

Do insect distributions fit our biomes?

S. Proches^{a,b} and R.M. Cowling^{a*}

An assessment of biome-specificity in southern African insect assemblages was undertaken using sweep collections in fynbos, grassland, subtropical thicket and Nama-karoo. Insect samples from the same biome generally cluster together in multidimensional scaling analyses, although there is a great variability between sites within each biome. Rich and distinctive insect faunas exist in each biome, including fynbos. In the Baviaanskloof Conservation Area of the southeastern Cape, where the four biomes marginally co-occur, some insect assemblages are enriched relative to sites at the core of the biomes, presumably through the mixing of faunas via transient or persistent establishment of populations recruited from adjacent biomes.

Introduction

South Africa has a relatively long tradition of recognizing biomes—high-order vegetation categories delimited on the basis of growth form mix and prevailing climate.^{1,2} Recent vegetation categorization for the country is firmly nested within these biome concepts.^{2,3} While some changes to biome concepts have occurred recently,³ most of the concepts can be regarded as stable.

The question arises: to what extent does the South African biota follow biome boundaries, given that they are delimited using non-taxic criteria? There is good evidence that some biomes represent centres of endemism for plant taxa, while others, such as the Nama-karoo, have transitional floras.⁴ It has been shown that the broad-scale distribution of other groups of organisms also tends to respect biome borders; regional assemblages of terrestrial vertebrates are to a great extent biome-specific^{5–8} (but see the case of taxa of aquatic affinities, where faunistic provinces are not congruent with biome delimitations⁹).

Comparing the structure of insect communities of southern African biomes has attracted only limited interest.^{10–12} Insects are particularly relevant in biome comparisons, since a large proportion of them may be host-specific herbivores, which is likely to make them vegetation-specific. On the other hand, assuming that there are biome-specific insect faunas, the high mobility and frequent dispersal events characteristic of winged

species may lead to an intermixing of the insect faunas specific to various biomes, either by tracking populations of interdigitating plant species, or by transient establishment at least around biome borders.

In a previous study,¹⁰ we collected data to compare insect diversity in fynbos and three neighbouring biomes. Here we use that data set to assess the compositional similarities and differences between the insect assemblages from those biomes, both in core localities and where they co-occur in the southeastern Cape, a region of complex biome interdigitation.¹³ Specifically, we tested the hypothesis that site richness would peak at the marginal biome sites, owing to the establishment of populations of species recruited from adjacent biomes. Enrichment due to transient establishment is referred to as the 'mass effect'.¹⁴

Methods

The study included sweep insect collections in 10 × 10 m plots, located in the core regions of the fynbos, grassland, subtropical thicket, and Nama-karoo biomes, and in the Baviaanskloof Conservation Area of the southeastern Cape, where all four biomes co-occur (Fig. 1). For comparison purposes, all plant species in every plot were also listed. In each of the eight sites, we sampled eight plots, in a spatial layout designed to cover assemblage variation across several spatial scales, from 10 m to 1 km.¹⁰ Collections were conducted in late morning, during the season of maximum biological activity at each site (February in core grassland, April in core Nama-karoo, October in the Baviaanskloof and core fynbos, and December in core thicket). Year-round collections in the Baviaanskloof¹⁰ indicate that peak-season collections cover the total diversity of insects reasonably well, but this may vary from site to site, and insects occurring seasonally may be under-represented at some sites. It could also be argued that sweep-net collections are more efficient in grassland, Nama-karoo and fynbos than in thicket. Species accumulation curves (not presented) suggest that this did not result in a serious bias in our samples, but these caveats need to be kept in mind when interpreting the data.

The complete data set we analysed included 636 insect species from eighteen orders (all major insect groups; see Table 1), but, because of the collection method, some functional groups are under-represented (for instance, soil insects and active flyers).

To illustrate the relationships (shared species) between the plant and insect assemblages of the four biomes, we used non-metric multidimensional scaling (MDS) analyses (samples clustered based on a Bray–Curtis dissimilarity matrix–group average linkage, PRIMER 6.2.4, 2001). This method provides a convenient way of representing visually the similarities and differences between the species assemblages, but without attaching a specific meaning to the graph axes.¹⁵

To search for a potential species enrichment effect in the southeastern Cape, we used untransformed abundance data to compute a predicted species richness indicator (ICE; EstimateS 6.0b1¹⁶), which we then regressed against the observed species

^aBotany Department, Nelson Mandela Metropolitan University, P.O. Box 77000, Port Elizabeth 6031, South Africa.

^bCentre for Invasion Biology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa.

*Author for correspondence. E-mail: rmc@kingsley.co.za

Table 1. Number of insect species collected in the four biomes,¹⁰ in the Baviaanskloof (B), and in the core area of each biome (C).

	Fynbos		Grassland		Thicket		Karoo		Total
	B	C	B	C	B	C	B	C	
Coleoptera	38	14	28	18	30	62	13	8	168
Hymenoptera	40	34	47	39	17	41	21	14	162
Hemiptera	27	20	35	19	20	24	21	17	129
Diptera	21	10	23	21	3	4	3	2	65
Other orders	26	16	22	26	14	27	18	14	113
All insects	152	97	155	123	84	158	76	55	636

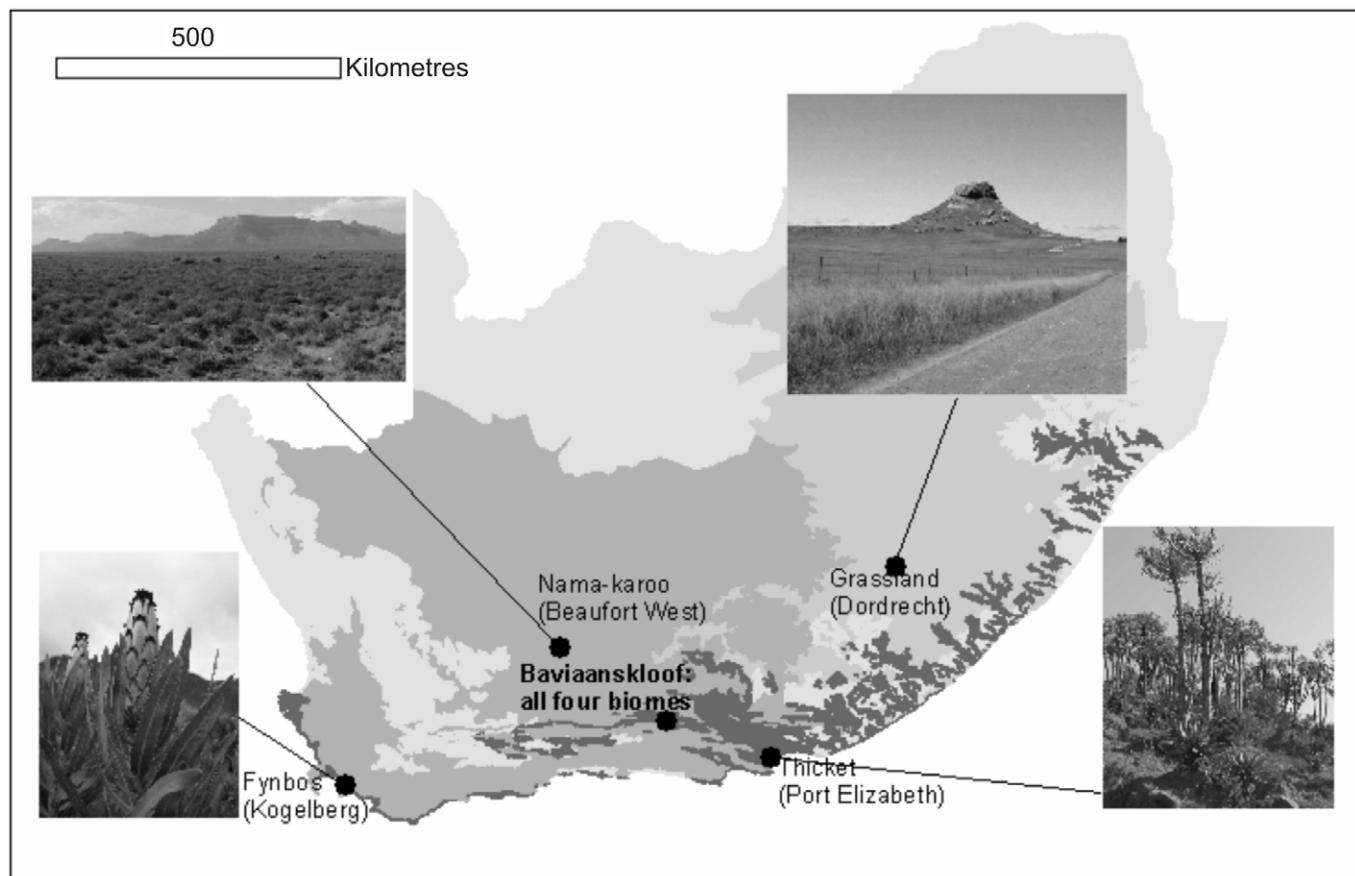


Fig. 1. Map of the collection localities.

richness values. If the predicted total species numbers in the Baviaanskloof sites were higher than in the core biome areas for a given observed number of species (owing to fewer individuals/species), then this provides support for the hypothesis that in the Baviaanskloof more insects are interlopers from other vegetation types, and therefore a species enrichment results from faunal mixing—a consequence of biome interdigitation.

Results and discussion

The MDS analysis for plants (Fig. 2a) had the tightest clustering. In all MDS analyses, the plots from each site and biome were clustered together, and seldom mixed with other sites/biomes (Fig. 2). The tightest clustering, and the lowest stress factor, were those observed for plants. The analysis for all insect species (Fig. 2b) thus had a high stress value, which would normally render the resulting plot unusable.¹⁵ However, the great similarity between this and the other MDS analyses (Fig. 2a, c, d), which had low stress values, suggests that this plot is a reasonably good representation of the relationships between samples, and can be further interpreted.

Clustering across sites was weakest for the thicket biome, where samples from the core and marginal sites were sometimes interspersed. This effect could be attributed to the closer proximity of the Baviaanskloof area to the Port Elizabeth site selected as core thicket site (Fig. 1). However, besides this observation, there was no obvious pattern that could be better explained by spatial autocorrelation than by vegetation type. The karoo samples were also relatively homogeneous, and differences between the core biome area (Beaufort West) and the Baviaanskloof sites were small, compared to those observed between the two fynbos sites.

Baviaanskloof sites were placed centrally in most analyses,

indicating an intermixing of plant and insect assemblages from various biomes. In particular, the Baviaanskloof grassland had a clear central position, especially in the plant analysis (Fig. 2a). It is worth mentioning that the grassy belt in the Baviaanskloof is not mapped as grassland on any of the national-level maps, where it is generally classified as grassy fynbos, although fynbos elements can be completely absent at the scale of kilometres.¹⁷ Floral and faunal mixing is probably a consequence of the small size of these grassy patches, and the distant location of core grassland area—a source of immigrants. Nevertheless, in the analysis including hemipteran insects alone, the core and Baviaanskloof plots appeared intermixed, indicating that the hemipteran grassland fauna is well represented in the Baviaanskloof, and at least in part restricted there to the grassy patches. However, the clusters were not more compact in the case of phytophagous insects, or hemipterans alone, than in the analysis for all insects, indicating that host-specificity does not play a major role in the structuring of phytophagous insect assemblages.¹⁸

Overall, there was a good linear relationship between observed and predicted insect species richness, suggesting comparable collection efficiency across biomes. For a given observed insect species richness value, diversity values predicted from abundance values were significantly higher in the Baviaanskloof than for the core biomes. Thus, the Baviaanskloof and core biome values described two distinct lines, with no difference in the slope ($F = 0.0060$; $P = 0.942$), and higher intercept in the Baviaanskloof ($F = 35.7$; $P = 0.0019$) (Fig. 3). This difference can most likely be attributed to a typical 'mass effect' (the establishment of species at sites where they cannot be self-maintaining^{14,19}). It is possible, however, that the establishment of insect species from neighbouring vegetation is in some cases persistent; long-term moni-

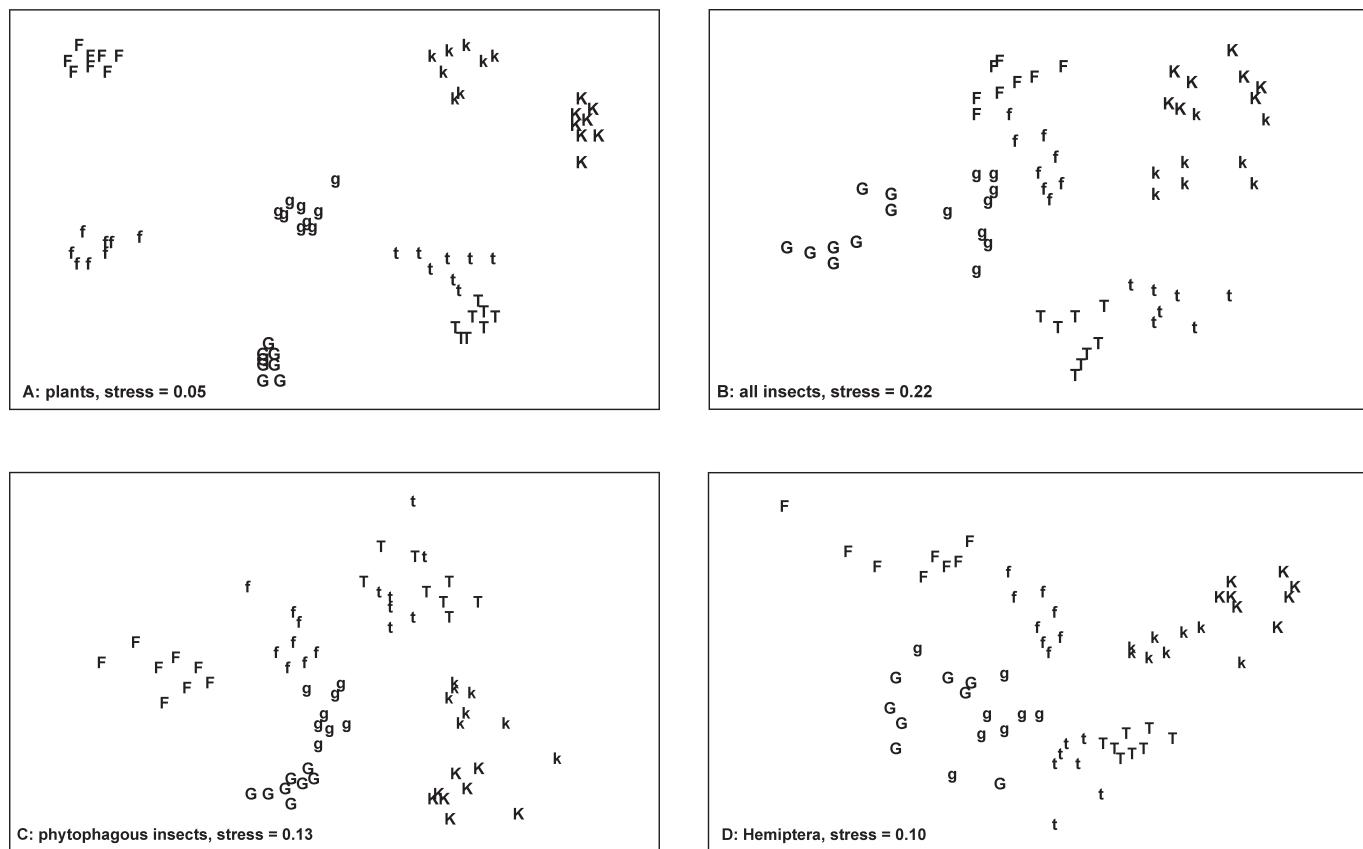


Fig. 2. Multidimensional scaling (MDS) analyses based on presence-absence data for the (a) plants, (b) all insects, (c) phytophagous insects only, and (d) hemipterans only from core fynbos (F), grassland (G), thicket (T) and karoo (K), as well as from the same four biomes in the Baviaanskloof Conservation Area (f, g, t, k).

toring is required to investigate this.

The observed site richness values for Baviaanskloof spanned a smaller range than that observed in the core areas (Fig. 3), suggesting that, in this mixed vegetation area, biomes with poor insect faunas get richer, but those with rich insect faunas get poorer. However, the species richness ranking of the biomes was different in the Baviaanskloof and the core areas. Among the core biomes, grassland was by far the richest, followed by thicket, fynbos and karoo; in the Baviaanskloof, fynbos and grassland showed similar values, followed at a much lesser degree by thicket and karoo. While the higher numbers in fynbos and grassland could be partly explained by higher collection efficiency, the differences between core biomes and Baviaanskloof must be regarded as real differences in faunal composition.

These values could indicate that the core (western) fynbos vegetation is somewhat impoverished in insect species, as suggested by several studies.^{20,21} At the plot scale, however,

comparisons showed no significant difference in insect diversity between western (core) and eastern (Baviaanskloof) fynbos (means and standard deviations for numbers of species: west: 27.1 ± 13.6 ; east: 38.8 ± 14.5 ; $P = 0.12$; $n = 8$). The large increase in total species numbers from west to east, observed when pooling samples (Fig. 3), suggests that most of the species gain in the east occurs across larger spatial scales (hundreds of metres to kilometres), where the effect of environmental gradients is felt. This could be explained by the mass effect mechanism we propose here, as different fynbos areas would be enriched with insects from different non-fynbos patches nearby. Insofar as more extensive sampling would show a significant difference at finer spatial scales, this could be partly attributed to the west-east gradient of increasing soil fertility and summer rain, these factors contributing to more productive vegetation that is able to support more complex food chains.²²

The similarly high insect numbers recorded in eastern fynbos and grassland are partly based on shared species. This is reflected to a limited extent in the MDS analyses (Fig. 2), where a transition can be followed from core grassland, through Baviaanskloof grassland and fynbos, to core fynbos. Nevertheless, the peripheral position of core fynbos in the MDS analyses confirms the existence of a characteristic fynbos insect fauna. This is especially obvious when limiting the analysis to phytophagous insects or the order Hemiptera.

Conclusion

Each of the biomes we considered contains some characteristic insects, not found elsewhere, but the overall differences between insect assemblages are clearly not as convincing as those between plant assemblages. This is what could be expected, considering the greater dispersal abilities of most

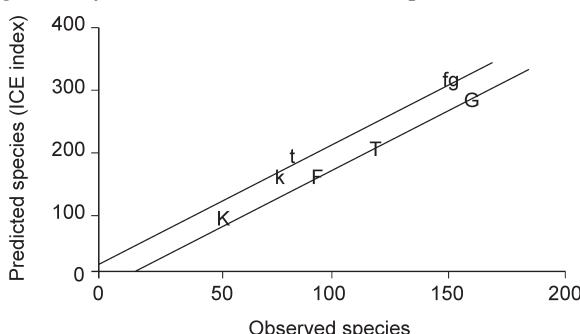


Fig. 3. Observed versus predicted insect species richness in the core biomes (capital letters) and the Baviaanskloof Conservation Area (small letters). F, fynbos; G, grassland; T, thicket; K, karoo.

insects. The transition from one biome to another appears smoother from an insect assemblage perspective. This study is based on a limited number of sites, and on a single collection method. Our conclusions will need future testing with other collection methods (pitfall traps, Malaise traps, etc.), and in multiple sites. Standardized insect collections in the biomes not included in this study, are also needed. Nevertheless, we hope that this study will provide a baseline for future research, and will raise interest in the characterization of South African insect assemblages.

We thank Steven Chown, Melodie McGeoch, Sarah Gess, Mike Picker, Michael Samways, Ruan Veldtman and John Wilson for discussion, Eileen Campbell, Derek Clark, Derek du Preez, and Graham Kerley for providing facilities, and Else Foster, Steffen Heelemann, Evert Jacobs, Abigail Kamineth, Andrew Knight, Marietjie Landman, Louise Visagie and Phil Whittington for assistance in the field. Comments from two anonymous referees helped improve the manuscript. We also thank the Department of Economic Affairs, Environment and Tourism (Eastern Cape), the Nelson Mandela Metropolitan Municipality, Cape Nature and private landowners (Ronald Kirkman, Wesley Berrington and the Lemoenfontein Guest Farm) for permission to collect on their holdings. This research was funded by the Nelson Mandela Metropolitan University and Claude Leon Foundation postdoctoral bursaries to S.P., and by National Research Foundation and NMMU grants to R.M.C. The Mazda Wildlife Fund provided the field vehicles.

Received 10 April. Accepted 12 August 2006.

1. Rutherford M.C. and Westfall R.H. (1986). Biomes of southern Africa. An objective characterisation. *Mem. Bot. Surv. S. Afr.* **54**, 1–98.
2. Low A.B. and Rebelo A.G. (1998). *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria.
3. Mucina L. and Rutherford M.C. (eds) (2006). The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* **19**. South African National Biodiversity Institute, Pretoria.
4. Van Wyk A.E. and Smith G.F. (2001). *Regions of Floristic Endemism in Southern Africa: a review with emphasis on succulents*. Umdaus Press, Pretoria.
5. van Rensburg B.J., Koleff P., Gaston K.J. and Chown S.L. (2004). Spatial congruence of ecological transition at the regional scale in South Africa. *J. Biogeogr.* **31**, 843–854.
6. De Klerk H.M., Crowe T.M., Fjeldså J. and Burgess N.D. (2002). Biogeographical patterns of endemic terrestrial Afrotropical birds. *Diversity and Distributions* **8**, 147–162.
7. de Klerk H.M., Crowe T.M., Fjeldså J. and Burgess N.D. (2002). Patterns of species richness and narrow endemism of terrestrial bird species in the Afrotropical region. *J. Zool.* **256**, 327–342.
8. Burgess N.D., Rahbek C., Larsen F.W., Williams P. and Balmford A. (2002). How much of the vertebrate diversity of sub-Saharan Africa is catered for by recent conservation proposals? *Biol. Cons.* **107**, 327–339.
9. Minter L.R., Burger M., Harrison J.A., Braack H.H., Bishop P.J. and Kloepfer D. (eds) (2004). *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland*. SI/MAB Series #9. Smithsonian Institution, Washington, D.C.
10. Proches S. and Cowling R.M. (2006). Insect diversity in Cape fynbos and neighbouring South African vegetation. *Global Ecol. Biogeogr.* **15**, 445–451.
11. Wright M.G. and Samways M.J. (1998). Insect species richness tracking plant species richness in a diverse flora: gall-insects in the Cape Floristic Region, South Africa. *Oecologia* **115**, 427–433.
12. Gess F.W. and Gess S.K. (1993). Effects of increasing land utilization on species representation and diversity of aculeate wasps and bees in the semi arid areas of southern Africa. In *Hymenoptera and Biodiversity*, eds J. LaSalle and I.D. Gauld, pp. 83–113. CAB International, Wallingford, Oxon.
13. Cowling R.M. (1983). Phytochorology and vegetation history in the south eastern Cape, South Africa. *J. Biogeogr.* **10**, 393–419.
14. Shmida A. and Wilson M.V. (1985). Biological determinants of species diversity. *J. Biogeogr.* **12**, 1–20.
15. Clarke K.R. and Warwick R.M. (1994). *Change in marine communities: an approach to statistical analysis and interpretation*. Plymouth Marine Laboratory, Plymouth.
16. Colwell R.K. (2001). EstimateS: Statistical estimation of species richness and shared species from samples. Version 6.0b1. User's Guide and application published online at: <http://viceroy.eeb.uconn.edu/estimates>
17. Euston-Brown D.I.W. (1995). *Environmental and dynamic determinants of vegetation distribution in the Kouga and Baviaanskloof Mountains, Eastern Cape*. M.Sc. thesis, University of Cape Town.
18. Novotny V., Basset Y., Miller S.E., Weiblein G.D., Bremer B., Èiek L. and Drozd P. (2002). Low host specificity of herbivorous insects in a tropical forest. *Nature* **416**, 841–844.
19. Eriksson O. (1996). Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos* **77**, 248–258.
20. Johnson S.D. (1992). Plant-animal relationships. In *The Ecology of Fynbos: Nutrients, fire and diversity*, ed. R.M. Cowling, pp. 175–205. Oxford University Press, Cape Town.
21. Johnson S.D. and Bond W.J. (1997). Evidence for widespread pollen limitation of fruiting success in Cape wildflowers. *Oecologia* **109**, 530–534.
22. Campbell B.M. (1983). Montane environments in the fynbos biome. *Bothalia* **4**, 283–298.

Genetic diversity of *Chrysoporthe cubensis* in eastern and southern Africa

Grace Nakabonge^a, Marieka Gryzenhout^a,
Brenda D. Wingfield^b, Michael J. Wingfield^a and
Jolanda Roux^{a*}

***Chrysoporthe cubensis* is an important fungal pathogen of *Eucalyptus* species worldwide. The fungus is also known on many other hosts, all residing in the order *Myrtales*. Previous studies have suggested that *Chr. cubensis* might be native to South America and southeast Asia and that it has been introduced into Africa. Recently, surveys have been conducted in eastern and southern Africa to assess the distribution of *Chrysoporthe* spp. in this region. *Chr. cubensis* was found on *Eucalyptus* spp. in Kenya, Malawi and Mozambique. The aim of the study reported here was to determine the genetic diversity of *Chr. cubensis* populations from these countries. Population diversity studies were conducted using five pairs**

of microsatellite markers previously developed for *Chr. cubensis*. Results show that there is a very low genetic diversity within the populations of *Chr. cubensis* from Kenya, Malawi and Mozambique, implying that the fungus was probably recently introduced in these countries. Based on phylogenetic analyses, the origin of East African *Chr. cubensis* is most likely Asia.

Introduction

Chrysoporthe cubensis (Bruner) Gryzenh. & M. J. Wingf., previously known as *Cryphonectria cubensis* (Bruner) Hodges,¹ is a fungal pathogen of *Eucalyptus* species in tropical and subtropical areas worldwide.² The canker disease caused by *Chr. cubensis* is characterized by the formation of stem cankers, wilting and death of trees.^{2–4} The disease is common on *Eucalyptus* spp. in areas with high temperatures and rainfall^{3–5} such as South America,³ Central and North America,⁶ Asia^{4,5,7} and Africa.^{8,9} The fungus also occurs in Australia.¹⁰ Cankers are generally found at the bases of trees, but are often also observed higher up on the stems.^{3,4,9} Management of the disease is most typically achieved by planting resistant hybrids and clones.^{2,4,11,12}

In Africa, *Chr. cubensis* has been identified on *Eucalyptus* spp. since the 1950s. The fungus is known from the Democratic Republic of Congo (Zaire), where it was thought to be *Cryphonectria havanensis* (Bruner) M.E. Barr,⁸ but later identified as *Chr. cubensis*.¹³ *Chr. cubensis* is also known from Cameroon⁸ and the Republic of Congo (Congo Brazzaville), on *E. grandis* and *E. urophylla* S.T. Blake.^{9,14}

^aDepartment of Microbiology and Plant Pathology, and ^bDepartment of Genetics, DST/NRF Centre of Excellence in Tree Health Biotechnology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria 0002, South Africa.

*Author for correspondence. E-mail: jolanda.roux@fabi.up.ac.za