quadrat
		Understory density	Number of understory plants per100 m^2 calculated for each quadrat
	Millipedes	Millipede species	Total number of millipede species per quadrat
		Cylindrical density	Number of *Centrobolus* spp., *Doratagonus* sp., *Spinotarsus anguiliferus,* and *Spirostreptidae* spp. per 100 m^2 calculated for each quadrat
		Keeled density	Number of *Gnomeskelus tuberosus* individuals per 100 m^2 calculated for each quadrat
		Pill density	Number of *Sphaerotheridae* spp. individuals per 100 m^2 calculated for each quadrat

Table 3 Dune morphological variables included in the most parsimonious models (based on Akaike Information Criteria (AIC) scores) explaining variance in abiotic and biotic variables for each of three seral stages and pooled stages, as well as the significance of the model ($p < 0.05$). Those response variables that were explained by dune morphological variables in the absence of age are highlighted in boldface text.

	Response variables	Seral stage	Explanatory variables: Dune morphology					ANCOVA results		
			Aspect	Elevation	Gradient	Position	Age	*df*	AIC	P
Soil	Soil pH	1	Insufficient cases							
		2					X	1	54.35	0.0005
		3	X	X		X	X	12	13.73	< 0.0001
		Pooled					X	1	157.54	< 0.0001
	Soil C:N	1	Insufficient cases							
		2			**X**			**4**	**284.46**	**0.119**
		3					X	1	186.59	0.745
		Pooled					X	1	542.26	0.778
Woody plants	Mean canopy height	1	X	X			X	9	23.03	< 0.0001
		2		X			X	5	23.77	< 0.001
		3	X		X	X	X	12	46.27	< 0.001
		Pooled		X			X	5	236.79	0.024
	Mean canopy tree CBH	1	X	X		X	X	10	158.23	< 0.0001
		2					X	1	280.81	< 0.001
		3	X		X		X	10	229.17	< 0.001
		Pooled	X	X	X		X	16	787.49	< 0.001
	Number of species in canopy	**1**	**X**	**X**	**X**	**X**		**13**	**125.49**	**0.002**
		2		X			X	5	195.20	< 0.001
		3			X		X	3	169.77	0.015
		Pooled		X		X	X	7	528.67	< 0.001

		1					X	1	-10.80	0.009
	Mean canopy tree density	2	X	X	X		X	15	-120.87	< 0.001
		3			**X**			**2**	**-120.89**	**0.0004**
		Pooled	X	X		X	X	14	-155.73	< 0.001
		1	X	X	X	X	X	14	97.78	0.009
	Number of species in understory	2			X		X	5	105.12	< 0.001
		3			X	X	X	5	57.26	0.0006
		Pooled	X		X		X	12	289.13	0.0008
		1					X	1	74.66	0.679
	Mean understory density	2	X	X	X		X	15	-171.69	< 0.001
		3					X	1	-113.38	0.0005
		Pooled					X	1	-305.24	0.003

Millipedes	Number of species	1	Insufficient cases							
		2				**X**		**2**	**126.00**	**0.016**
		3	X	X	X	X	X	14	83.35	< 0.001
		Pooled				X	X	3	271.23	< 0.001
	Cylindrical millipede density	1	Insufficient cases							
		2		X			X	6	92.18	< 0.0001
		3	X	X		X	X	13	-18.05	< 0.001
		Pooled	X	X	X	X	X	20	183.63	<0.001
	Keeled millipede density	1	Insufficient cases							
		2	X	X	X	X	X	15	-114.18	< 0.0001
		3	X	X		X	X	12	-96.33	0.0004
		Pooled	**X**	**X**	**X**	**X**		**9**	**-235.50**	**< 0.001**
	Pill millipede density	1	Insufficient cases							
		2	X	X	X		X	14	-221.88	0.004
		3	X		X	X	X	12	-110.06	0.0001
		Pooled	X	X	X		X	18	-400.40	< 0.001

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Table 4 Characteristic tree species (taller than 2 m) forming the canopies on slopes of different gradients in seral stage two based on similarity percentage analysis (SIMPER).

Species	Family	Average abundance	Average similarity	Similarity SD	Percentage contribution	Cumulative percentage
0-5 degree slope						
Average similarity: 54.91						
Acacia karroo Hayne	Mimosaceae	3.26	39.44	6.11	71.83	71.83
Celtis africana Burm.f.	Celtidaceae	0.92	7.70	1.12	14.02	85.85
Allophylus natalensis Sond.	Sapindaceae	0.76	4.90	0.88	8.93	94.78
6-10 degree slope						
Average similarity: 48.96						
Acacia karroo	Mimosaceae	3.39	35.83	2.44	73.18	73.18
Allophylus natalensis Sond.	Sapindaceae	0.70	4.41	0.98	9.01	82.19
Celtis Africana Burm.f.	Celtidaceae	0.99	3.32	0.78	6.78	88.97
Cestrum laevigatum Schltdl.	Solanaceae	0.52	1.19	0.41	2.42	91.39
11-15 degree slope						
Average similarity: 52.42						
Acacia karroo Hayne	Mimosaceae	3.44	40.69	4.33	77.62	77.62
Celtis Africana Burm.f.	Celtidaceae	0.70	3.71	0.72	7.07	84.70
Brachylaena discolour (DC.)	Asteraceae	0.35	1.67	0.45	3.19	87.89
Allophylus natalensis Sond.	Sapindaceae	0.47	1.54	0.37	2.94	90.82
16-20 degree slope						

Average similarity: 50.52						
Acacia karroo Hayne	Mimosaceae	3.49	26.86	4.48	53.17	53.17
Celtis Africana Burm.f.	Celtidaceae	2.08	14.93	5.77	29.55	82.72
Grewia occidentalis L.	Tiliaceae	0.87	2.47	0.56	4.89	87.61
Chaetachme aristata Planch.	Ulmaceae	0.55	1.03	0.37	2.04	89.66
Teclea gerrardii I.Verd.	Rutaceae	0.30	0.87	0.39	1.72	91.38
>20 degree slope						
Less than two samples in a group						

Table 5 Characteristic species occurring in the understory of each elevation category within seral stage three based on similarity percentage analysis (SIMPER).

Species	Family	Average abundance	Average similarity	Similarity SD	Percentage contribution	Cumulative percentage
21-40 m.a.s.l.						
Less than 2 samples in group						
41-60 m.a.s.l.						
Average similarity: 44.51						
Rhoicissus revoilii Planch.	Vitaceae	1.49	27.25	1.10	61.23	61.23
Scutia myrtina Burm.F.	Rhamnaceae	0.95	12.50	0.69	28.09	89.32
Chromolaena odorata L.	Asteraceae	0.57	4.75	0.46	10.68	100.00
61-80 m.a.s.l.						
Average similarity: 30.00						
Scutia myrtina Burm.F.	Rhamnaceae	0.87	30.00	0.76	100.00	100.00

Figures

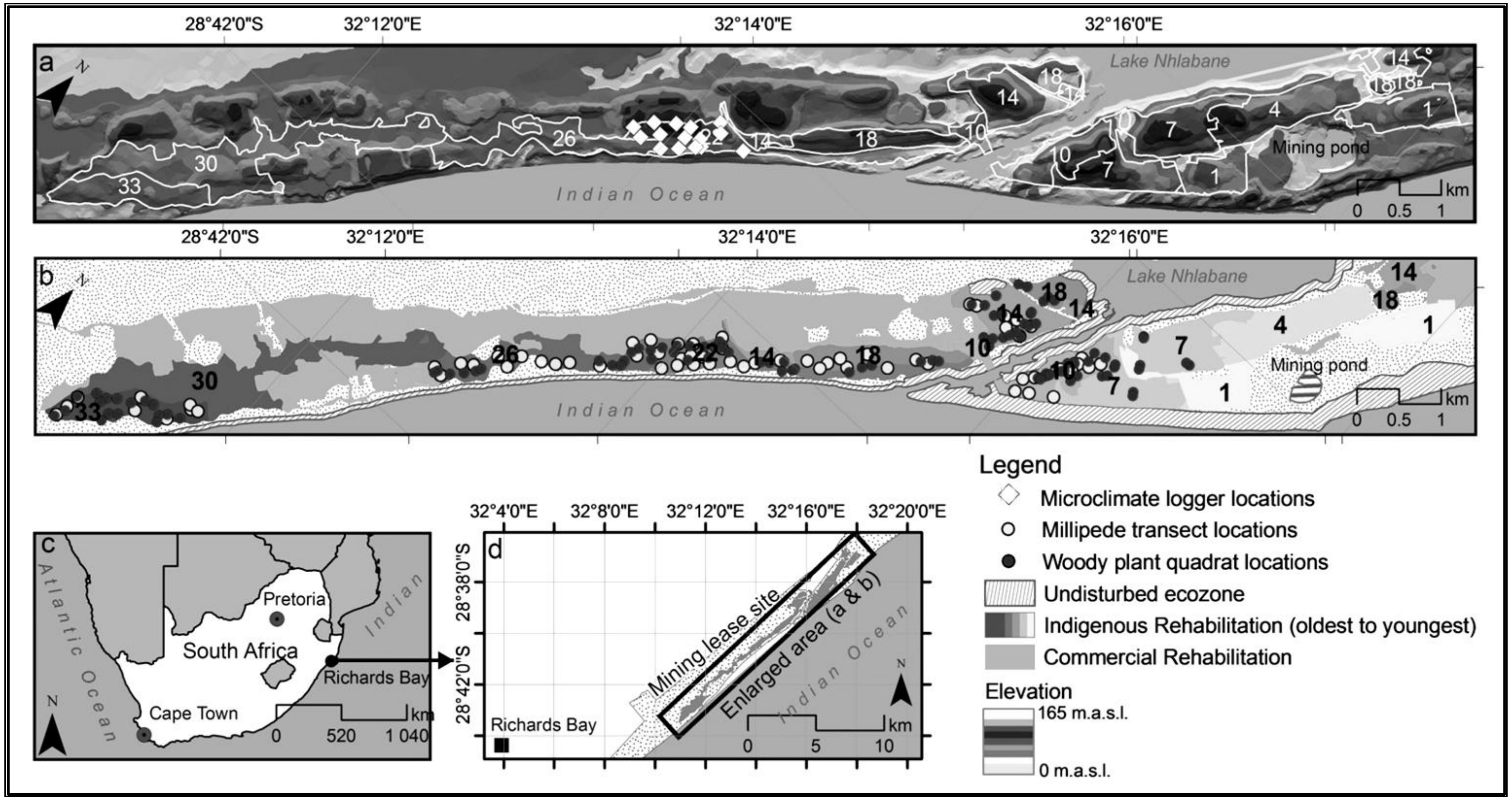

Fig. 1 Digital elevation model of the study area also showing the delineation of rehabilitating stands according to age, and the sites where data loggers were deployed (a). The locations of woody plant quadrats and millipede transect surveys were conducted are shown in relation to stand age (b). Inset maps provide geographical context (c & d).

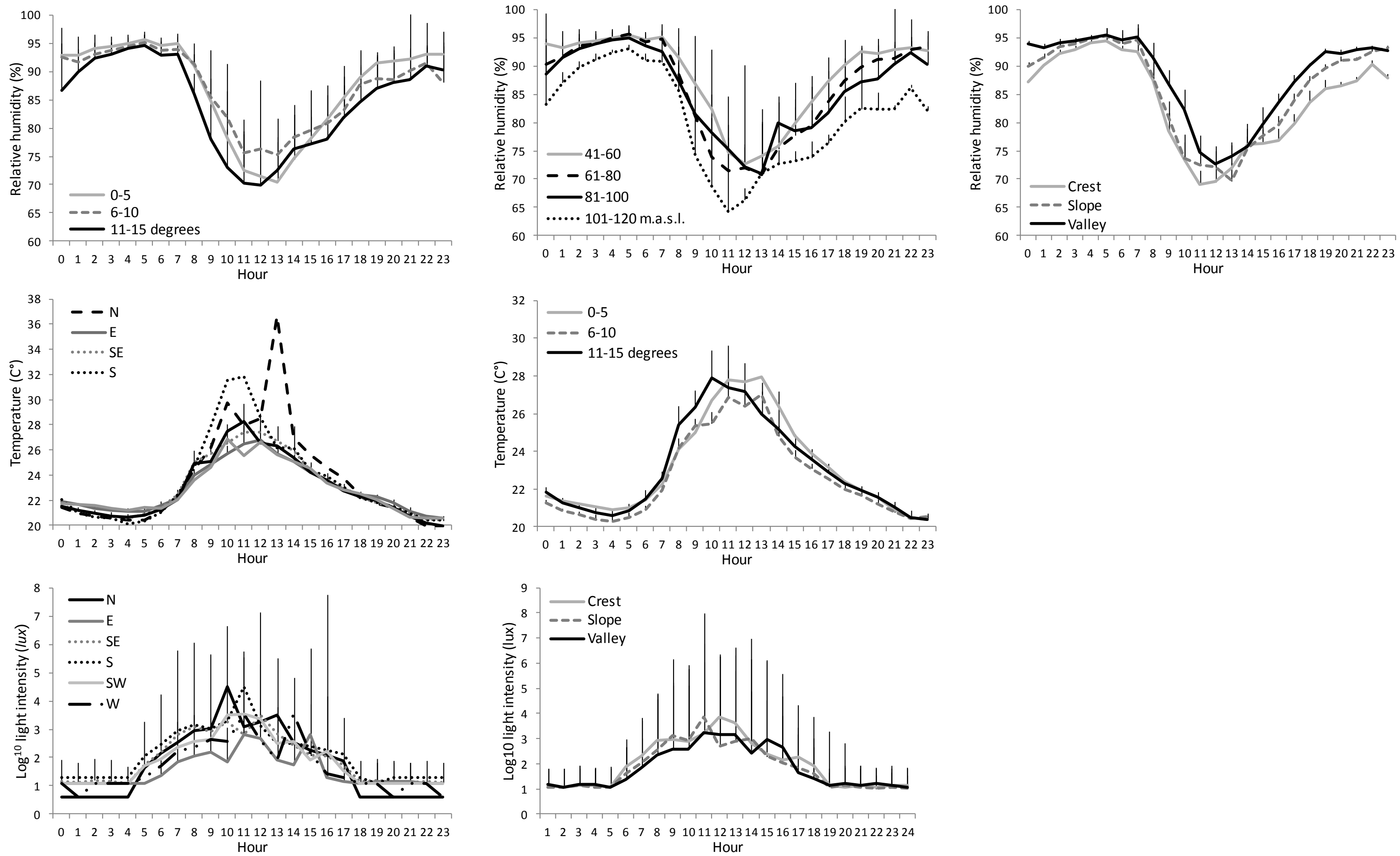

Fig. 2 Mean ± one standard deviation of the mean of three microclimatic variables (relative humidity, temperature, and light intensity, from top to bottom, respectively) that showed significant responses to variables of dune morphology according to the repeated measures ANOVA, as recorded between 01h00 and 24h00 on the 29th of January 2011.

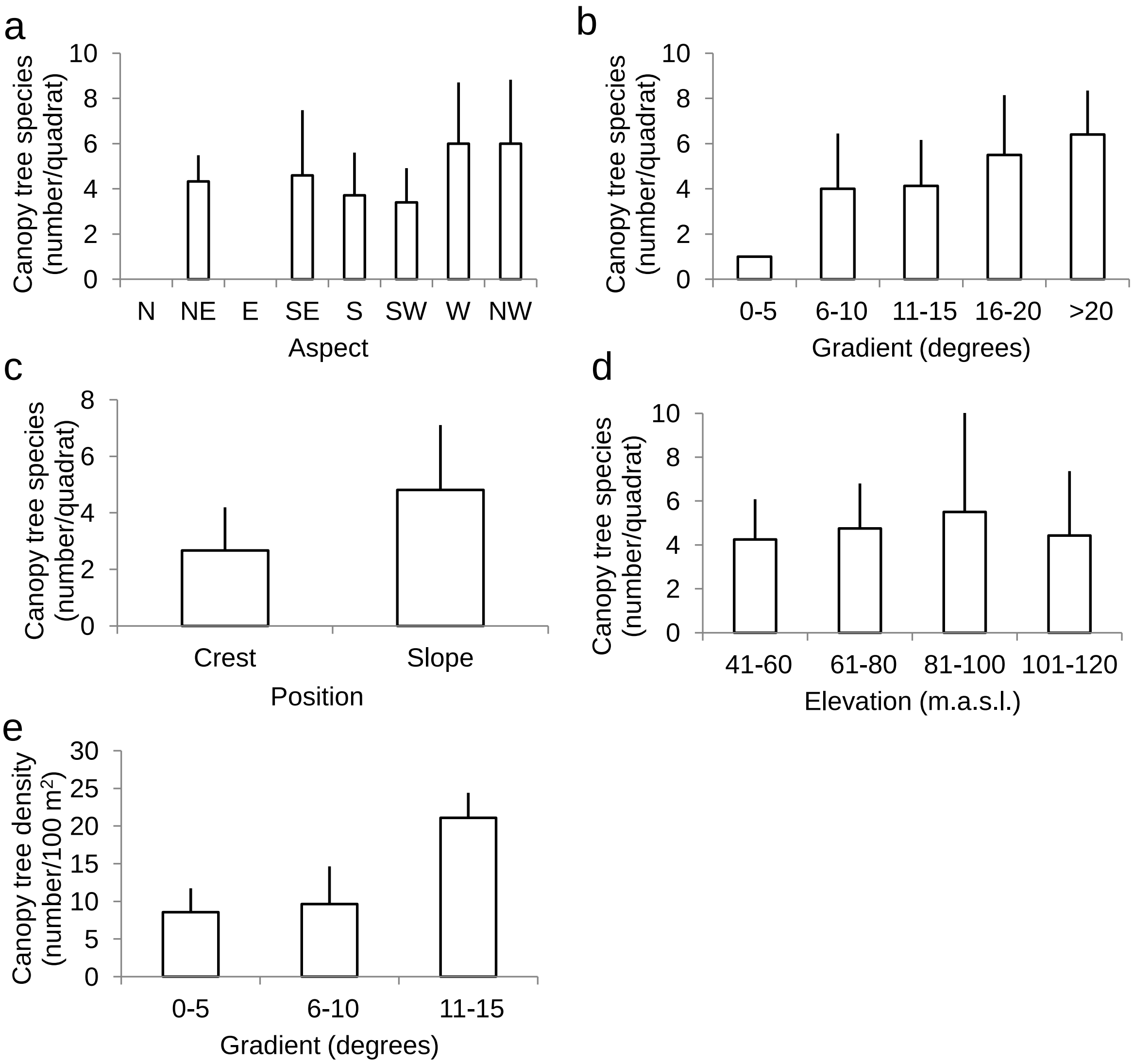

Fig. 3 Mean ± one standard deviation of the mean of woody plant response variables presented as a function of those variables that best-explained their variability significantly despite stand age (see Table 2).

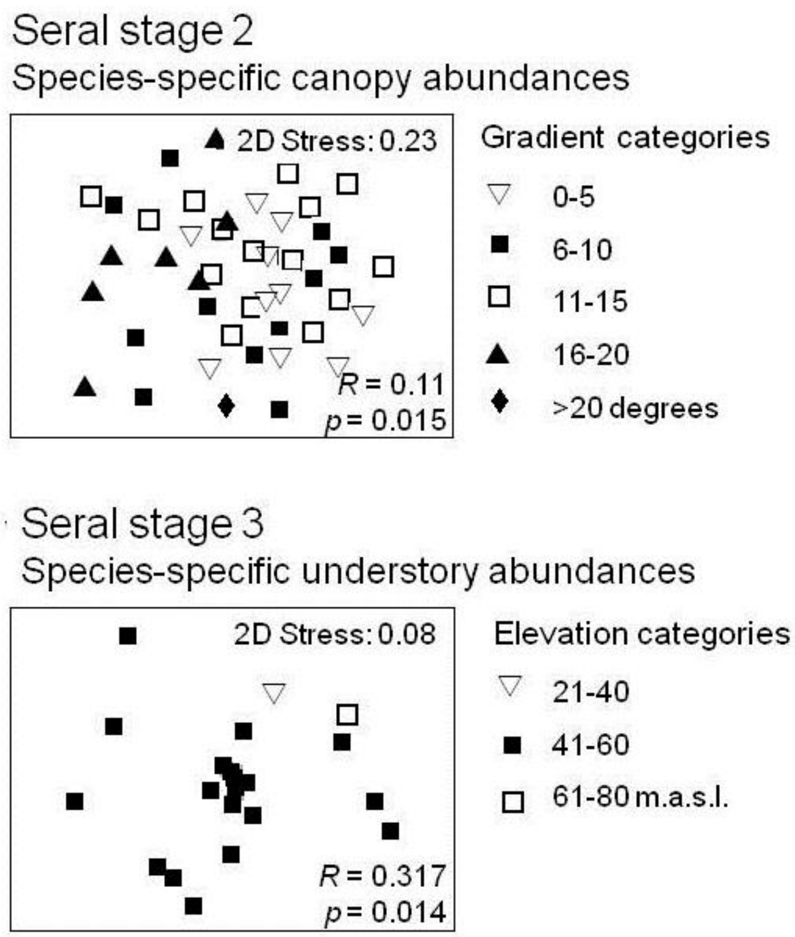

Fig. 4 Non-metric multi-dimensional scaling (NMDS) plots of woody plant abundances in the canopy (top) and understory (bottom) where analysis of similarity revealed significant ($p < 0.05$) community separation attributable to dune morphological characteristics (elevation, gradient, position) according to seral stages two (11-25) and three (>25 years), respectively.

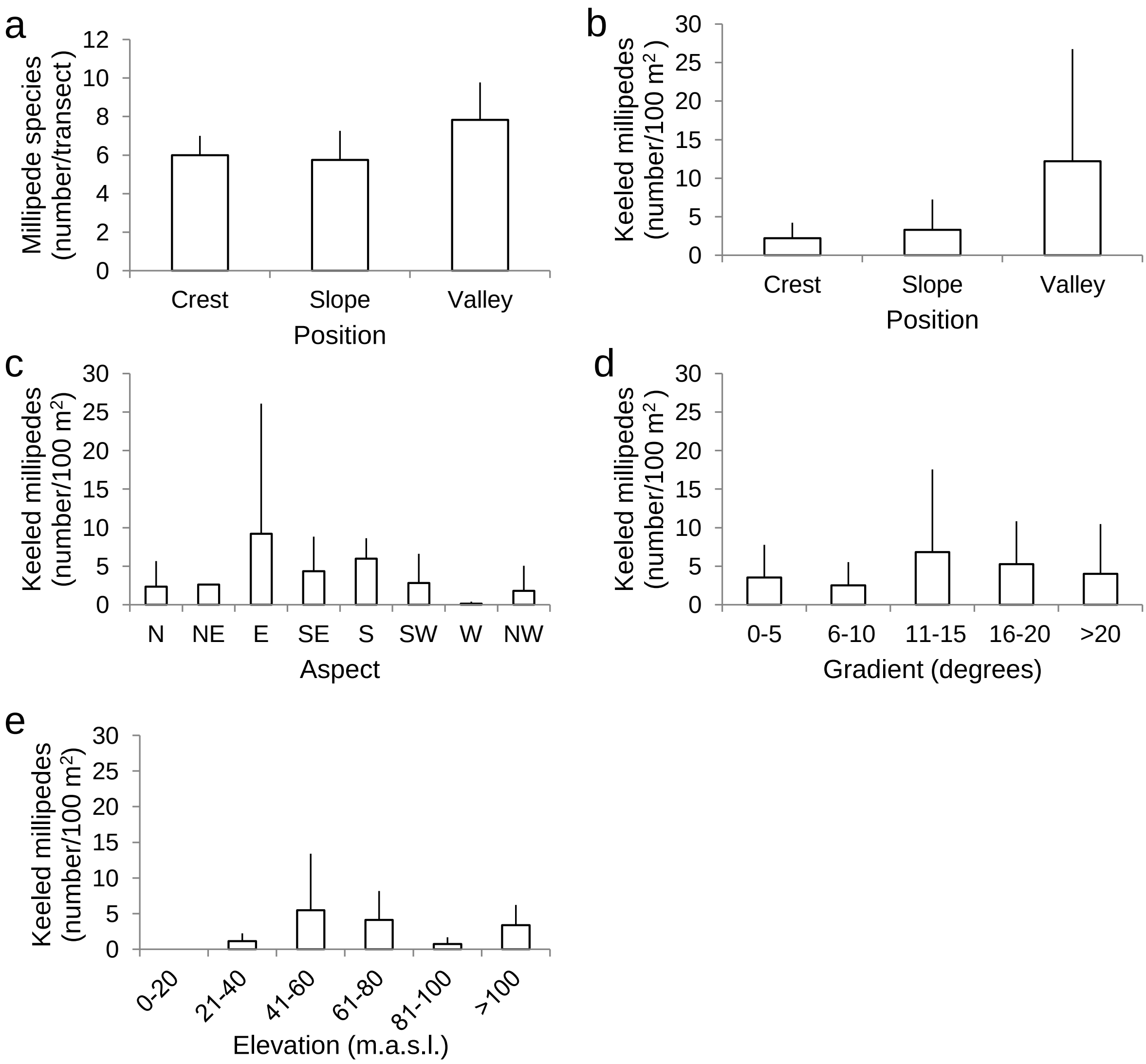

Fig. 5 Mean ± one standard deviation of the mean of millipede response variables presented as a function of those variables that best-explained their variability significantly despite stand age (see Table 2).