

Research Article

Nocturnal hawkmoth pollination in fynbos vegetation: A critical re-appraisal and first observations from the Cape Peninsula

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Abstract

Pollination by nocturnal hawkmoths is considered rare in the hyper-diverse fynbos vegetation, but it is also hard to detect. Here, we present evidence for hawkmoth pollination of an orchid in fynbos vegetation on the Cape Peninsula, where this pollination system has not yet been recorded. Both direct observations and motion-activated camera footage revealed hawkmoths, several of which were identified as *Hyles livornica* (Esper, 1780), foraging from the long nectar spurs of flowers of *Satyrium candidum*. Several individuals carried pollinaria, suggesting they are legitimate pollinators. These observations add to a growing number of studies that document interactions between flowers and nocturnal hawkmoths in fynbos, and the presence of a small guild of native sphingophilous plants in fynbos vegetation suggests that hawkmoths must have been present in the region over evolutionary time scales. Although fynbos supports fewer hawkmoth species involved as pollinators compared to other regions, and fewer plant species representing fewer lineages in this vegetation type are known to rely on hawkmoth pollination, further quantitative analyses and field studies are required to evaluate whether hawkmoths represent a less-favored pollination niche for fynbos plants.

Key words: Cape Floristic Region, *Hyles livornica*, Orchidaceae, *Satyrium candidum*, Sphingidae, Sphingophily

“Hawkmoth flowers are easy to predict but difficult to document. Our documented knowledge of hawkmoth flowers in most floras consequently lags behind our knowledge concerning other pollination classes.”
Grant (1983)

Introduction

Nocturnal hovering hawkmoths (Sphingidae p.p.) are a well-known group of insects involved in numerous specialized pollination mutualisms globally (Johnson et al. 2017). Although plant lineages involved in the mutualism span a large portion of the angiosperm phylogeny, their flowers are considered to

be uniformly characterized by relatively long nectar-containing floral tubes and strong (and mostly nocturnal) scent production, often referred to as the sphingophilous pollination syndrome (Vogel 1954; Faegri and van der Pijl 1979). South Africa has a large number of specialized pollination niches, including hawkmoths (Johnson 2010). However, it has been suggested that hawkmoth-flower interactions are more common in the eastern summer-rainfall region compared to the winter- and all year-rainfall regions in the west of South Africa, and that they are particularly rare in the fynbos biome (Johnson 1997b; Manning and Snijman 2002; Johnson and Raguso 2016). This regional paucity appears to apply to moth pollination systems in general (Johnson 2004), and also to butterflies (Cottrell 1985). A compelling explanation for the apparent under-representation of specialized Lepidoptera-plant interactions in Cape fynbos in particular is that the nutrient-poor soils, sclerophyllous foliage and absence of many of the angiosperm families that are larval hosts for Lepidoptera act as barriers for colonization (Cottrell 1985).

The suggested rarity of hawkmoth pollination in fynbos is largely extrapolated from a relatively low number of plant species with the sphingophilous syndrome. (Manning and Snijman 2002; Johnson 2004). Nevertheless, several recent studies present evidence for hawkmoth-flower interactions in fynbos, including for species of the largest fynbos genus *Erica* that lack flowers with the typical sphingophilous syndrome (Van der Niet and Cozien 2022, 2024). This suggests that the frequency of hawkmoth pollination may be underestimated in fynbos. However, when comparing all hitherto published records of species pollinated by nocturnal hawkmoths within and outside fynbos vegetation across South Africa, this number is substantially smaller in fynbos, both in terms of number of species and lineages represented by these species (Table 1).

The Cape Peninsula is one of the most botanically diverse areas worldwide (Simmons and Cowling 1996) and contains a few species with a sphingophilous floral syndrome (Marloth 1913–1915), such as *Bonatea speciosa*, which occurs in coastal thicket and scrub and which has been confirmed to be pollinated by hawkmoths in coastal forest bordering fynbos vegetation in the southern Cape (Johnson and Liltved 1997). However, no hawkmoth-flower interactions have been hitherto recorded from the peninsula. Although this region has been extensively researched from an ecological point of view (Pauw and Johnson 1999), the challenges associated with observing interactions between flowers and nocturnal hawkmoths (Grant 1983) may offer a reasonable explanation for the current absence of cases. Focused studies, specifically targeting species with a sphingophilous floral syndrome, and implementing novel techniques such as use of motion-activated cameras, may be useful to uncover hawkmoth pollination (e.g. Van der Niet et al. 2025).

Here we use the orchid *Satyrium candidum* Lindl. as a test species to determine the presence of hawkmoth pollination on the Cape Peninsula. This species has floral tubes that are longer (c. 30 mm) than other fynbos *Satyrium* species with otherwise similar floral traits, and which have been shown to be pollinated by settling moths that typically have a shorter proboscis (Johnson 1997a). In general, *Satyrium* species with a sphingophilous syndrome (i.e. white, scented flowers with relatively long spurs) have been found to be pollinated by hawkmoths (Johnson et al. 2011; Van der Niet et al. 2011, 2015, 2025). Previous attempts to directly observe pollinators of *S. candidum* on the Cape Peninsula in the 1990s were unsuccessful and the only previous observation of hawkmoths visiting *S. candidum*

flowers comprises a single record in fynbos of the Cape mountains off the peninsula, but this observation was insufficient to confirm the role of hawkmoths as pollinators (see Liltved and Johnson 2012). Confirmation of hawkmoth pollination of this species would add a further case in fynbos vegetation and also shed light on whether hawkmoth pollination systems occur on the Cape Peninsula. Given that previous biogeographical analyses of hawkmoth pollination focused on plants with a sphingophilous floral syndrome, we further investigate the presence of hawkmoths in fynbos through their appearance in scientific collections and on citizen science platforms. We use these records to provide a pollinator-focused assessment of the presence of hawkmoths in the fynbos region versus other regions in South Africa to evaluate the purported rarity of hawkmoth pollination from the former and to provide potential explanations thereof.

Table 1. Plant species pollinated by hawkmoths and their vegetation type from the Cape Floristic Region and elsewhere in South Africa.

Region	Plant Family	Plant species	Vegetation type	References
Cape Floristic Region	Amaryllidaceae	<i>Brunsvigia bosmaniae</i>	Karoo scrub	(Raimundo 1998)
		<i>Crinum variable</i>	Karoo scrub	(Manning and Snijman 2002)
	Ericaceae	<i>Erica cylindrica</i>	Fynbos	(Van der Niet and Cozien 2022)
		<i>E. infundibuliformis</i>	Fynbos	(Van der Niet and Cozien 2024)
	Iridaceae	<i>Gladiolus emiliae</i>	Fynbos, Renosterveld	(Goldblatt and Manning 2002)
		<i>G. recurvus</i>	Renosterveld	(Goldblatt and Manning 2002)
		<i>Tritoniopsis nervosa</i>	Fynbos	(Manning and Goldblatt 2005)
	Orchidaceae	<i>Bonatea speciosa</i>	Forest	(Johnson and Liltved 1997)
		<i>Satyrium acuminatum</i>	Fynbos	(Van der Niet et al. 2015)
		<i>S. candidum</i>	Fynbos	This study
		<i>S. eurycalcaratum</i>	Fynbos	(Van der Niet et al. 2025)
		<i>S. jacottetae</i>	Fynbos	(Botes et al. 2020)
		<i>S. membranaceum</i>	Fynbos	(Botes et al. 2020)
		<i>S. pallens</i>	Fynbos/ Karoo scrub	(Van der Niet et al. 2015)
Rest of South Africa	Amaryllidaceae	<i>Crinum bulbispermum</i>	Grassland	(Johnson and Raguso 2016)
		<i>C. delagoense</i>	Grassland	(Johnson and Raguso 2016)
		<i>C. macowanii</i>	Grassland	(Johnson and Raguso 2016; Johnson et al. 2020)
		<i>Pancratium tenuifolium</i>	Savanna	(Manning and Smith 2017)
	Bignoniaceae	<i>Catophractes alexandri</i>	Savanna	(Vogel 1954)
	Capparaceae	<i>Crateva kirkii</i>	Savanna	(Johnson and Raguso 2016)
	Iridaceae	<i>Gladiolus longicollis</i>	Grassland	(Goldblatt and Manning 1998; Alexandersson and Johnson 2002; Goldblatt and Manning 2002; Johnson et al. 2009; Anderson et al. 2010; Johnson and Raguso 2016)
	Malvaceae Orchidaceae	<i>Adansonia digitata</i>	Savanna	(Taylor et al. 2020; Karimi et al. 2022; Venter et al. 2025)
		<i>Bonatea antennifera</i>	Savanna	(Johnson et al. 2020; Johnson et al. 2024)
		<i>B. polypodantha</i>	Savanna	(Balducci et al. 2020)
		<i>Disa cooperi</i>	Grassland	(Johnson 1995)

Region	Plant Family	Plant species	Vegetation type	References
		<i>Habenaria clavata</i>	Grassland	(Johnson et al. 2019; Johnson et al. 2020)
		<i>H. epipactidea</i>	Grassland	(Vogel 1954; Peter et al. 2009)
		<i>Mystacidium venosum</i>	Savanna	(Luyt and Johnson 2001)
		<i>Rangaeris muscicola</i>	Grassland	(Johnson and Raguso 2016)
		<i>Satyrium hallackii</i> subsp. <i>ocellatum</i>	Grassland	(Johnson 1997b)
		<i>S. longicauda</i>	Grassland	(Johnson et al. 2009; Johnson et al. 2011; Castañeda-Zárate et al. 2021; Johnson et al. 2020)
	Orobanchaceae	<i>Cynium adonense</i>	Grassland	(Vogel 1954)
		<i>Harveya speciosa</i>	Grassland	(Johnson and Raguso 2016)
	Pedaliaceae	<i>Holubia saccata</i>	Savanna	(Vogel 1954)
		<i>Sesamothamnus lugardii</i>	Savanna	(Johnson and Raguso 2016; Johnson et al. 2020)
	Plumbaginaceae	<i>Plumbago zeylanica</i>	Savanna	(Vogel 1954)
	Rubiaceae	<i>Conostomium zoutpansbergense</i>	Savanna	(Vogel 1954)
		<i>Gardenia thunbergii</i>	Savanna	(Johnson and Raguso 2016; Johnson et al. 2020)
		<i>Oxyanthus pyramidalis</i>	Forest	(Johnson et al. 2004; Johnson and Raguso 2016)
	Scrophulariaceae	<i>Zaluzianskya elongata</i>	Grassland	(Johnson et al. 2002)
		<i>Z. natalensis</i>	Grassland	(Johnson et al. 2002; Johnson et al. 2009)
		<i>Z. pulvinata</i>	Grassland	(Johnson et al. 2002)
	Apocynaceae	<i>Araujia sericifera</i> ¹	Urban gardens	(Coombs and Peter 2010)
	Convolvulaceae	<i>Ipomoea alba</i> ¹	Savanna	(Johnson and Raguso 2016)
	Liliaceae	<i>Lilium formosanum</i> ¹	Grassland	(Rodger et al. 2010; Johnson and Raguso 2016)
	Zingiberaceae	<i>Hedychium gardnerianum</i> ¹	Forest	(Johnson and Raguso 2016)

¹ Species invasive in South Africa.

Materials and methods

To evaluate whether hawkmoths pollinate the sphingophilous flowers of *Satyrium candidum*, fieldwork was conducted between 18 October and 1 November 2025 in a population of circa 40 plants that grew in a flat sandy area among rocky sandstone outcrops, c. 1 km north-east of St. James Peak in Table Mountain National Park on the Cape Peninsula. The area supports fynbos vegetation and had burnt two years previously.

To record flower visitors we performed direct observations (3 evenings, for a duration of 45 minutes after sunset, which is peak activity for several hawkmoth species (Johnson et al. 2020), and two day-time periods of 30 minutes each around mid-day). In addition, we also used between one and three Bushnell HD NatureView (model 119740) motion-activated cameras (present on 12 evenings). Cameras were set to record at night only to preserve battery life that would otherwise be depleted by excessive day-time recording due to wind-triggering. Cameras were placed circa 30 cm from an orchid inflorescence, and sensitivity was set to high to maximize opportunities to record visiting insects, including various kinds of moths (Johnson et al. 2020). All recordings were reviewed for the presence of insect visitation to flowers. Activity time, the number of flowers probed, and whether visitors carry orchid pollinaria on their proboscis were recorded.

Several plant traits were measured to compare these with those of other hawkmoth-pollinated *Satyrium* species (Johnson et al. 2011; Van der Niet et al. 2015, 2025; Castañeda-Zárate et al. 2021). The functional length of the nectar spur on one flower each from 24 different plants was measured from the tip of the spurs to the rostellum. For ten of these flowers the nectar volume was measured by gently squeezing nectar from a cut spur into a glass capillary tube; sugar concentration was measured with a hand-held 0–50% Bellingham & Stanley refractometer. The distance from the top of the nectar column in the spur to the rostellum, representing the minimum proboscis length required to consume any nectar, was also measured. Finally, pollination success of the 24 flowers was measured by recording whether pollinaria had been removed and massulae deposited on the stigmas.

Further observations of crepuscular visitors to *S. candidum* in fynbos were conducted in the first flowering season after fire on 16 November 2008 along Franschhoek Pass (southern side) and on 9 October 2011 in the mountains south-east of the Mount Hebron nature reserve. Observations commenced at sunset and lasted for circa 1 hour. At these sites no further measurements were taken.

To evaluate the historical and current presence of hawkmoths in the fynbos versus other regions of South Africa, we accessed the digital database of Sphingidae that are held in the Iziko Museum in Cape Town (SAMC) on 22 October 2025. Although this does not provide an exhaustive list of hawkmoth collections in South Africa, the Iziko collection is the most relevant one for studying Cape hawkmoths due to its geographical location. To compare hawkmoth species presence in the fynbos versus other South African regions, we used the records from the Western Cape Province as a proxy for fynbos distribution and compared it to the remainder of South Africa. We also accessed the database of iNaturalist records to compare Sphingidae species between the Western Cape Province and the rest of South Africa from all Researchgrade records downloaded on 10 November 2025. For both datasets we distinguished the Cape Peninsula from the rest of the Western Cape Province. Finally, the resulting list of hawkmoth species in both areas was further evaluated for their role as pollinators of South African plants based on a literature survey of pollination studies. We performed a search on ISI Web of Knowledge with “sphingid*” OR “hawkmoth*” OR “moth*”, in combination with “Africa” AND “pollinat*” as search terms. The resulting list was interrogated for studies of hawkmoth pollination performed in South Africa. We then recorded whether these studies were of species that occur in the fynbos. We also considered the meta-analysis performed by Johnson and Wester (2017), and included all empirical studies of hawkmoth pollination referred to therein. Finally, the search was supplemented with publications such as unpublished theses, dissertations and magazine articles that are not on ISI Web of Knowledge, but comprise studies of hawkmoth pollination.

Results

During the two-week period of field observations on the Cape Peninsula, four visits by hawkmoths to *S. candidum* flowers during three nights were recorded: one visit from direct observations and three from camera traps (Fig. 1). In all cases hawkmoths foraged extensively from the nectar spurs of the orchid, and



Figure 1. Observed and potential hawkmoth-flower interactions on the Cape Peninsula. **A.** Painting of a presumed interaction between *Harveya capensis* and *Hippotion celerio* (adapted from a painting in Marloth (1913-1915)); **B.** *Hyles livornica* probing a *Satyrium candidum* flower in Table Mountain National Park on 18 October 2025; **C.** Motion-activated camera screengrab of the same interacting species on 31 October 2025. Hawkmoth individuals in both cases carried orchid pollinaria on their proboscis (not clearly visible on images).

in two cases hawkmoths visibly carried pollinaria of the orchid on their proboscides (Suppl. material 1). Three of the four hawkmoths could be identified as *Hyles livornica*, while the fourth individual could not reliably be identified (but could also be *H. livornica*). Camera trap footage (N = 7) and direct observations also revealed several settling moths, which either only approached inflorescences or very briefly landed on an inflorescence to probe one or a few flowers during very brief bouts. None of the observed settling moths could be identified, and none carried orchid pollinaria. At Franschoek Pass one large unidentified hawkmoth was observed visiting several *S. candidum* flowers, whereas at Mount Hebron three visits by large hawkmoth individuals (2 of which carried pollinaria), one visit by a small hawkmoth species and several visits by settling moths (none of which carried pollinaria) were observed.

Table 2. Nocturnal hawkmoth species that have been recorded as pollinators in the Western Cape Province (largely comprising the fynbos) and the rest of South Africa. The numbers are based on the number of iNaturalist records (Researchgrade only) and the number of pinned specimens in the SAMC. All species present in the Western Cape are also present on the Cape Peninsula, unless stated otherwise.

Hawkmoth species	Western Cape Province		Rest of South Africa	
	Present (iNaturalist/SAMC)	Pollinator (number of plant species)	Present (iNaturalist/SAMC)	Pollinator (number of plant species)
<i>Agrius convolvuli</i>	Yes (53/3)	Yes (2)	Yes (413/15)	Yes (23) ²
<i>Basiothia charis</i>	No	No	Yes (9/5)	Yes (1)
<i>Basiothia medea</i>	No	No	Yes (213/12)	Yes (1)
<i>Basiothia schenki</i>	Yes (13/0) ¹	No	Yes (83/10)	Yes (8)
<i>Coelonia fulvinotata</i>	Yes (207/17)	No	Yes (146/6)	Yes (4)
<i>Daphnis nerii</i>	Yes (42/2)	No	Yes (149/11)	Yes (1)
<i>Hippotion celerio</i>	Yes (170/9)	Yes (3)	Yes (436/16)	Yes (9)
<i>Hippotion eson</i>	Yes (582/21)	Yes (1)	Yes (281/9)	Yes (6)
<i>Hippotion osiris</i>	Yes (5/0) ¹	No	Yes (34/3)	Yes (3)
<i>Hippotion rosae</i>	No	No	Yes (17/1)	Yes (1)
<i>Hyles livornica</i>	Yes (105/11)	Yes (8)	Yes (135/8)	Yes (3)
<i>Nephele accentifera</i>	No	No	Yes (50/7)	Yes (4)
<i>Nephele comma</i>	Yes (22/0)	Yes (1)	Yes (204/4)	Yes (5)
<i>Oligographa juniperi</i>	No	No	Yes (96/10)	Yes (1)
<i>Temnora plagiata</i>	Yes (13/3)	No	Yes (22/1)	Yes (1)
<i>Temnora pylas</i>	Yes (90/25)	Yes (3)	Yes (13/10)	Yes (1)
<i>Theretra cajus</i>	Yes (104/14)	Yes (2)	Yes (23/2)	Yes (3)
<i>Theretra capensis</i>	Yes (134/13)	Yes (4)	Yes (196/13)	Yes (2)

¹ Not recorded on the Cape Peninsula.

² In some cases this species is a nectar robber, and not a pollinator.

Mean $\pm$ SD spur length of *S. candidum* was 28.7 ± 2.4 mm, and the volume of the standing crop of nectar was 0.70 ± 0.36 μ l with a sugar concentration of $41.8 \pm 9.0\%$ (representing a minimum mean, since the concentration in three flowers exceeded 50% and could therefore not be reliably measured). The distance from the rostellum to the top of the nectar column was 21.2 ± 2.8 mm. Nineteen out of 24 flowers had at least one pollinarium removed, and 12 flowers had massulae deposited on their stigma. Only 5 flowers (21%) did not show any signs of pollination.

Seventy-four hawkmoth species have been recorded in South Africa on iNaturalist, all of which are present in the area outside the Western Cape Province, whereas only 30 of these were recorded in the Western Cape Province (Suppl. material 2). Fifty-three species featured in the SAMC collection, all of which are present in the area outside the Western Cape Province, with only 21 of these recorded in the Western Cape Province (Suppl. material 2). Therefore, not a single hawkmoth species in South Africa is unique to the Western Cape Province. Of the 78 hawkmoth species recorded in South Africa in total, 18 have been recorded as pollinators of South African plants in general (Tables 1, 2) and 8 of these species occur in the Western Cape Province (Table 2).

Discussion

Observations from this study revealed hawkmoth pollination in *S. candidum* in accordance with its typical sphingophilous floral syndrome. These observations are consistent with hawkmoth pollination systems in several other *Satyrrium* species

with similar floral traits that are fully or partially pollinated by hawkmoths (Johnson et al. 2011; Van der Niet et al. 2015, 2025). The nectar spur length of *S. candidum* closely matches the proboscis length of *H. livornica* measured as 30.5 mm in another study (Johnson and Liltved 1997), and is similar in length to the floral tube of distantly related plant species that belong to the short-tongued hawkmoth pollination guild (Johnson et al. 2017). The spur length and nectar depth suggest that the reward may be largely inaccessible to settling moths in the Cape region, which usually have a proboscis shorter than 20 mm (Johnson 1997a), and may explain the observed difference in flower visiting behavior between hawkmoths and settling moths. The sugar concentration in the nectar is relatively high and would render the nectar rather viscous, which could explain the long duration of foraging bouts by hawkmoths (Josens and Farina 2001). Together, this suggests that the floral traits of *S. candidum* represent typical adaptations for hawkmoth pollination. However, we did not mirror the nocturnal observations with systematic diurnal observations. We therefore cannot exclude the possibility that additional visits by diurnal pollinators, such as long-proboscid flies, may occur, although hawkmoths and long-proboscid flies usually constitute mutually exclusive specialized pollination systems (e.g. Campbell et al. 2016; Johnson et al. 2026). Further observations, and experiments that quantify the contribution of diurnal versus nocturnal pollinators are required to confirm whether *S. candidum* is specialized for exclusive pollination by hawkmoths (Van der Niet et al. 2015, 2025).

The observations of hawkmoth pollination of *S. candidum* in the fynbos of the Cape Peninsula represent the first confirmed case of this pollination system in the region. Marloth's (1913–1915) records of hawkmoth pollination of species that occur there cannot be verified due to lack of spatiotemporal details and, in the case of *Gethyllis* (Amaryllidaceae), his misinterpretation of the long floral tube as a nectar reservoir (Manning and Snijman 2002; Kiepiel and Johnson 2024). One possibility is that hawkmoths have only recently appeared in the region, for instance due to the availability of larval food provided by ornamental plants in urban gardens and parks of the Cape Town metropolitan area. Indeed, iNaturalist features hundreds of recent citizen scientist records of hawkmoth presence from the urban areas of the Cape Peninsula. However, historical collections of hawkmoths from the Cape Peninsula in the SAMC date back as far as 1862. Furthermore, several other native plant species on the Cape Peninsula, such as *Bonatea speciosa*, are likely similarly pollinated by hawkmoths, based on observations of interactions with hawkmoths away from the Cape Peninsula, (Johnson and Liltved 1997). Finally, based on similarities in floral traits with closely related plant species that are known to be pollinated by hawkmoths elsewhere (Johnson and Raguso 2016), species on the Cape Peninsula such as *Harveya capensis* are also likely to be pollinated by hawkmoths (Table 1, Fig. 1). Together, this suggests that hawkmoth pollination on the Cape Peninsula is not of recent anthropogenic origin and that the focused effort of observing hawkmoths for this study has resulted in an extension of known hawkmoth pollination in the fynbos region.

Along with hawkmoth pollination of other typical fynbos plants, the observations presented here are consistent with the long-term presence of hawkmoths as a reliable pollination niche in the fynbos biome. Nevertheless, the number of hawkmoth-pollinated plant species and lineages is substantially smaller compared to elsewhere in South Africa (Table 1). Although this is consistent with

previous suggestions that hawkmoth pollination is relatively rare in fynbos, several alternative explanations for this discrepancy must be considered. First of all, the fynbos region is substantially smaller compared to the rest of South Africa. Nevertheless, other relatively small areas, such as the coastal and montane regions of KwaZulu-Natal, are rich in hawkmoth-pollination systems (e.g. Johnson et al. 2020; Castañeda-Zárate et al. 2021), suggesting that surface area alone does not explain the patterns. Similarly, the number of plant species in fynbos is smaller compared to the rest of South Africa. However, this difference does not account for the almost 3-fold larger number of species observed to be hawkmoth pollinated outside fynbos (Table 1). On the other hand, the currently available studies do not necessarily reflect a random sample or similar sampling effort of the species pools, rendering quantitative comparisons vulnerable to sampling bias.

Similar to the apparent smaller number of hawkmoth-pollinated plant species in fynbos, this region also contains fewer hawkmoth species (Table 2, Suppl. material 2). A smaller number of pollinator species may be indicative of a smaller number of plant species that rely on a particular functional pollinator group. This has been indirectly considered in the context of parallel declines in plant and pollinator species (Biesmeijer et al. 2006), but evidence from South African pollinator groups is inconclusive. On the one hand, the larger number of oil-collecting bee species in the winter-rainfall region appears to be matched by a larger number of plant species that depend on these bees (Johnson et al. 2015; Pauw et al. 2017; Kuhlmann et al. 2020). On the other hand, two specialized nectarivorous bird species alone pollinate dozens of plant species in fynbos *Erica* and *Proteaceae* (Rebelo 1987). Furthermore, unlike in oil-bee pollination systems, pollination by short-tongued hawkmoths is usually not specialized at the hawkmoth species-level and a small number of functionally similar species may sustain a relatively large number of plant species that depend on them. The absolute number of pollinator species may therefore not represent the breadth of the pollination niche (e.g. Johnson and Raguso 2016).

In addition to arguments supported by quantitative data, there has been a long-standing idea that a lack of suitable host plants for hawkmoth larvae in fynbos may limit their presence (cf. Johnson 1997b), as has also been argued in the case of butterflies (Cottrell 1985). Many plant groups that are key larval hosts for hawkmoths are rare or absent from fynbos, and hawkmoth larvae tend to feed on broad soft leaves whereas fynbos plants tend to have sclerophyllous foliage (Ballesteros Mejia et al. 2020). The relatively large number of hawkmoth records in museums and on citizen science platforms may partly reflect the presence of exotic plants in human-altered landscapes that are suitable larval hosts. For instance, *Theretra capensis* feeds on *Vitaceae* including *Vitis vinifera*, and its presence in a wine-growing region may be artificially high. However, the host plants of the polyphagous larvae of *H. livornica* comprise a diverse range of taxa, including taxa that occur in the fynbos (Pinhey 1975), whereas *T. pylas* larvae also feed on a Cape plant, *Anthospermum aethiopicum* (Dickson 1953). Finally, commonly recorded pollinating hawkmoth species in the Western Cape Province of the genus *Hippotion* use *Zantedeschia aethiopica* as host plant (Pinhey 1975), a species that is widespread in the Cape Floristic Region and beyond. Therefore, although the pool of potential host plants in fynbos appears relatively minor, they are not altogether absent. Interestingly, even though the floral

syndrome of pollination by settling moths in fynbos appears less common than outside the region (Johnson 2004), a number of species in several relatively large genera are apparently pollinated by settling moths (Makholela and Manning 2006), and a potential settling moth pollination guild may occur in fynbos (Van der Niet 2026). Unlike Sphingidae, several species of settling moths appear to have specialized larval host associations with typical fynbos plants in *Erica*, *Cliffortia*, and Proteaceae (Staude et al. 2023), which may facilitate a more important role as pollinators compared to hawkmoths, but further quantitative work is needed to confirm this.

Altogether, it appears that the hawkmoth pollination niche is available for fynbos plants, including those on the Cape Peninsula, but current quantitative evidence suggests that it appears to be more restricted than in other regions of South Africa. This is in line with personal observations which suggest that flower visitation rates are higher, and hawkmoth-flower interactions are easier to record outside the fynbos vegetation (compare Johnson et al. 2020; Van der Niet et al. 2025). However, objective comparisons of potential hawkmoth pollination systems inside and outside fynbos vegetation are needed, and should ideally be supplemented with similar analyses of other pollination systems. Pollination network studies could be potentially useful for obtaining such data, but these are rare for the South African flora, and they would require appropriate effort in terms of nocturnal pollinator observations. Perhaps more useful would be implementation of novel methods for studying pollination, such as the use of motion-activated cameras (e.g. Johnson et al. 2020), as well as implementation of objective methods to quantify hawkmoth abundance in pristine ecosystems such as light trapping and identification of plant species representing hawkmoths' pollen loads through metabarcoding (Macgregor et al. 2019).

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Supplementary material 1

Supplementary video

Authors: Timotheüs Van der Niet

Data type: mp4

Explanation note: *Hyles livornica* visiting flowers of *Satyrium candidum* in Table Mountain National Park. The arrow indicates a large mass of pollinaria affixed to the hawkmoth's proboscis and touching the flower's stigma.

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Link: <https://doi.org/10.3897/AfrInvertebr.67.181280.suppl1>

Supplementary material 2

Supplementary table

Authors: Timotheüs Van der Niet, Steven D. Johnson

Data type: xlsx

Explanation note: Records of Sphingidae in South Africa based on collections in the SAMC and observations on iNaturalist.

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Link: <https://doi.org/10.3897/AfrInvertebr.67.181280.suppl2>

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.

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Author contributions

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.