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Patterns of diversity, endemism and distribution of bees (Insecta: Hymenoptera: Anthophila) in southern Africa

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Abstract

For southern Africa, patterns of bee diversity and endemism were studied with a special focus on South Africa and the Cape Floral Kingdom. Based on distribution records of 645 species incorporated in the “Southern African Bee Database” (SouthABees), the pattern of bee diversity was analysed on a $2^\circ \times 2^\circ$ grid. The resulting map shows a bicentric pattern, with highest species diversity located in the arid west and in the relatively moist east. The investigation of distribution patterns of 516 South African species identified twelve distribution types that largely coincide with patterns in the seasonality of precipitation: winter rainfall, early to mid summer rainfall, late to very late summer rainfall and rain all year. The largest number of bee species is associated with the winter rainfall area (46.3% of the fauna) and with the early to mid summer rainfall area (36.5% of the fauna). Consequently South Africa is a centre of bee diversity of global significance. The most important centres of endemism are the winter rainfall area in the west (27.3% of total fauna endemic) and the early to mid summer rainfall area (29.1% of total fauna endemic) in the east. The relationship between bee/plant diversity patterns and speciation is discussed.

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1. Introduction

Worldwide some 25,000 bee species exist (Michener, 2007). They are the most important pollinators of the 240,000 species of flowering plants and of more than half of the 3000 crop species. Bees are ecological keystone species and the economic value of their pollination service to agriculture is estimated at 70 billion U.S. \$ annually (Corbet et al., 1991; Allen-Wardell et al., 1998; Klein et al., 2007). Furthermore, by coevolving with the angiosperms bees contributed decisively to the explosive adaptive radiation of flowering plants and, thus, to the present phytodiversity and the structure of the terrestrial vegetation and ecosystems (Friis et al., 1987; Grimaldi, 1999).

Notwithstanding the great ecological and economic value of wild bees, knowledge of this most important group of pollinators

is still poor. Only two third of the world's estimated bee fauna is currently described (Michener, 2007). The percentage may be even lower for Africa where until recently very little was known about bee biogeography and ecology (Prins, 1978) and where few studies on pollination ecology have been conducted so far (Whitehead et al., 1987; Gemmill et al., 2004; Harris and Johnson, 2004 and references therein). Eardley (1989a) and Kuhlmann (2005) were the first to shed some light on bee species diversity, endemism and distribution patterns in southern Africa, although North Africa has been investigated much more thoroughly (Patiny and Michez, 2007; Patiny et al., 2009).

Pollinators are believed to have played an important role in plant speciation in southern Africa and especially in the Cape Floral Kingdom (CFK) (Kreft and Jetz, 2007; Van der Niet and Johnson, 2008; Waterman et al., 2008). Interestingly, the CFK is the only place on earth where a centre of bee diversity coincides with a plant diversity hotspot (Kuhlmann, 2005). This is due to the fact that the CFK is the only centre of phytodiversity in an arid to semi-arid environment (Cowling and Hilton-Taylor,

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1997; Cowling et al., 1998), the kind of environment where bees are generally most diverse (Michener, 1979, 2007). This unique situation probably influenced the evolution and speciation of both bees and plants as indicated by the frequent occurrence of unusual pollination syndromes and unusual pollinator adaptations in this region (Johnson and Steiner, 2003; Johnson, 1996, 2004; Ollerton et al., 2006).

The environmental conditions of the winter rainfall region create a unique selective regime: The predictability of precipitation and relatively mild temperatures during winter facilitate a thriving flora and a spectacular mass flowering which is world-renowned (Cowling et al., 1999; Esler and Rundel, 1999). But these conditions during the peak flowering season also provide an unfavourable environment for pollinating insects leading to reduced flight activity and widespread pollen limitation of the flora (Johnson and Bond, 1997). A striking feature of this region is the weak synchronization of bee activity with their food plants' flowering (Mayer and Kuhlmann, 2004). However, casual observations and experimental data from North America show that the emergence particularly of specialized bees in desert areas is controlled by rainfall events (Danforth, 1999; literature reviewed therein). Synchronization of bee and host-plant phenology is seen as a possible mechanism for the elevated speciation rate in desert bees (Minckley et al., 2000; Danforth et al., 2003) and might have had an impact on plant evolution as well. Thus, knowledge about bee biogeographical patterns may help to improve our understanding of the evolution and speciation processes of bees and plants in southern Africa and to foster studies on plant–pollinator interactions.

In the present study, the biogeography of the bee fauna of southern Africa is analysed with special emphasis on South Africa and the CFK. The main goals are: (1) to estimate the scale of bee diversity and endemism; (2) to identify and describe regional distribution patterns; and (3) to discuss these patterns in relation to patterns shown by flowering plants as the principal food source.

2. Methods

2.1. Geographical framework

The region dealt with in the present study is Africa south of the rivers Kunene and Okavango in the west and the river Zambezi in the east, comprising Namibia, Botswana, Zimbabwe, the southern part of Mozambique, South Africa, Lesotho and Swaziland (Fig. 1). A detailed study of distribution patterns was undertaken for South Africa and Lesotho, where sufficient bee records were available. Also South Africa has the richest flora of southern Africa and encompasses the majority of the centres of bee endemism (Fig. 5c) and the CFK (Cowling et al., 1997; Van Wyk and Smith, 2001).

2.2. Origin of data and analysis

An extensive survey of potential sources of biogeographical data for bees was undertaken prior to the present study. Only

reliable and comprehensive sources of taxonomic information providing full distribution data of all examined specimens (i.e. taxonomic revisions and data from the author's study of the genus *Colletes*) were used. Revisions lacking full documentation were excluded from the study to avoid a geographical bias within these taxa. Thus, the genera *Megachile* s.l. (Pasteels, 1965) and *Coelioxys* (Pasteels, 1968) as well as the tribe Anthidiini (Pasteels, 1984) were not included. Distribution records and additional data have been included in the South-ABees database held by the author. It comprises 11,310 data records of which 10,958 (96.9%) are georeferenced. Collecting sites were georeferenced using geographical coordinates directly given with published records or by using Microsoft Encarta® Weltatlas. For southern Africa a total of 2852 collecting sites were identified (Fig. 1).

For the analysis of diversity patterns in southern Africa the final dataset included 645 bee species representing 56 genera and 97 subgenera and belonging to all of the higher lineages of bees occurring in the study region (Table 1). The number of species recorded as present per $2^{\circ} \times 2^{\circ}$ grid was recorded and mapped. Distribution patterns in South Africa were analysed using a subset of 516 species. For all species records were mapped using DMAP V7.2 by Alan Morton. Distributions of species showing similar patterns are superimposed to identify general distribution types. These were subsequently manually compared with climatic factors (Schulze, 1997), patterns of phytodiversity and phytogeography, distribution of biome and vegetation types (Cowling et al., 1997) and centres of plant endemism (Van Wyk and Smith, 2001).

Classification on generic and subgeneric level as well as higher classification of bees follows Michener (2007).

3. Results

3.1. Diversity patterns

Of the seven bee families known worldwide, all but the Australian endemic Stenotritidae are represented in the Afrotropical region (Table 2). An overview of the number of genera and subgenera as well as the numbers of bee species in the Afrotropical region, southern Africa and South Africa is given in Tables 2 and 3. From southern Africa, 89 bee genera and 174 subgenera (82% and 75% respectively of the Afrotropical fauna) are known, of which 85 genera and 165 subgenera (78% and 71% respectively of the Afrotropical fauna) occur in South Africa (Table 2).

About 2800 bee species are currently described from the Afrotropics, of which ca. 1400 (50%) are known from southern Africa (Table 3). The number of bee species in the Afrotropics is unevenly distributed among the families. The Halictidae and Megachilidae have the highest diversity, followed by the Apidae and Colletidae, while Melittidae and Andrenidae are least speciose (Table 3). On generic and subgeneric level the picture is slightly different, with Megachilidae and Apidae having the highest number of taxa, followed by Halictidae and Melittidae. Least diverse are Andrenidae and Colletidae (Table 2).

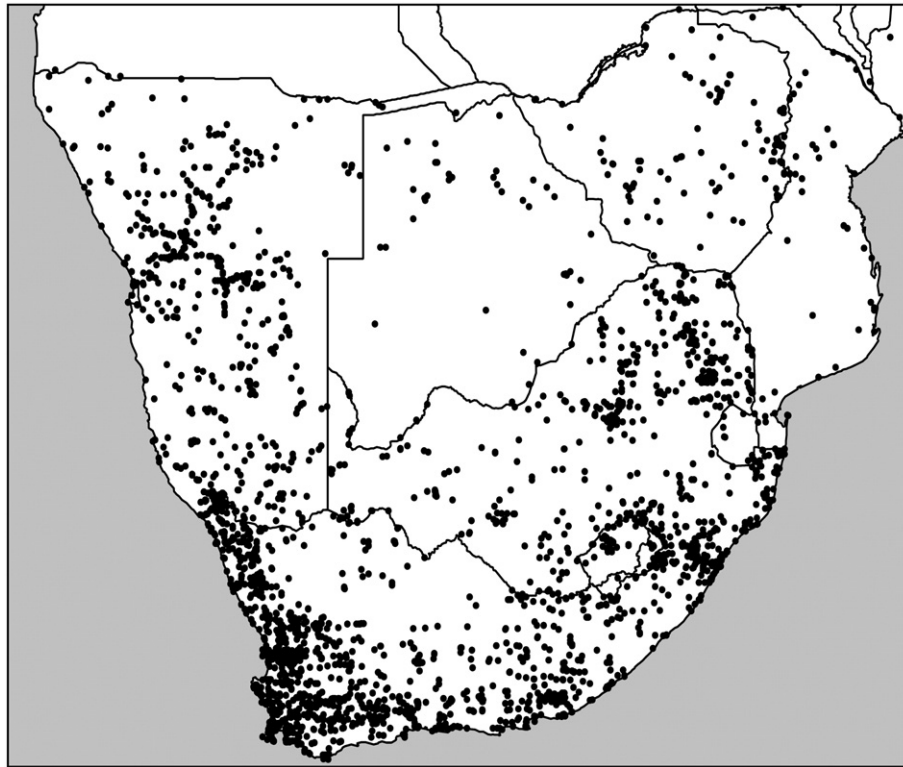


Fig. 1. Distribution of the 2852 Southern African collecting sites of the 645 bee species included in the SouthABees database.

The diversity of bees in southern Africa plotted as number of species per $2^\circ \times 2^\circ$ square is shown in Fig. 2. Bees show a bicentric diversity pattern in South Africa with highest species numbers located in the western (maximum 167 species per grid square) and southern parts, but less pronounced in the east of the country. Few species are known from the Karoo region in the interior of South Africa. The number of records in central Namibia and in parts of Zimbabwe is moderately high while very few bee species have been recorded from Botswana and Mozambique so far.

3.2. Distribution patterns

As a result of the present study, twelve main distribution types of South African bees could be identified (Fig. 3). The fauna shows clear climatic associations with the rainfall regime (Fig. 5a). Most bee species (64.2%) are restricted to a single region with either winter rainfall, early to mid summer rainfall, late to very late summer rainfall, or rain all year respectively. A small number of species (18.9%) live in the southern South African region with rain all year but also intruding into either the winter rainfall, early to mid summer rainfall, or late to very late summer rainfall areas respectively. Only 13.3% are frequently found in three or more precipitation zones, or show no preferences at all (3.6%). The majority of bee species is either more or less restricted to the winter rainfall area (46.3%), or to the early to mid summer rainfall area (36.5%). Of the 516 bee species analysed here, 317 (60.2%) are known to occur in the winter rainfall area and 265 (50.3%) were found in the early to

mid summer rainfall area. Proportions of species associated with each distribution type are given in Fig. 4.

There is no general congruence of biome types and bee distribution. However, the Succulent Karoo biome, and to a lesser extend the Fynbos biome, are associated with the winter rainfall area, while the Nama Karoo biome is almost congruent with the late to very late summer rainfall area (Fig. 5b). There is no obvious coincidence of bee distribution with phytogeographical regions (Fig. 5d).

3.3. Endemism

The degree of endemism for the southern African bee fauna is generally high, with the most important centres of endemism (highest number of endemic species) located in the winter rainfall area in the west and the early to mid summer rainfall area in the east of South Africa (Fig. 4). In southern Africa 89 genera and 174 subgenera occur, of which 10 genera (11%) and 35 subgenera (20%) are endemic. Most of the endemics belong to the Megachilidae (3 genera, 19 subgenera) and the Melittidae (4 genera, 9 subgenera) (Table 2). With the exception of *Mermiglossa*, *Ceratomonina* and *Rediviva* (the latter has a substantial number of endemic species in the summer rainfall area) all endemic genera and subgenera are restricted to the winter rainfall area.

In the winter rainfall area, 141 species (27.3%) are strictly endemic, while in the early to mid summer rainfall area 150 (29.1%) are endemics. The degree of endemism in the other

Table 1

Bee genera included in the Southern African Bee Database (SouthABees) used to analyse biogeographical and diversity patterns in southern Africa (south of the rivers Cunene and Zambezi: Namibia, Botswana, Zimbabwe, Mozambique (southern part), South Africa, Lesotho, Swaziland).

| Genus | N species | | % | References | Comments |
|---|-----------------|-------------|------|---|---|
| | Southern Africa | Afrotropics | | | |
| Colletidae | | | | | |
| <i>Colletes</i> | 101 | 126 | 80 | Kuhlmann (2007), Kuhlmann (unpubl.) | |
| <i>Hylaeus (Alfkenylaus)</i> | 2 | 4 | 50 | Snelling (1985) | |
| <i>Hylaeus (Cornylaues)</i> | 2 | 2 | 100 | Snelling (1985) | |
| <i>Hylaeus (Metylaues)</i> | 1 | 5 | 20 | Snelling (1985) | |
| <i>Hylaeus (Prosopisteron)</i> | 1 | 1 | 100 | Snelling (1985) | Introduced |
| <i>Hylaeus incertae sedis</i> | 1 | 1 | 100 | Snelling (1985) | |
| <i>Scrapter</i> | 47 | 47 | 100 | Eardley (1996), Davies et al. (2005), Davies and Brothers (2006) | Endemic in southern Africa (1 species in Kenya) |
| Andrenidae | | | | | |
| <i>Andrena</i> | 1 | 3 | 33 | Eardley (2006) | |
| <i>Melitturga</i> | 3 | >3 | <100 | Eardley (1991a) | |
| <i>Melitturgula</i> | 7 | >12 | <55 | Eardley (1991a), Patiny (2000) | |
| <i>Mermiglossa</i> | 1 | 1 | 100 | Eardley (1991a) | Endemic in southern Africa |
| Halictidae | | | | | |
| <i>Cellariella</i> | 4 | 5 | 80 | Pesenko and Pauly (2005) | |
| <i>Ceylactis</i> | 3 | 5 | 60 | Pesenko and Pauly (2005) | |
| <i>Eupetersia</i> | 1 | 12 | 8 | Pauly (1981) | |
| <i>Lasioglossum (Ctenonomia)</i> (metallic species) | 1 | 6 | 17 | Pauly (1980) | |
| <i>Lasioglossum (Ctenonomia)</i> (as <i>Ipomactis</i>) | 2 | 2 | 100 | Pauly (2001) | |
| <i>Lipotriches (Afronomia)</i> | 6 | 7 | 86 | Pauly (1990) | |
| <i>Lipotriches (Maynenomia)</i> | 1 | 1 | 100 | Pauly (1990) | |
| <i>Lipotriches (Trinomia)</i> | 5 | 6 | 83 | Pauly (1999) | |
| <i>Nomia</i> s.str. | 1 | 3 | 33 | Pauly (1990) | |
| <i>Nomia (Acunomia)</i> | 4 | 9 | 44 | Pauly (1990) | |
| <i>Nomia (Crocisaspida)</i> | 5 | 9 | 55 | Pauly (1990) | |
| <i>Nomia (Leuconomia)</i> | 10 | 25 | 40 | Pauly (2000) | |
| <i>Nomioides</i> | 1 | 6 | 17 | Pesenko and Pauly (2005) | |
| <i>Patellapis (Chaetalictus)</i> | 43 | 46 | 94 | Timmermann and Kuhlmann (2009) | Most species endemic in southern Africa |
| <i>Patellapis (Dictyohalictus)</i> | 1 | 12 | 8 | Michener (1978), Pauly (1989) | |
| <i>Patellapis (Lomatalictus)</i> | 1 | 1 | 100 | Timmermann and Kuhlmann (2009) | Endemic in southern Africa |
| <i>Patellapis (Patellapis)</i> | 23 | 23 | 100 | Timmermann and Kuhlmann (2009) | Endemic in southern Africa |
| <i>Pseudapis</i> s.str. | 5 | 19 | 26 | Pauly (1990) | |
| <i>Pseudapis</i> s.str. (as <i>Ruginomia</i>) | 1 | 1 | 100 | Pauly (1990) | Endemic in southern Africa |
| <i>Pseudapis</i> s.str. (as <i>Stictonomia</i>) | 4 | 9 | 44 | Pauly (1990) | |
| <i>Pseudapis (Pachynomia)</i> | 3 | 4 | 75 | Pauly (1990) | |
| <i>Spatunomia</i> | 1 | 2 | 50 | Pauly (1990) | |
| <i>Steganomus</i> | 1 | 4 | 25 | Pauly (1990) | |
| Melittidae | | | | | |
| <i>Afrodasyypoda</i> | 1 | 1 | 100 | Engel (2005) | Endemic in southern Africa |
| <i>Ceratonomia</i> | 1 | 1 | 100 | Michener (1981) | Endemic in southern Africa |
| <i>Haplomelitta</i> | 8 | 10 | 80 | Michener (1981), Michez et al. (submitted for publication) | Most species endemic in southern Africa |
| <i>Hesperapis</i> | 13 | 13 | 100 | Michez et al. (2007), Michez and Kuhlmann (2007) | Endemic in southern Africa |
| <i>Meganomia</i> | 2 | 4 | 50 | Michener (1981) | |
| <i>Melitta</i> | 6 | 7 | 86 | Eardley and Kuhlmann (2006) | |
| <i>Rediviva</i> | 24 | 24 | 100 | Whitehead and Steiner (1992, 2001), Whitehead et al. (2008) | Endemic in South Africa |
| <i>Redivivoides</i> | 1 | 1 | 100 | Michener (1981) | Endemic in South Africa |
| Megachilidae | | | | | |
| <i>Aglaoapis</i> (as <i>Dioxoides</i>) | 1 | 1 | 100 | Michener (1996) | Only species in southern hemisphere |
| <i>Fidelia</i> | 11 | 11 | 100 | Whitehead and Eardley (2003), Engel (2002) | Endemic in southern Africa but single Palearctic species |
| <i>Lithurgus</i> | 2 | 4 | 50 | Eardley (1988) | |
| <i>Stelis</i> | 1 | 1 | 100 | Griswold and Parker (2003) | |
| Apidae | | | | | |
| <i>Allodape</i> | 17 | 28 | 61 | Michener (1975) | |

(continued on next page)

Table 1 (continued)

| Genus | N species | | % | References | Comments |
|-----------------------------------|-----------------|-------------|-----|--|---|
| | Southern Africa | Afrotropics | | | |
| Apidae | | | | | |
| <i>Allodapula</i> | 13 | 13 | 100 | Michener (1975) | Endemic in southern Africa? |
| <i>Amegilla</i> | 31 | >60 | <50 | Eardley (1994) | |
| <i>Ammobates</i> | 1 | 1 | 100 | Eardley and Brothers (1997) | The only species in the southern hemisphere |
| <i>Anthophora (Heliophila)</i> | 16 | ? | ? | Eardley and Brooks (1989) | |
| <i>Anthophora (Paramegilla)</i> | 8 | ? | ? | Eardley and Brooks (1989) | |
| <i>Anthophora (Pyganthophora)</i> | 7 | ? | ? | Eardley and Brooks (1989) | |
| <i>Braunsapis</i> | 17 | 38 | 45 | Michener (1975) | |
| <i>Ceratina</i> | 29 | ? | ? | Eardley and Daly (2007) | |
| <i>Ceratina (Ctenoceratina)</i> | 8 | 13 | 62 | Daly (1988) | Endemic in Afrotropical region |
| <i>Cleptotrigona</i> | 1 | 1 | 100 | Eardley (2004) | |
| <i>Compsomelissa s.str.</i> | 1 | 4 | 25 | Michener (1975) | |
| <i>Compsomelissa (Halterapis)</i> | 3 | 3 | 100 | Michener (1975) | Endemic in southern Africa? |
| <i>Ctenoplectra</i> | 4 | 6 | 67 | Eardley (2003) | |
| <i>Ctenoplectrina</i> | 1 | 2 | 50 | Eardley (2003) | Endemic in Afrotropical region |
| <i>Epeolus</i> | 10 | 11 | 91 | Eardley (1991c) | |
| <i>Eucondylops</i> | 2 | 2 | 100 | Michener (1970, 1975) | Endemic in southern Africa |
| <i>Hypotrigona</i> | 3 | 4 | 75 | Eardley (2004) | |
| <i>Liotrigona</i> | 2 | 2 | 100 | Eardley (2004) | |
| <i>Macrogalea</i> | 1 | 3 | 50 | Michener (1975) | |
| <i>Meliponula</i> | 3 | 8 | 38 | Eardley (2004) | |
| <i>Nasutapis</i> | 1 | 1 | 100 | Michener (1970, 1975) | Endemic in southern Africa |
| <i>Nomada</i> | 3 | 3 | 100 | Eardley and Schwarz (1991) | |
| <i>Pachymelus</i> | 3 | 20 | 15 | Eardley (1993) | |
| <i>Pasites</i> | 10 | 17 | 59 | Eardley and Brothers (1997) | |
| <i>Plebeina</i> | 1 | 1 | 100 | Eardley (2004) | |
| <i>Sphecodopsis</i> | 13 | 13 | 100 | Eardley and Brothers (1997), Eardley (2007) | Endemic in southern Africa |
| <i>Tetralonia s.str.</i> | 3 | 5 | 60 | Eardley (1989b) | |
| <i>Tetralonia (Eucara)</i> | 3 | 7 | 43 | Eardley (1989b) | |
| <i>Tetralonia (Tetraloniella)</i> | 19 | 28 | 68 | Eardley (1989b) | |
| <i>Thyreus</i> | 22 | >30 | <73 | Eardley (1991b) | |
| <i>Xylocopa</i> | 24 | 126 | 19 | Eardley (1983, 1987) | |
| Σ | 645 | >950 | <68 | | |

Generic and subgeneric systematics follows Michener (2007).

regions is much lower, with 23 species (4.5%) in the late to very late summer rainfall area and 17 species (3.3%) in the area with rain all year. When species that occur in neighbouring rainfall regions are included, the number of winter rainfall endemics increases to 239 species (46.3%) and to 188 species (36.5%) for the early to mid summer rainfall endemics (Fig. 4).

The two main centres of endemism are rich in endemic species. Currently 317 out of the 516 bee species included in this analysis are recorded from the South African winter rainfall area, of which 141 (44.5%) are strictly endemic. A total of 239 (75.4%) are endemic only in the broader sense, as they intrude into the adjacent rainfall areas. For the 265 bee species of the early to mid summer rainfall area, 150 (56.6%) seem to be strictly endemic and 188 (70.9%) are broadly endemic.

4. Discussion

4.1. Diversity patterns

The present study had to rely on existing taxonomic information and is biased towards the families Apidae and Colletidae,

while relatively few species were included of the two largest families Megachilidae and Halictidae (Table 3). However, the lack of information about these families is expected to have little influence on the general diversity pattern, because the less well known species generally share similar habitat preferences with the species included here (Michener, 1979, 2007).

With respect to bee generic and subgeneric diversity, southern Africa in general (and especially South Africa) is unusually rich. Comprising a land area of 1.2 million km², about one twentieth (5%) of the Afrotropical region, two thirds of all genera and subgenera and an estimated 50% of all Afrotropical bee species (Eardley, 1989a,b) occur in South Africa (Table 2). This can be explained by the fact that South Africa is topographically and climatically diverse, including different xeric and warm-temperate regions, which generally have the highest bee diversity (Michener, 1979, 2007).

The number of genera and subgenera recorded from the Afrotropics and southern Africa presumably largely reflects the real situation, although there are indications that the species diversity is grossly underestimated. Recent taxonomic studies by the author on speciose and widely distributed genera like

Table 2

Number of genera and (subgenera) of the Afrotropical region, continental Africa (excluding Madagascar and Sokotra), southern Africa, South Africa and endemic to South Africa (in case of *Rediviva* including Lesotho; all (sub)genera confined to or centred at the winter rainfall area in western South Africa) and Namibia (except for *Mermiglossa* and *Ceratonomia* all (sub)genera in northern extension of the South African winter rainfall area).

| Family | Afrotropical region | % fauna | Continental Africa | % fauna | Southern Africa | % fauna | South Africa | % fauna | endemic South Africa/Namibia | %/family |
|--------------|---------------------|-------------|--------------------|-------------|-----------------|-------------|--------------|-------------|------------------------------|------------|
| Andrenidae | 5 (5) | 4.6 (2.2) | 5 (5) | 5.0 (2.3) | 4 (4) | 4.5 (2.3) | 3 (3) | 3.5 (1.8) | 1 (1) | 20 (20) |
| Apidae | 35 (61) | 32.1 (26.3) | 32 (56) | 31.7 (25.9) | 31 (50) | 34.8 (28.7) | 30 (48) | 35.4 (29.1) | 2 (5) | 6 (8) |
| Colletidae | 4 (9) | 3.7 (3.9) | 4 (9) | 4.0 (4.2) | 3 (8) | 3.4 (4.6) | 3 (7) | 3.5 (4.2) | 0 (0) | 0 (0) |
| Halictidae | 19 (45) | 17.4 (19.3) | 16 (39) | 15.8 (18.1) | 14 (31) | 15.7 (17.8) | 14 (31) | 16.5 (18.8) | 0 (1) | 0 (2) |
| Megachilidae | 35 (94) | 32.1 (40.5) | 33 (91) | 32.6 (42.1) | 29 (68) | 32.6 (39.1) | 28 (64) | 32.9 (38.8) | 3 (19) | 9 (20) |
| Melittidae | 11 (18) | 10.1 (7.8) | 11 (16) | 10.9 (7.4) | 8 (13) | 9.0 (7.5) | 7 (12) | 8.2 (7.3) | 4 (9) | 36 (50) |
| | 109 (232) | | 101 (216) | | 89 (174) | | 85 (165) | | 10 (35) | 9.3 (15.1) |

Colletes and *Patellapis* discovered many undescribed species. Even within South Africa, that is the best investigated area within the Afrotropical region, the number of described species in these two genera will more than double. Thus, the total number of bees in the Afrotropical region is likely to reach 3500–4000 once the continent is thoroughly investigated. Besides southern Africa, and especially for East and NE Africa, a larger number of undescribed species is expected, while tropical Central and West Africa probably is relatively poor in bees (Michener, 1979, 2007).

The southern African bee diversity pattern as shown in Fig. 2 is clearly influenced by uneven sampling (Fig. 1). In the past, collecting was mainly concentrated around urban centres and along main roads. There is still a serious lack of information for the rural central and northern parts of South Africa, as well as for vast areas of Namibia, Zimbabwe, and especially for Botswana and Mozambique. Nevertheless, studies on the much better known pollen wasps (Gess, 1992; Gess and Gess, 2004) and beetles (Endrödy-Younga, 1978) reveal similar patterns. Consequently, I agree with Eardley (1989a,b) that the recorded patterns are likely to reflect the true situation.

The high diversity of bees found for the CFK contradicts Giliomee (2003), who reported no elevated diversity in herbivorous insects in this region. But a recent study by Procheş et al. (2008) revealed a positive relationship between plant diversity and insect diversity, which agrees with the present results.

4.2. Distribution patterns

The distribution types identified for bees seem to represent general patterns that are found in other insects as well. Identical

patterns related to the precipitation regime have been found in pollen wasps (Vespidae: Masarinae) (Gess, 1992), antlions (Neuroptera, Myrmeleontidae) (Erasmus et al., 2000), dung beetles (Coleoptera: Scarabaeidae) (Davis, 1997), buprestid and cetoniine beetles (Coleoptera: Buprestidae, Scarabaeidae) (Holm, 1990), and beetles in general (Endrödy-Younga, 1978).

However, some of the species that fall within the broad definition of the distribution types described here occur within what is sometimes only a small subregion of any particular precipitation zone. This is especially conspicuous in the winter rainfall area and can be observed frequently in bee genera like *Rediviva*, *Scapter* and *Patellapis*. As far as currently known, species with a more restricted distribution are often associated with the Richtersveld and the Bokkeveld Plateaux in western South Africa and with the Drakensberg Mountains in the east. Similarly, small ranges are known from certain pollen wasps (Gess, 1992). The species with more restricted distributions might have special climatic requirements or they might be dependent on specific resources like particular nesting sites or host plants.

Temperature and humidity regime play a critical role for bee development, so that mutations changing thermal tolerance range can alter habitat requirements, ultimately leading to population divergence and speciation (Mazzucco and Mazzucco, 2007). Thus, the observed distribution patterns and the high degree of endemism might also reflect adaptations to regional climate conditions and recent speciation.

4.3. Endemism and origin of the fauna

At the generic and subgeneric rank the degree of endemism in the winter rainfall area of western South Africa and SW Namibia

Table 3

Bee species in the Afrotropical region and southern Africa (based on personal catalogue of C.D. Eardley, version June 2005, unpubl.) and number of species included in biogeographical analyses for South Africa (SouthABees database of author, unpubl.).

| Family | Afrotropical region | % | Southern Africa | % records | % total fauna | South Africa (SouthABees) | % records | % total fauna |
|--------------|---------------------|------|-----------------|-----------|---------------|---------------------------|-----------|---------------|
| Andrenidae | 29 | 1.1 | 14 | 1.0 | 48.3 | 6 | 1.1 | 20.7 |
| Apidae | 717 | 26.0 | 312 | 22.6 | 43.5 | 237 | 45.0 | 33.1 |
| Colletidae | 179 | 6.5 | 137 | 9.9 | 76.5 | 121 | 23.0 | 67.6 |
| Halictidae | 913 | 33.1 | 391 | 28.5 | 42.8 | 101 | 19.1 | 11.1 |
| Megachilidae | 856 | 31.1 | 479 | 34.7 | 56.0 | 14 | 2.7 | 1.7 |
| Melittidae | 61 | 2.2 | 46 | 3.3 | 75.4 | 48 | 9.1 | 78.7 |
| | 2755 | | 1379 | | 50.1 | 527 | | 19.1 |

The real number of described species for the entire Afrotropical region and southern Africa is higher than shown as recently published revisions are not included.

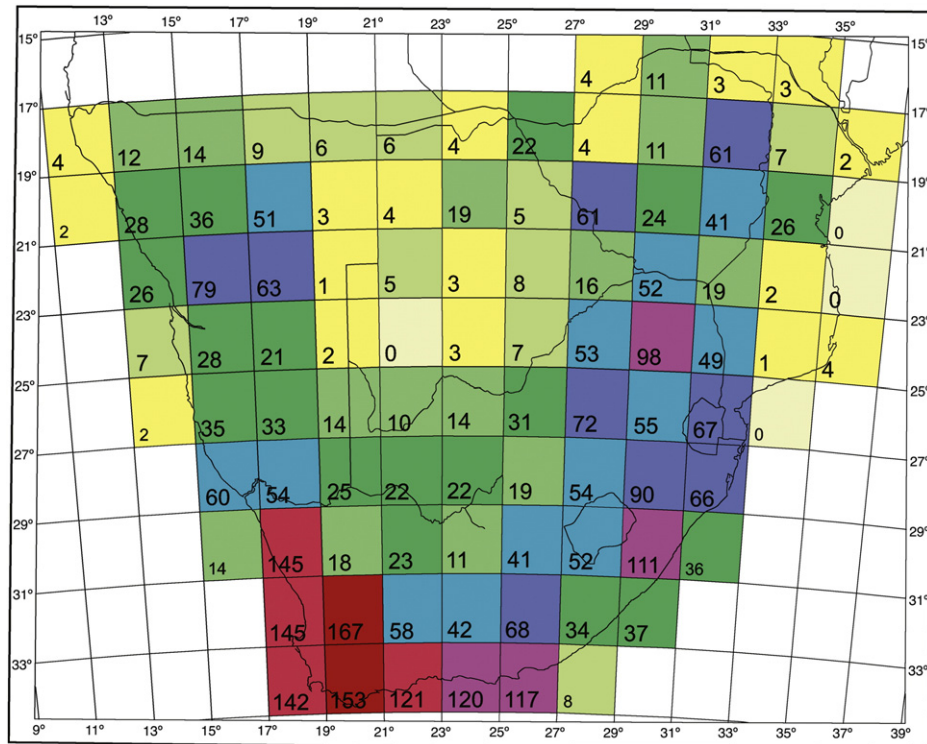


Fig. 2. Number of bee species in southern Africa recorded on a $2^{\circ} \times 2^{\circ}$ grid based on 645 species of 56 genera. Numbers in small print indicate grid cells with less than 10% land.

is surprisingly high. On a land area of about 150,000 km² (0.5% of the Afrotropical region), 10 genera (11%) and 35 subgenera (20%) are endemic, comprising 256 species (Michener, 2007). This exceeds the bee endemism of Madagascar, which has more different types of ecosystems (rainforest to desert) than the winter rainfall area suggesting higher bee diversity. Also it has almost four times the size of the winter rainfall area and is renowned for its unique fauna and flora. A total of 244 bee species (90% endemic) are recorded from Madagascar, representing 38 genera and 64 subgenera, of which 7 genera (18%) and 15 subgenera (23%) are endemic (Pauly et al., 2001). The winter rainfall area, with its special climatic conditions, is like an island surrounded by a markedly different precipitation regime. The unique climate, in connection with factors like an ancient landscape with a varied topography and geology, has contributed to an extraordinary diversity of habitats in this region, and has probably lead to a specially adapted fauna and an increased rate of speciation (Cowling et al., 1999; Goldblatt and Manning, 2002).

Among the genera endemic to the winter rainfall area are a few presumably palaeo-endemics that represent basal lineages

within their families. These are the genera *Scapter* (Colletidae) (Eardley, 1996), *Fidelia* and *Fideliopsis* (Engel, 2002), *Afroheriades* (Peters, 1978; Praz et al., 2008), *Aspidosmia* (Peters, 1972) (Megachilidae) and *Haplomelitta* (Danforth et al., 2006) (Melittidae), which are of special interest for the understanding of bee phylogeny and evolution.

In contrast to the clearly delimited winter rainfall area, little is known about the northerly distribution of many bees that at present are only recorded from the South African part of the summer rainfall area. Some bees of this region extend far north (e.g. East Africa) and often reach the southern extreme of their distribution in the Durban area (Eardley, 1989a,b). Thus, it is very likely that the degree of endemism in the summer rainfall area is considerably lower than described here.

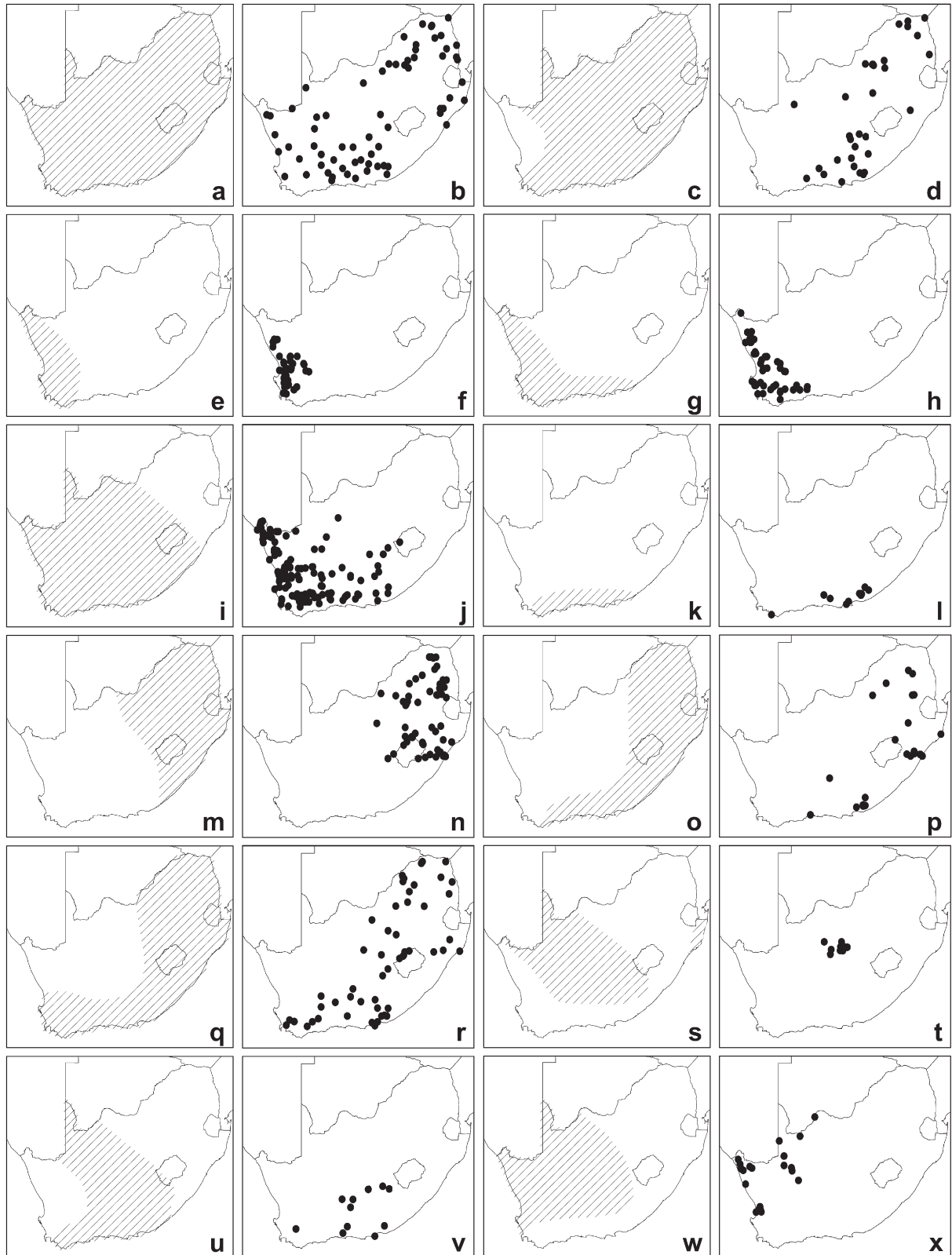
The southern part of South Africa, with rain all year, is a transitional zone where the faunas of the highly endemic winter and summer rainfall areas meet, resulting in a high bee diversity (Fig. 2) but a low degree of endemism (Fig. 4).

The southern African bee fauna is a mixture of different faunal elements that consist of widespread genera, endemics and a few isolated species that probably are descendants of genera with

Fig. 3. Principal distribution types of South African bees and distribution maps of species representing them. (a) Occurring everywhere. (b) *Thyreus delumbatus* (Vachal) (Apidae). (c) Outside winter rainfall area. (d) *Nomia* (*Leuconomia*) *candida* Smith (Halictidae). (e) Endemic in winter rainfall area. (f) *Rediviva intermixta* (Cockerell) (Melittidae). (g) Winter rainfall area and area with rain all year. (h) *Rediviva rufipes* (Friese) (= *bicava* Whitehead and Steiner) (Melittidae). (i) Distribution centred in winter rainfall area and area with rain all year. (j) *Colletes capensis* (Cameron) (Colletidae). (k) Endemic in area with rain all year. (l) *Allodape quadrilineata* (Cameron) (Apidae). (m) Endemic in early to mid summer rainfall area. (n) *Colletes marleyi* Cockerell (Colletidae). (o) Early to mid summer rainfall area and area with rain all year. (p) *Ceratina* (*Ctenoceratina*) *penicillata* Friese (Apidae). (q) Early to mid summer rainfall area and area with rain all year intruding into southern part of winter rainfall area. (r) *Amegilla atrocincta* (Lepelletier) (Apidae). (s) Endemic in late to very late summer rainfall area. (t) *Fidelia* (*Parafidelia*) *friesei* (Brauns). (Megachilidae). (u) Late to very late summer rainfall area and area with rain all year. (v) *Anthophora* (*Pyganthophora*) *braunsiana* Friese (Apidae). (w) Late to very late summer rainfall area and winter rainfall area. (x) *Fidelia* (*Fideliopsis*) *hessei* Whitehead and Eardley (Megachilidae).

origin in the northern hemisphere. The latter group comprises genera like *Aglaopis* (Michener, 1996), *Ammobates* (Eardley and Brothers, 1997), *Nomada* (Eardley and Schwarz, 1991), and

six species of the subgenus *Colletes* (*Elecolletes*) (Kuhlmann, unpubl.), all genera that are represented in southern Africa only by a few species. These species inhabit xeric habitats and probably



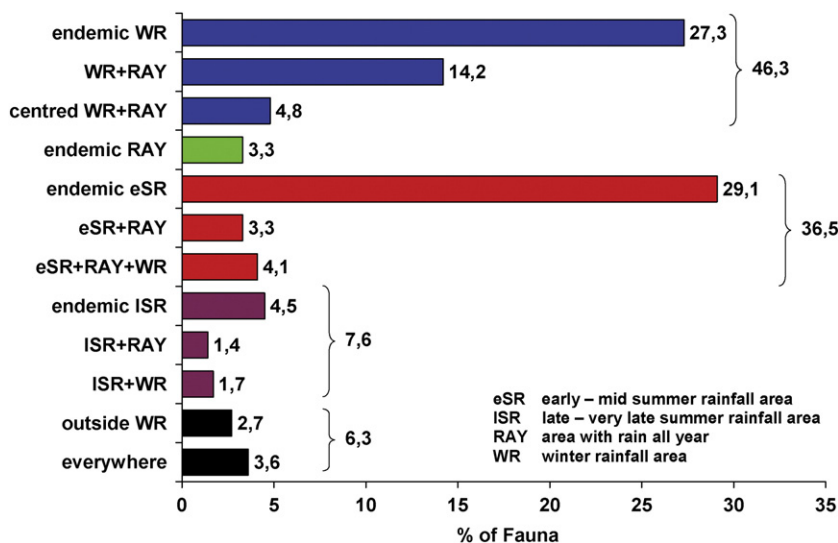


Fig. 4. Composition of the South African bee fauna with respect to distribution types of 516 species.

colonized southern Africa using the Pleistocene “arid corridor” via East Africa (Balinsky, 1962; Verdcourt, 1969; Poynton, 1995).

4.4. Relation of bee and plant diversity patterns

In southern Africa a general coincidence can be observed for patterns in diversity and endemism of bees and plants. Both have their centres of highest species diversity in the winter rainfall area in western South Africa that is largely identical with the Cape Floral Kingdom (Jürgens, 1997; Goldblatt and Manning, 2002; Steenkamp et al., 2005; Born et al., 2007). However, on a finer scale the situation is more complex and at present there is little evidence for the existence of clearly delimited smaller subcentres of endemism in bees or other insects (Procheş and Cowling, 2007) as known for plants (Fig. 5c; Van Wyk and Smith, 2001).

Examples for a coincidence of bee distribution ranges with subcentres of phytodiversity are scarce. This might be partially caused by the lack of sufficient distribution data (a number of species is only known from the type locality) and due to the fact that even endemic bees generally have larger distribution ranges than many plant endemics, which are often restricted to only a few localities (Van Wyk and Smith, 2001). The best documented example so far is the recently described bee *Patellapis doleritica*, which seems to occur only from the Bokkeveld Plateau to the Hantam Mountains around Calvinia, an area within the Hantam-Roggeveld centre (Fig. 5c, region 2.5). This relatively large and conspicuous communal nesting bee (Timmermann and Kuhlmann, 2008) can be very abundant locally and it is unlikely that it has escaped the attention of entomologists elsewhere. The same is true for *Rediviva rufocincta* in the Drakensberg Alpine Centre (Fig. 5c, region 5), while too little is known about the distribution of bees in the Richtersveld/Gariep Centre (Fig. 5c, region 2.1) and the Chimanimani–Nyanga Centre in eastern Zimbabwe (Fig. 5c, region 10) to be sure of the status of some of their bees as endemics.

Regional endemism of bees, as well as the existence of groups of very closely related species in a relatively small area,

is believed to be a sign for recent and ongoing speciation (Mazzucco and Mazzucco, 2007). The latter is known from a number of bee taxa in the winter rainfall area (Kuhlmann, pers. obs.) and thus is of special interest for improving our understanding of speciation processes in bees.

A lack of broad coincidence of patterns in diversity and endemism between bees and plants does not necessarily mean that plant–pollinator interactions only play a secondary role in plant speciation in the CFK. A potential but mostly unexplored scenario is pollinator-facilitated local adaptation (Waser and Campbell, 2004): due to area-restricted foraging, pollinators move most pollen over relatively short distances reducing gene flow between populations. Coupled with restricted seed dispersal (common for most plant species), this would allow adaptation of conspecific plants in different populations to different local environments, because gene flow is insufficient to counterbalance local adaptation. In this scenario, pollinator behaviour could facilitate speciation especially when environmental heterogeneity is as high as in the CFK (Cowling et al., 2008). Recent studies highlighted the importance of a geographical mosaic of pollinator availability for plant diversification in the winter rainfall area (Johnson, 1997; Anderson and Johnson, 2008; Pauw et al., 2009). Bee endemism in combination with the unusually small foraging ranges of female bees in the CFK (Kuhlmann, 2008) might create such a mosaic leading to increased speciation. This hypothesis deserves further investigation.

The flora of the CFK is known for the unusually rich radiation of some plant taxa, with twelve genera having more than 100 species. The 10 largest genera (about 2000 species) contribute over 21% to the flora and the 20 largest genera (about 2900 species) represent over 31% of the total species. The largest genus alone, *Erica* (657 species), comprises more than 7% of the species in the entire flora (Goldblatt and Manning, 2002). As presently known, the taxonomic composition of the bee fauna in the CFK is more balanced and does not show such a pronounced bias in favour of a few genera. However, preliminary faunistic

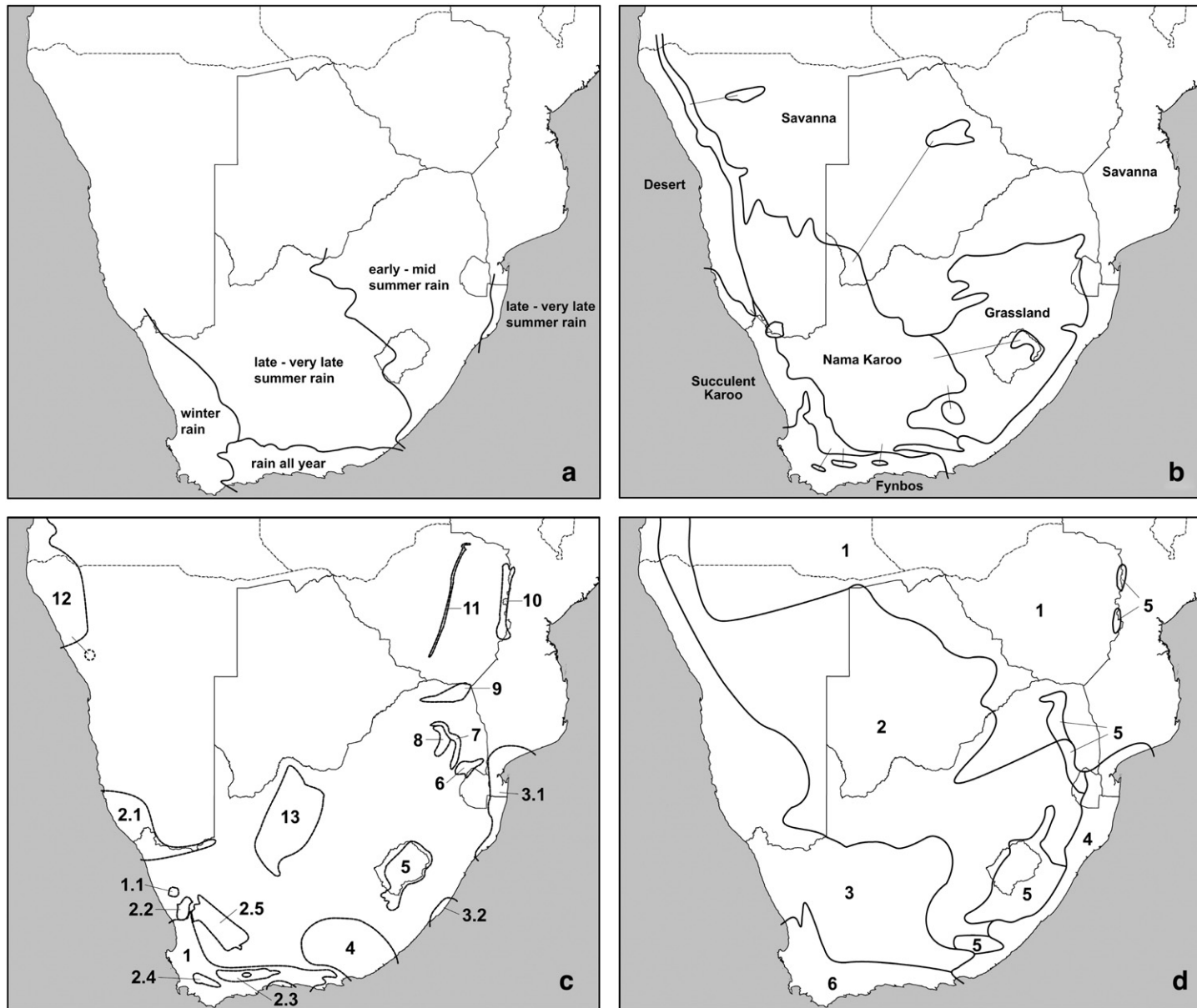


Fig. 5. (a) Simplified principal rainfall areas of South Africa (after Schulze, 1997). (b) The biomes of southern Africa (after Rutherford, 1997). (c) Centres of plant endemism (after van Wyk and Smith, 2001). 1 Cape Floristic Region; 1.1 Kamiesberg Centre; 2 Succulent Karoo Region; 2.1 Gariiep Centre; 2.2 Knersvlakte Centre; 2.3 Little Karoo Centre; 2.4 Worcester–Robertson Karoo Centre; 2.5 Hantam–Roggeveld Centre; 3 Maputaland–Pondoland Region; 3.1 Maputaland Centre; 3.2 Pondoland Centre; 4 Albany Centre; 5 Drakensberg Alpine Centre; 6 Barberton Centre; 7 Wolkberg Centre; 8 Sekhukhuneland Centre; 9 Soutpansberg Centre; 10 Chimanimani–Nyanga Centre; 11 Great Dyke Centre; 12 Kaokoveld Centre; 13 Griqualand West Centre. (d) Phytogeographical regions of southern Africa (after Cowling and Hilton-Taylor, 1997). 1 Zambezian Region; 2 Kalahari–Highveld Transition Zone; 3 Karoo–Namib Region; 4 Tongaland–Pondoland Region; 5 Afromontane Region; 6 Cape Region.

and taxonomic work on speciose genera like *Scapter* and *Pa-tellapis* has discovered many undescribed species, which might alter the picture when more comprehensive data are available.

Some specialist (oligolectic) bee species are dependent on a wider spectrum of host plants for collecting pollen or plant oils than others. They can have a close relationship with their host plants and show congruent distributions, like some narrow oligolectic oil-collecting *Rediviva* bees with oil-secreting orchids or Scrophulariaceae of the genera *Colpias*, *Diascia* and *Hemimeris* (Whitehead and Steiner, 2001; Pauw, 2006; Whitehead et al, 2008; Kuhlmann, unpubl.). The proportion of oligolectic species can exceed 30–40% of the bee fauna in xeric regions with temporally unpredictable rainfall (Moldenke, 1979), but little is known about the host plant relationships of many southern African bees.

5. Conclusions

Sound knowledge of bee diversity and ecology can provide new perspectives for a better understanding of pollinator-driven evolutionary processes and speciation, especially in the CFK, and facilitates research on plant–pollinator interactions. The results presented here are a first step towards a better understanding of patterns in diversity and endemism among southern African bees. To investigate the finer biogeographical structure of the bee fauna and its plant relationships, an improved database is necessary based on additional fieldwork, thorough faunal inventories, and especially on taxonomic research, which is needed to describe and properly document the rich southern African bee fauna.

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