TOPIC 5. **Plant-pollinator interactions**

Sílvia Castro, Marta Barberis, Marta Galloni

TOPIC 5. **Plant-pollinator interactions**

Pollination and pollinators Pollination syndromes The generalist specialist continuum Pollination limitation	45’ + 15’
Pollinator behaviour in flowers	45’ + 15’
Practical approaches	45’ + 15’

Pollination - a key mutualism
The importance of pollinators and pollination

A note on terminology

Plant-pollinator interactions

Pollination – process of transference (whatever the vector) of pollen from the anthers to the stigma

Pollination system – flower characteristics (colour, shape, size, odour, rewards, etc.) plus the animals that effectively transfer pollen

Pollination syndrome – phenotypic expression of traits in a flower, i.e. colour, shape, size, odour, rewards, etc.

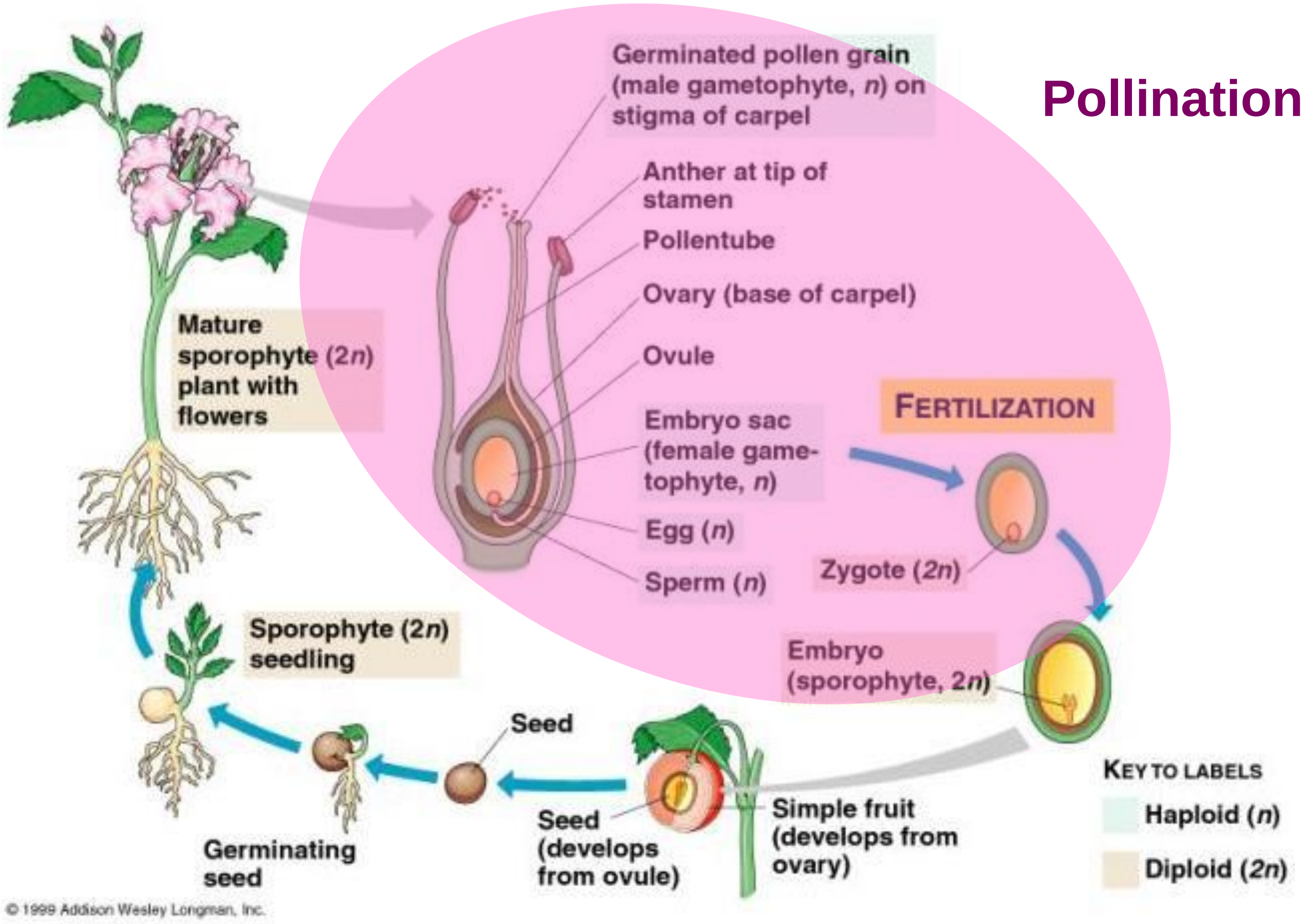
Pollinator guild(s) or **Pollinator functional group(s)** – floral visitors to a given plant species (or plant community)

Pollination - a key mutualism
The importance of pollinators and pollination

'It's easy to underestimate, and impossible to exaggerate, the importance of pollinators and the pollination services they provide to plants.' Ollerton 2021

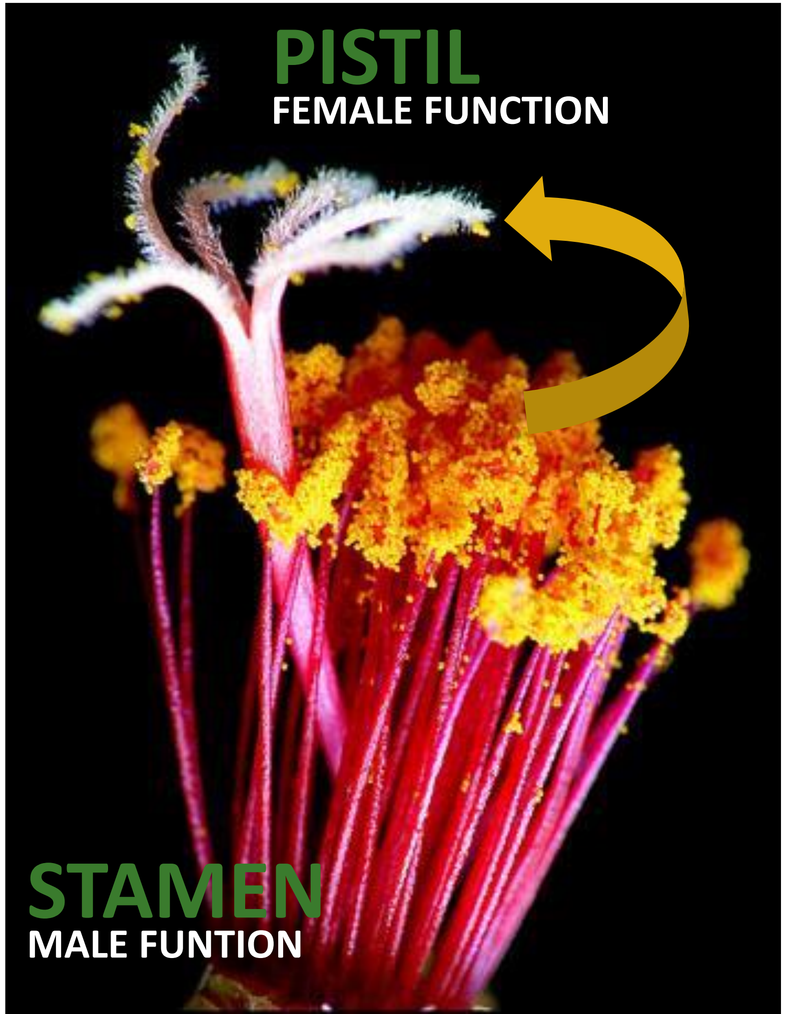
Pollination - a key mutualism
The importance of pollinators and pollination

Ecosystem service



Pollination - a key mutualism
The importance of pollinators and pollination

Pollination is the process of **transference of pollen from the anthers to the stigma** (from the same flower - self-pollination - or from a flower of a different plant - cross-pollination) that, when successful, culminates in fertilization and subsequent seed production.



… process far from being simple!

Pollination - a key mutualism
The importance of pollinators and pollination

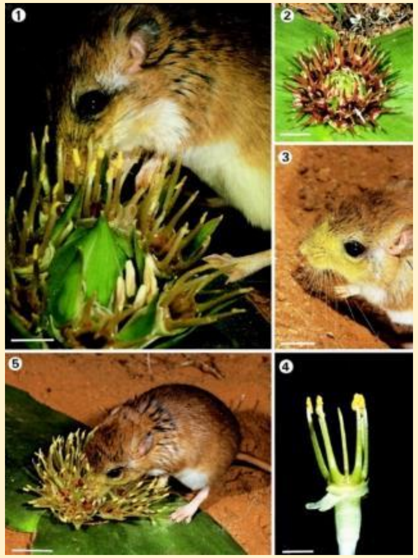
Pollination vectors

*'(…) plants have a **singular disadvantage** compared to animals when it comes to sex: **they can't just get up and find themselves a mate**.'* Berenbaum 1995

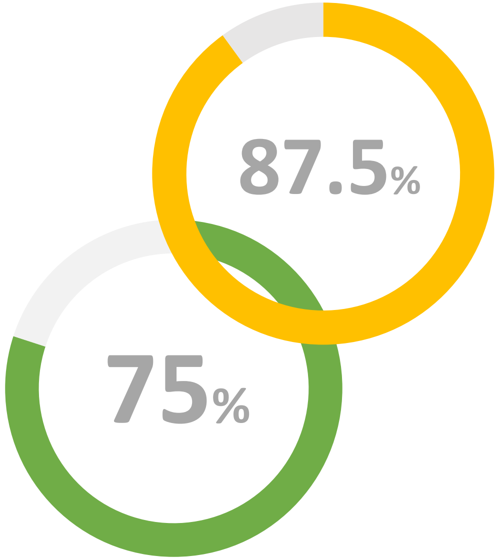
Pollination - a key mutualism
The importance of pollinators and pollination

Abiotic vectors (12.5%)

Biotic vectors (87.5%): insects (**entomophily**), birds, e.g., hummingbirds (tropics), felosa-comum (Iberian Peninsula), mammals, reptiles (islands), and *new interaction to discover*



87.5% das plantas silvestres dependem de polinização animal



75% das principais culturas dependem total ou parcialmente da polinização por insetos

Ollerton et al. 2011
Klein et al. 2011

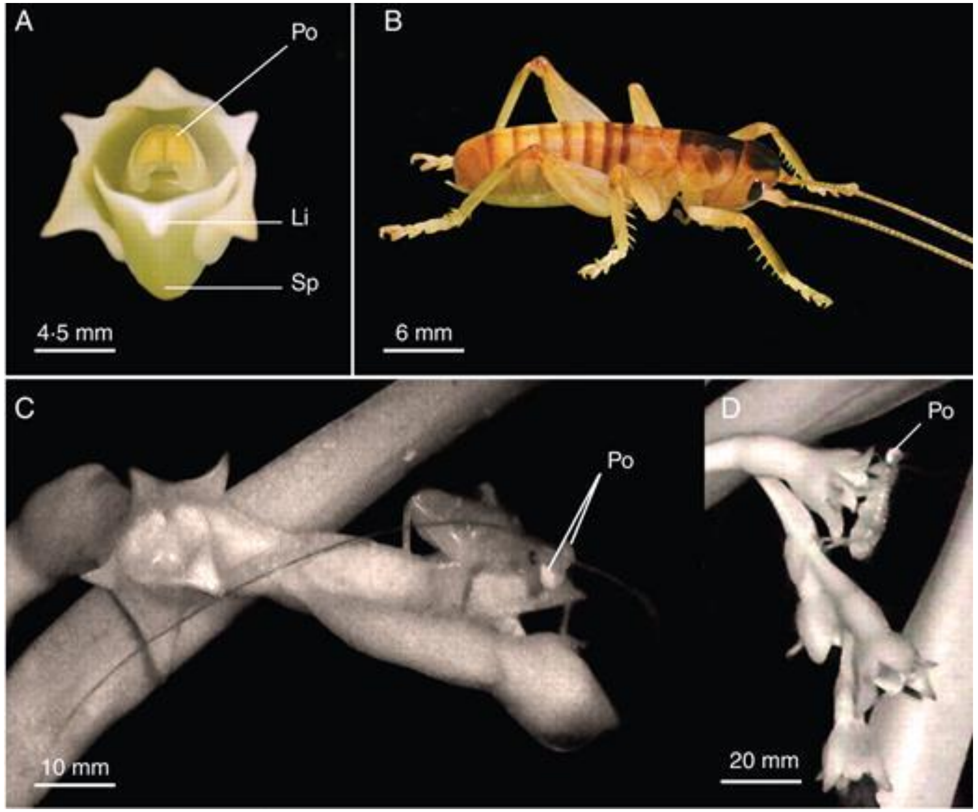
Pollination - a key mutualism
The importance of pollinators and pollination

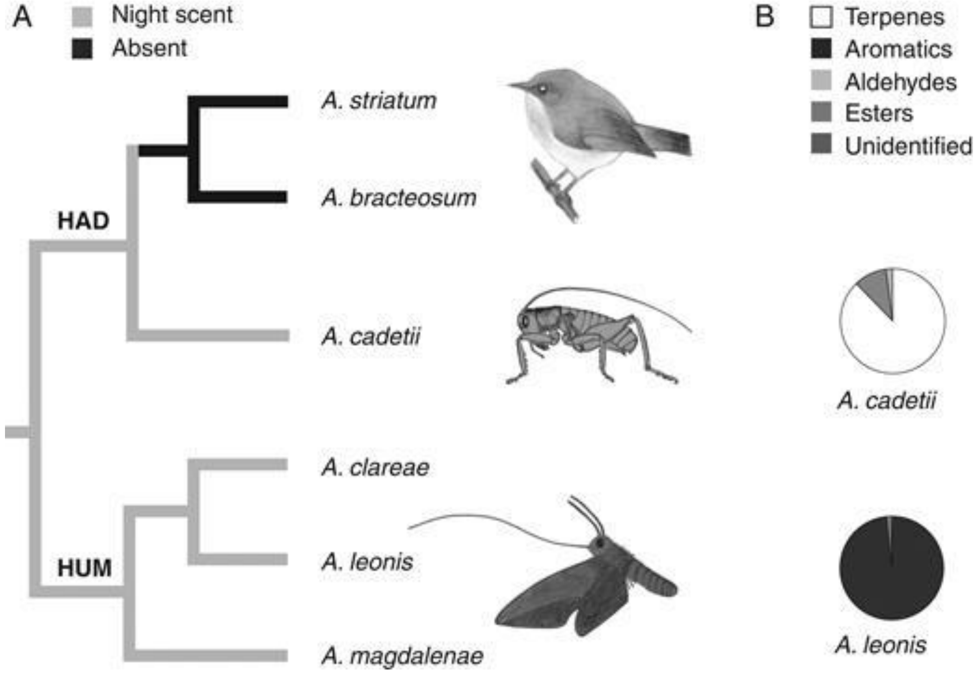
Ambophily

e.g. *Actinidea* spp. (kiwifruit) flowers have two main pollination systems, **wind pollination** marked by pendulous flowers with large and fleshy stigmas, production of high quantities of pollen and synchronous mass flower production lasting a short period of time, and **insect-pollination**, specifically **buz- pollination**, marked by the production of attractive flowers, floral scent, high amounts of pollen as reward, gradually maturing anthers and large number of ovules

Pollination - a key mutualism
The importance of pollinators and pollination

… more importantly, new pollinators are continuously being discovered, especially in areas of the globe that are less known and explored





Angraecum (Vandeae, Epidendroideae)

Micheneau et al. 2010 Orthoptera a new order of pollinators

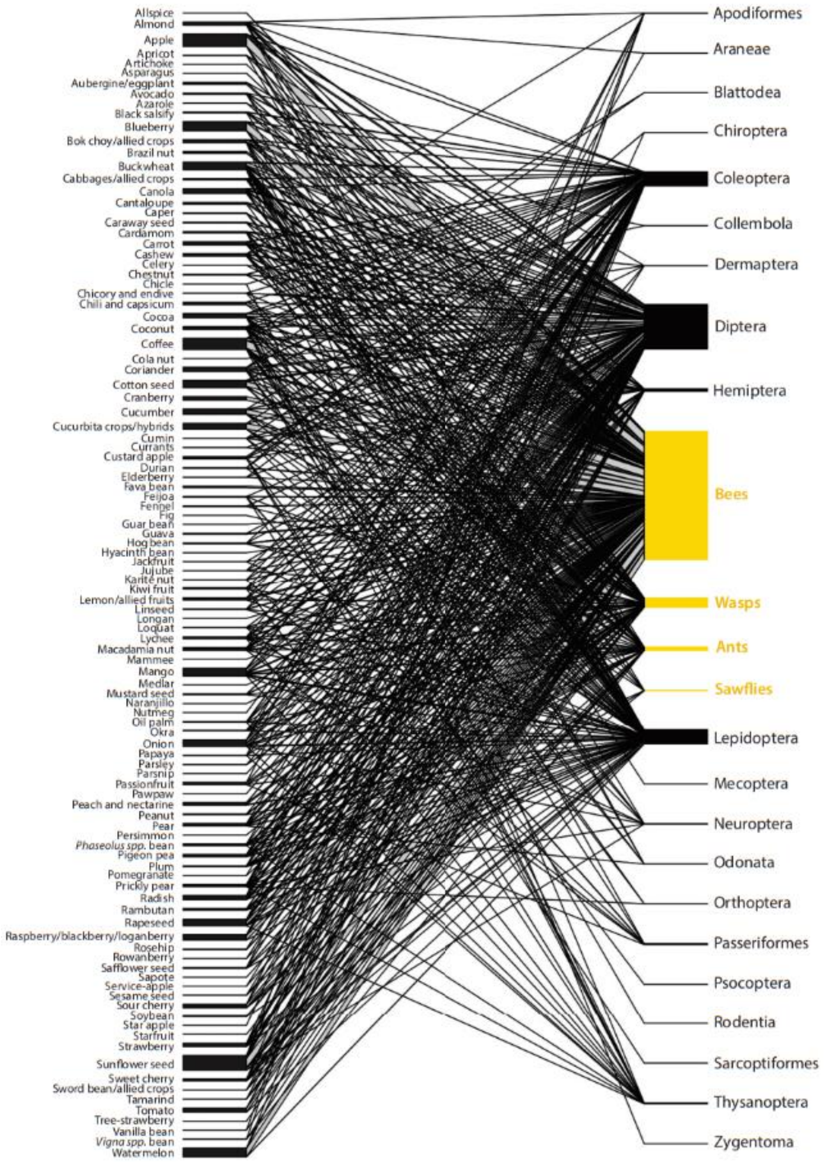
TABLE 2.1 The estimated number of described species in the major pollinator groups.

Taxon	Estimated number of pollinating species in the major groups	Diversity of significant subgroups	Sources
Lepidoptera (butterflies and moths)	141,600		Wardhaugh (2015)
• Moths (Heterocera)		123,100	
• Butterflies (Rhopalocera)		18,500	
Coleoptera (beetles)	77,300		Wardhaugh (2015)
• Flower chafers (Cetoniinae)		4,000	Sakai & Nagai (1998)
Hymenoptera (bees, wasps, ants)	70,000		Wardhaugh (2015)
• Bees (Anthophila)		20,446	Ruggiero *et al.* (2020)
• Spider wasps (Pompilidae)		5,000	Pitts *et al.* 2005
• Social wasps (Vespidae)		5,000	
Diptera (flies)	55,000		Wardhaugh (2015)
• Hoverflies (Syrphidae)		6,000	
• Bee-flies (Bombyliidae)		4,500	
Thysanoptera (thrips)	1,500		Wardhaugh (2015)
Aves (birds)	1,089		Regan *et al.* (2015)
• Hummingbirds (Trochilidae)		365	
• Honeyeaters (Meliphagidae)		177	
• Sunbirds (Nectariniidae)		124	
• White eyes (Zosteropidae)		100	
• Parrots (Psittacidae)		93	
Hemiptera (bugs)	1,000		Wardhaugh (2015)
Collembola (springtails)	400		Wardhaugh (2015)
Blattodea (termites and cockroaches)	360		Wardhaugh (2015)
Mammalia (mammals)	344		Regan *et al.* (2015)
• Bats (Chiroptera)		236	
• Non-flying mammals (various)		108	
Neuroptera (lacewings)	293		Wardhaugh (2015)
Trichoptera (caddisflies)	144		Wardhaugh (2015)
Orthoptera (crickets)	100		Wardhaugh (2015)*
Mecoptera (scorpionflies)	76		Wardhaugh (2015)
Psocoptera (barkflies)	57		Wardhaugh (2015)
Plecoptera (stoneflies)	37		Wardhaugh (2015)
Lacertilia (lizards)	37		Olesen & Valido (2003)
Dermaptera (earwigs)	20		Wardhaugh (2015)
Crustacea (mainly Isopoda)	11		Ollerton (1999), van Tussenbroek *et al.* (2016)
Polychaeta (marine worms)	3		van Tussenbroek *et al.* (2016)
Total	**349,371**		

* Possibly an overestimate, as only one species confirmed as a pollinator (Micheneau *et al.* 2010).

Pollinator guilds

More than just bees, the diversity of pollinators, but…



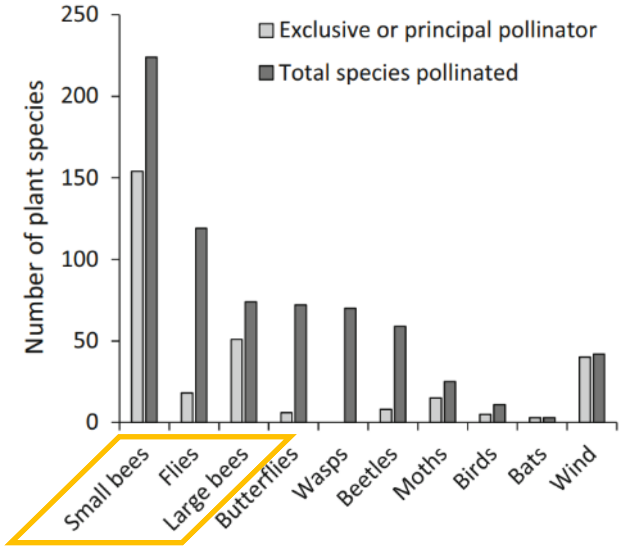


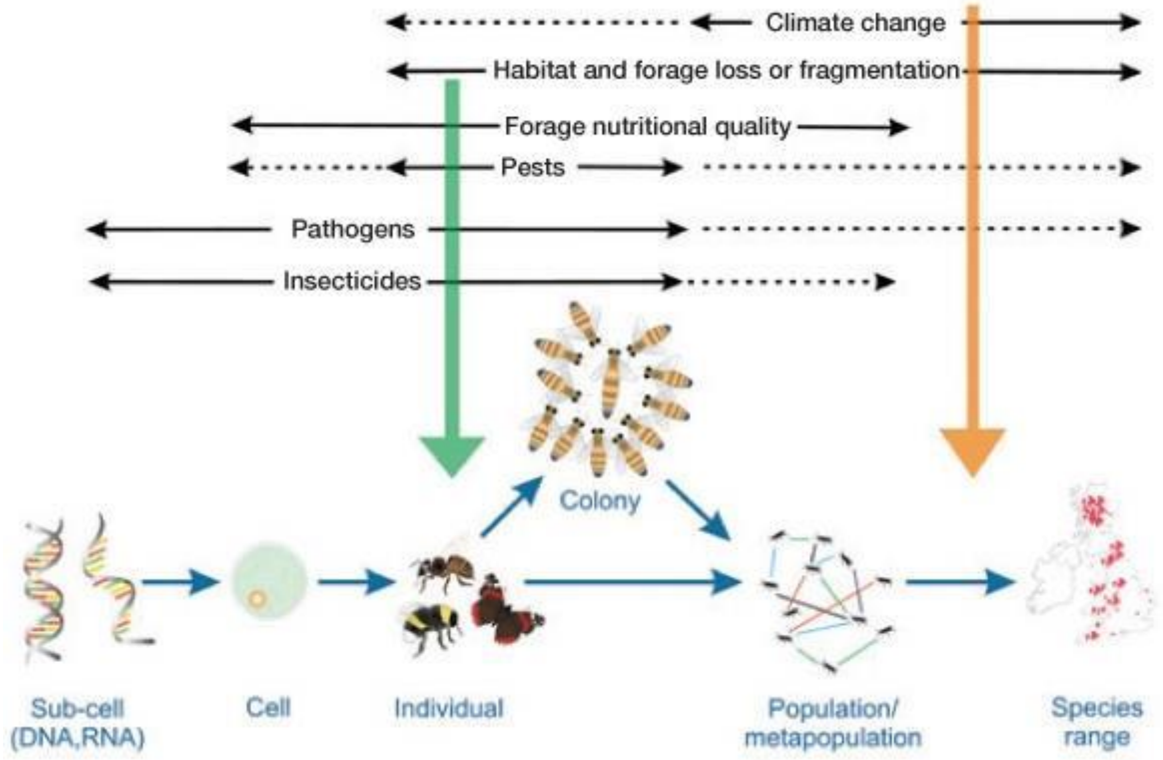
Fig. 1 Number of plant species (total 301) from Brazilian cerrado pollinated exclusively or principally by different flower-visiting taxa, and the total number of plant species that each group pollinates. Data from Gottsberger and Silberbauer-Gottsberger (2006)

Wardhaugh 2015, Ollerton 2017, Rader et al. 2019

Pollination - a key mutualism
Pollinator loss and conservation

Current drivers of pollinator declines

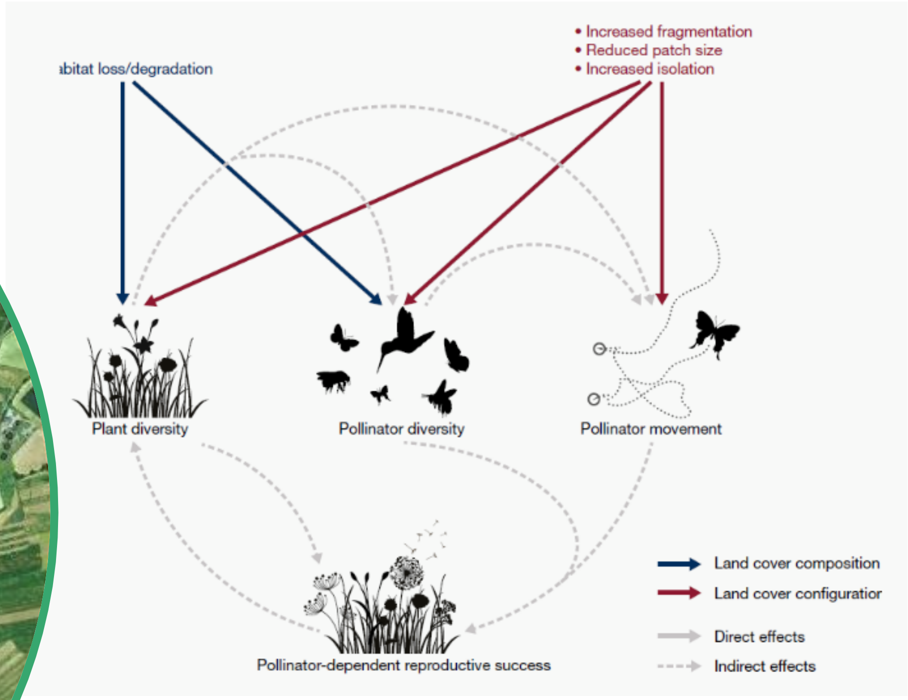
- Climate change
- Habitat loss and fragmentation
- Management intensification
- Agrochemicals use
- Pathogens, pests and invasive species

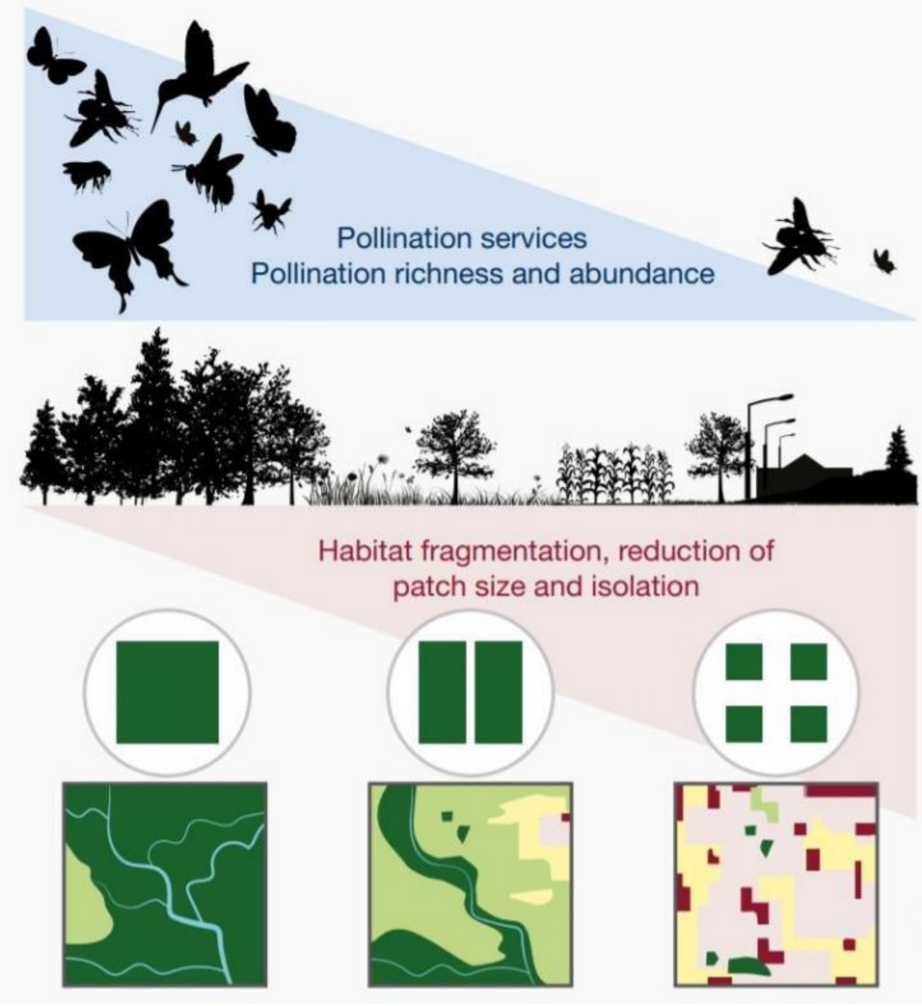


Vanbergen & Insect Pollinators Initiative 2013

Pollination - a key mutualism
Pollinator loss and conservation

Landscape effects

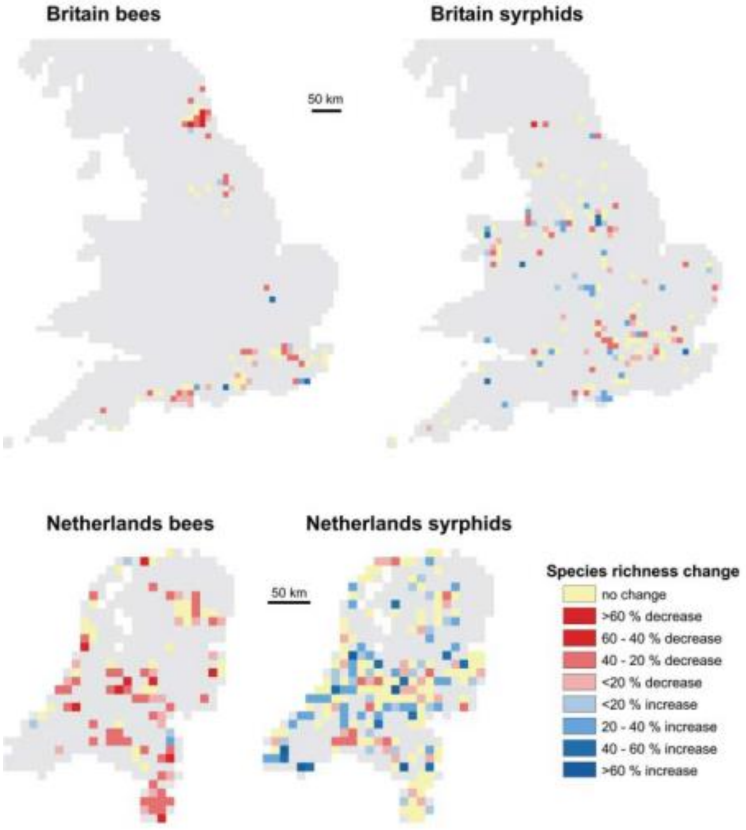


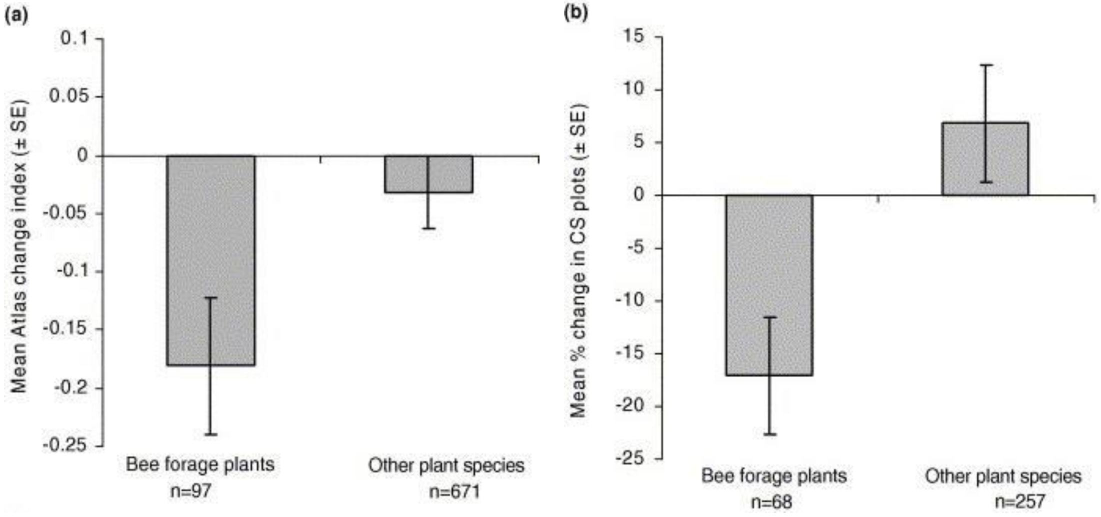


Ricketts et al 2008; Steffab-Dewenter & Westphal 2008; IPBES 2016; Hadley & Betts 2012

Pollination - a key mutualism
Pollinator loss and conservation

- **Parallel declines** in pollinators and insect-pollinated plants





	Obligatory outcrossing, insect pollinated	Obligatory outcrossing, wind or water pollinated	Predominantly self pollinating	*P*
Britain	−0.22 ± 0.06* (*n* = 75)	+0.18 ± 0.14† (*n* = 30)	−0.003 ± 0.70*† (*n* = 116)	0.009
Netherlands	+0.10 ± 0.08 (*n* = 182)	+0.18 ± 0.08 (*n* = 160)	−0.08 ± 0.11 (*n* = 143)	0.091
NL bee plants	−0.12 ± 0.13* (*n* = 42)	+0.18 ± 0.08† (*n* = 160)	−0.08 ± 0.11*† (*n* = 143)	0.036

Biesmeijer et al. 2006
Carvell et al. 2006

Pollination - a key mutualism
Pollinator loss and conservation

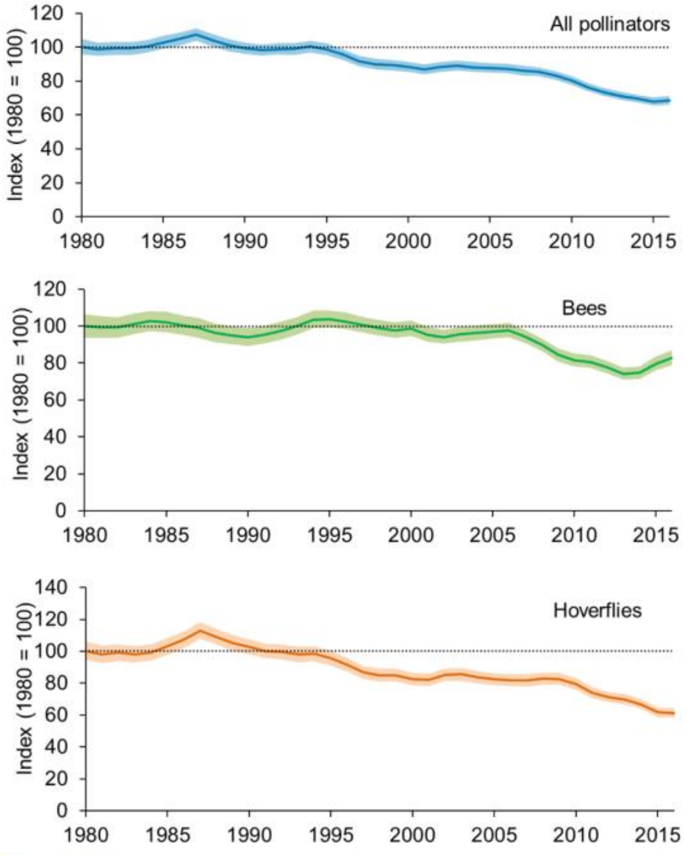


FIGURE 10.3 Changes in the distribution of all bee and hoverfly pollinators (top graph), bees (n = 137 species, middle graph) and hoverflies (n = 228 species, bottom graph) in the UK between 1980 and 2016. Data from Powney *et al.* (2019a)

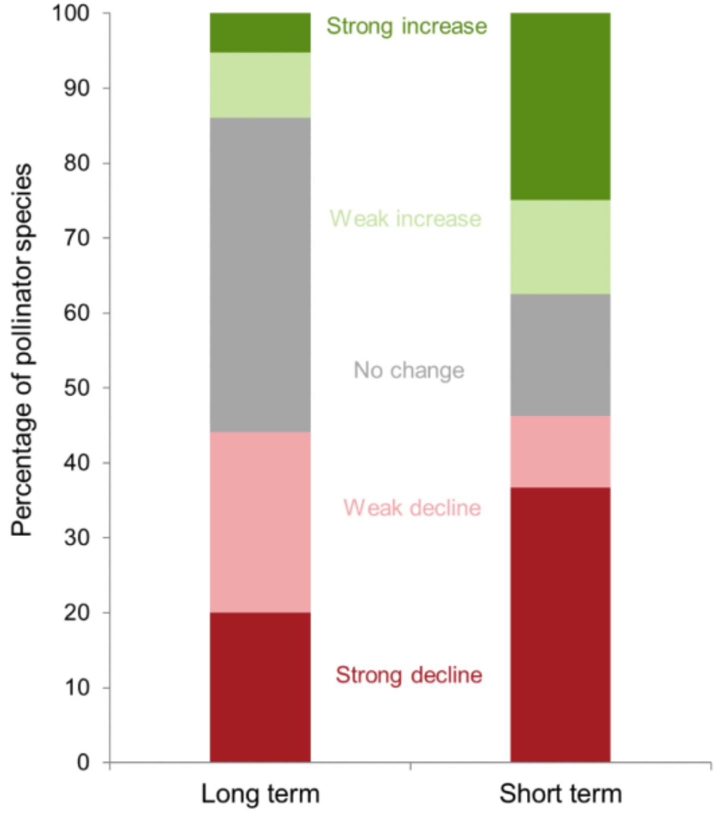


FIGURE 10.4 The percentage of UK bee and hoverfly species in each of five trend categories, calculated using the mean annual change over (a) the long term (1980–2016) and (b) the short term (2011–2016). Data from Powney *et al.* (2019a).

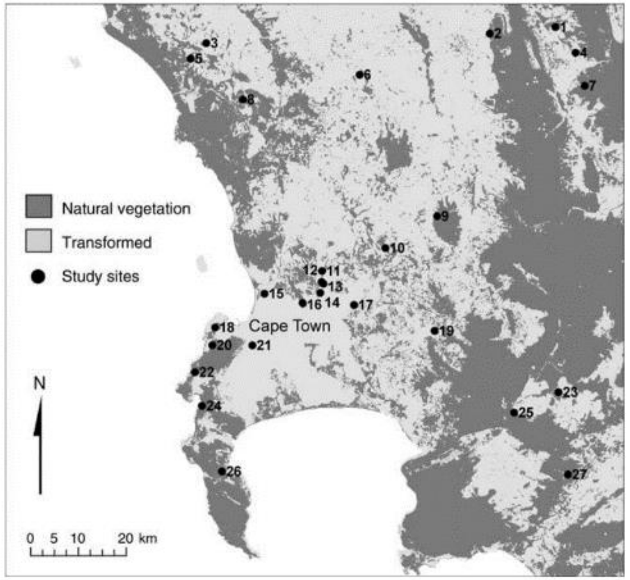
What changes are we facing?

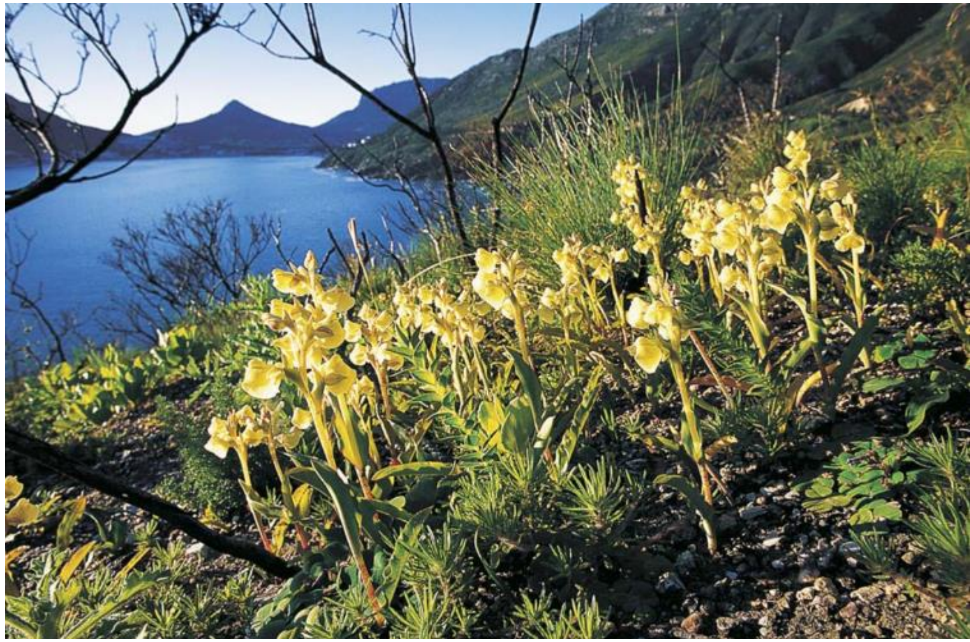
- Declines in insect communities
- Species extinctions

But, some species may cope under changing scenarios

Pollination - a key mutualism
Pollinator loss and conservation

- **System:** generalist oil-collecting bee and a community of oil-secreting plants Pauw 2007
- Local extinction of the bee pollinator has **negative effects on the reproduction of plants** specialized in this bee, while generalist plants replaced their pollinators

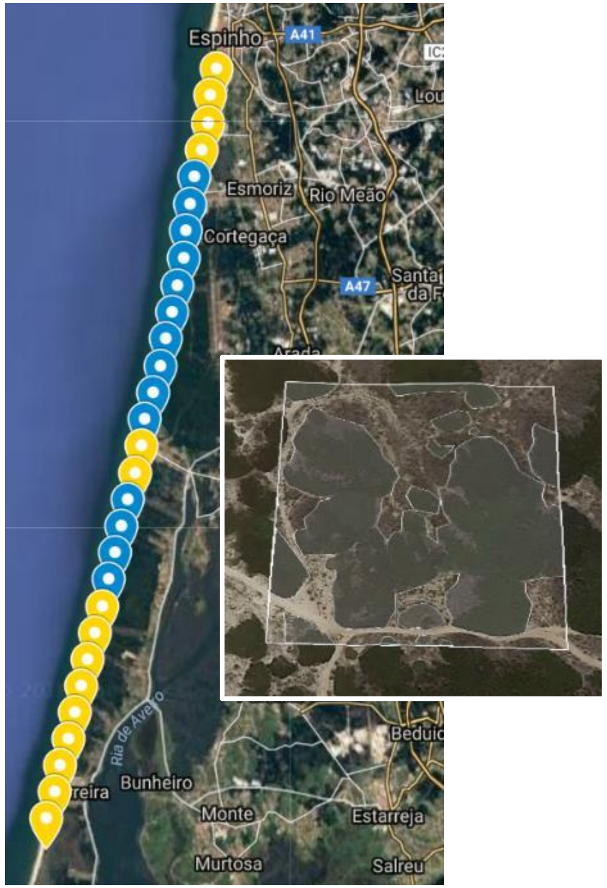


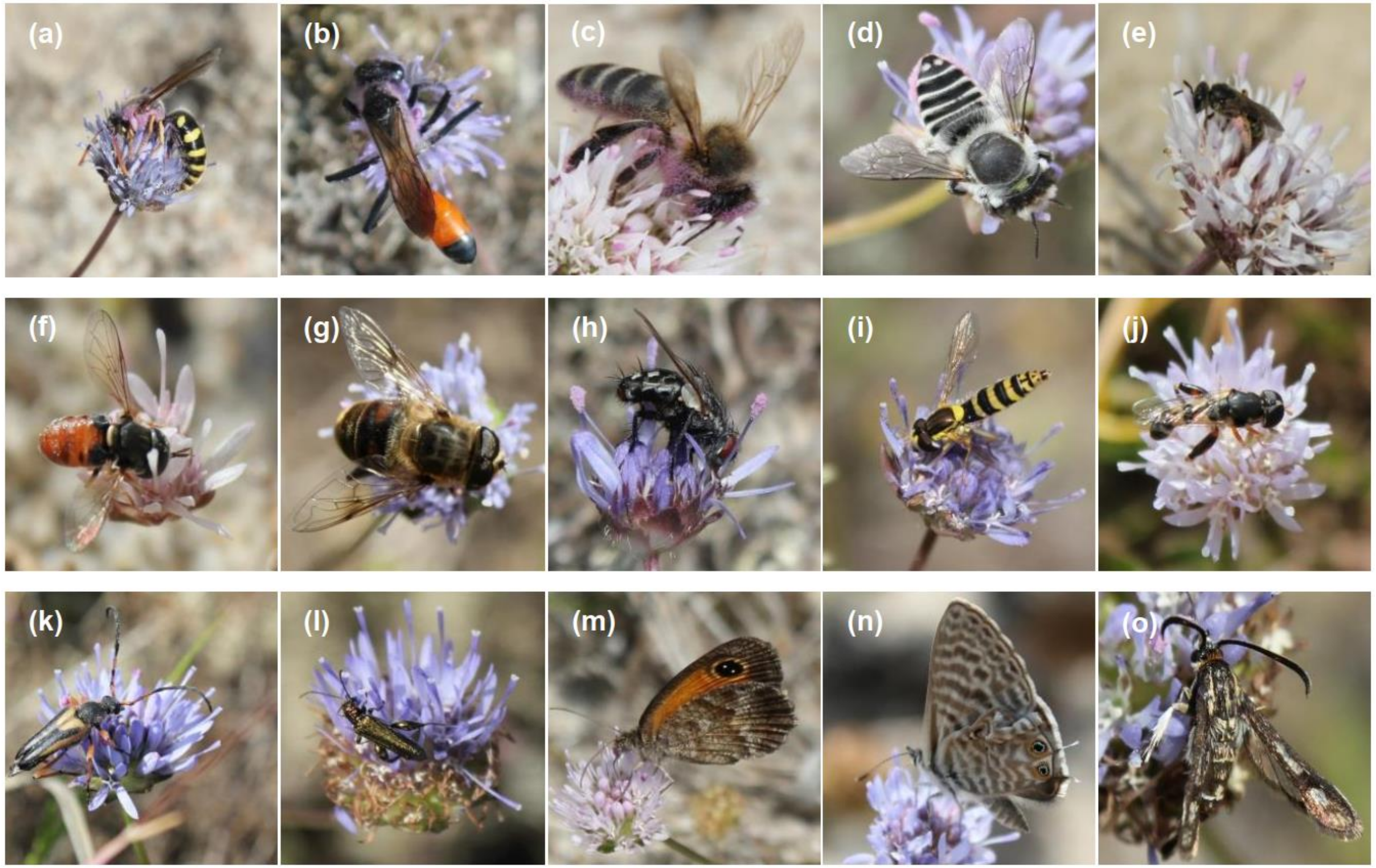


Pauw 2007

Pollination - a key mutualism
Pollinator loss and conservation

Jasione maritima **var.** ***sabularia***
NT, Red List of Vascular Flora

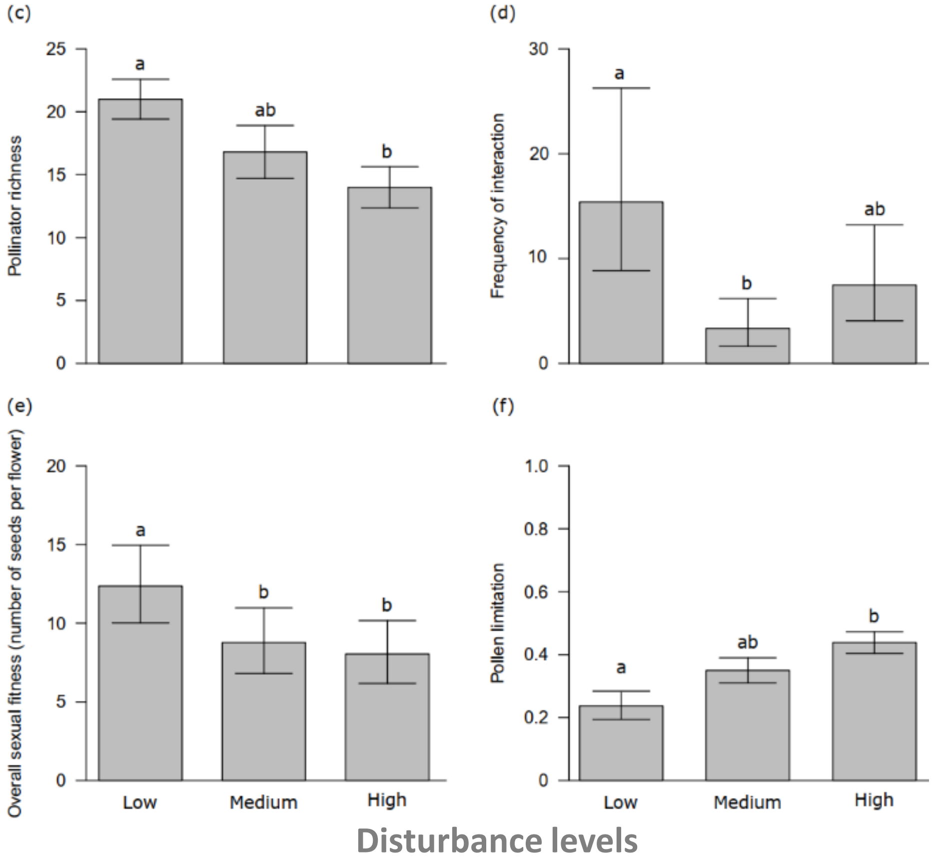


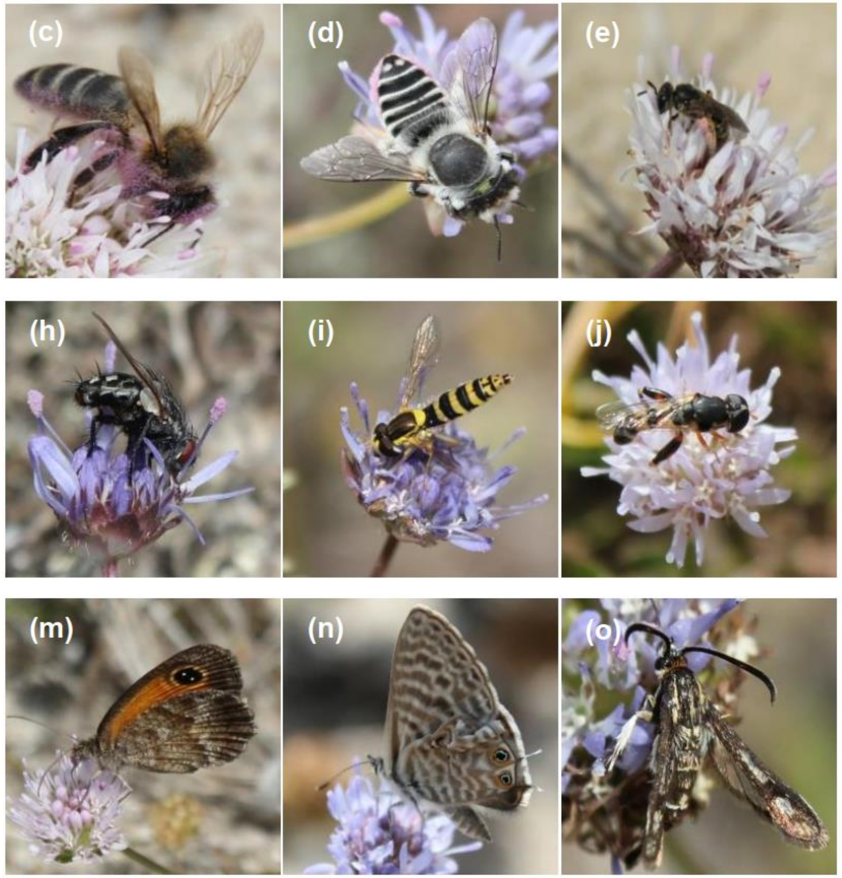


Mendes 2018; Mendes et al. (submitted)

Pollination - a key mutualism
Pollinator loss and conservation

Jasione maritima* var. *sabularia
NT, Red List of Vascular Flora





Mendes 2018; Mendes et al. (submitted)

Pollination - a key mutualism
Pollinator loss and conservation

- Decline in **quantity** and **quality** of pollination services through time

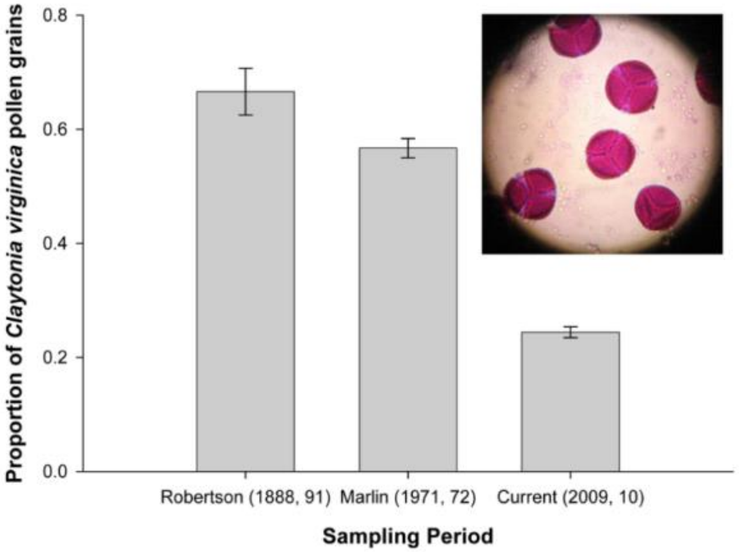
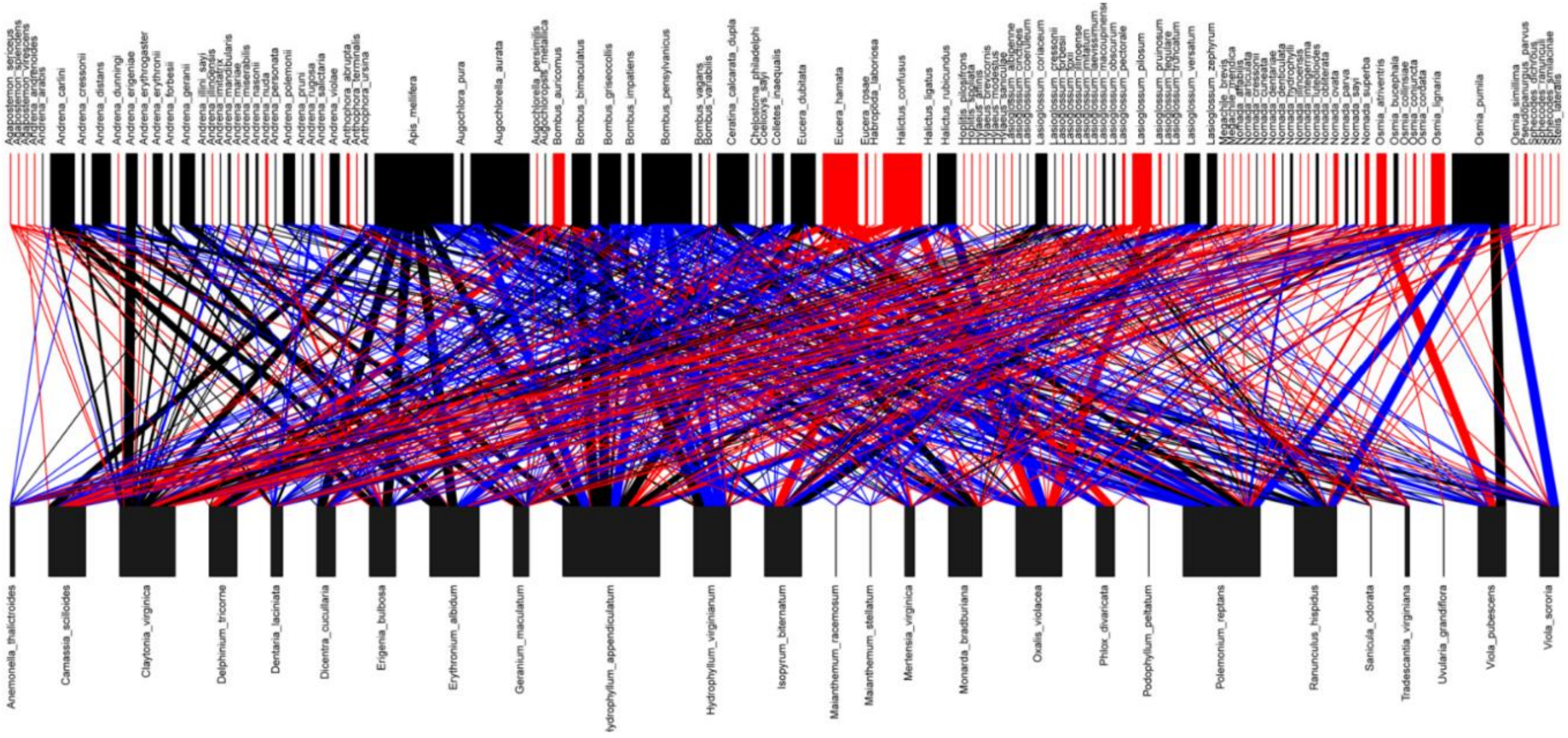


Fig. 4. Across 6 bee species, the proportion of *Claytonia virginica* pollen grains on the bodies of bee individuals captured visiting open flowers of that forb species declined over time, suggesting decreased fidelity and probability of successful pollination. Least-squared means are reported ± SE. Inset is a photo of *C. virginica* pollen grains.

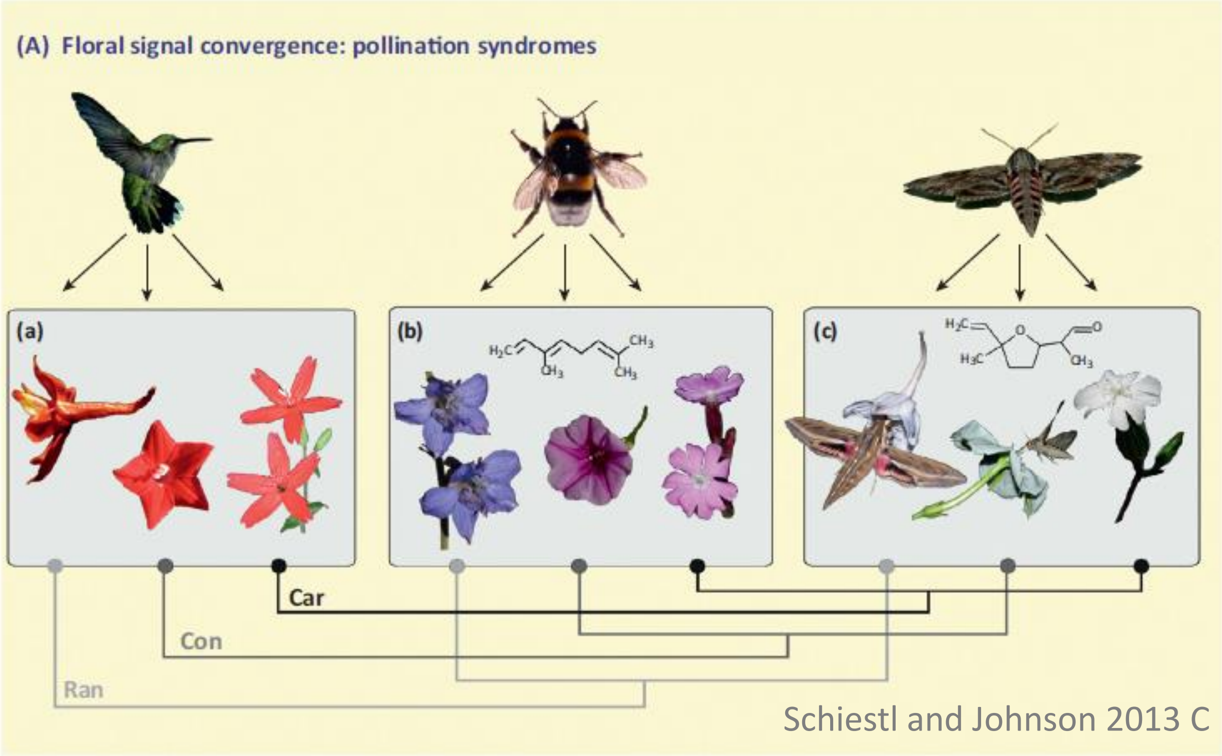


Burkle et al. 2013 Plant-pollinator interactions over 120 years

Pollination syndromes

Phenotypic expression of traits in a flower, i.e. colour, shape, size, odour, rewards, etc. – example of **convergent evolution**

- Concept that is a good model for studies of adaptive evolution and provide a focus for understanding key processes of natural selection
- **Controversial terminology** Wase 2006
- Syndromes are not laws , but just (fairly weak) trends, with links between floral traits and observed pollinators being far more complex



Schiestl and Johnson 2013 C

Pollination syndromes

Table 11.1
Classical Pollination Syndromes

Syndrome	*Pollinator*	*Timing of anthesis*	*Main colors*	*Nectar guides*	*Scent*	*Shape*	*Nectar site*	*Nectar volume and concentration*	*Pollen amount*	*Pollen deposited*
Cantharophily	Beetles	Day or night	Cream, green, usually dull	No	Strong, fruity or fermenting	Radial, flat or bowl-shaped	Exposed	Low V—mid C	Mid/high	Face, legs, underside
Myophily	Flies	Usually day	White, yellow, greenish	No	Usually mild, not sweet	Radial, flat; or flat inflorescence	Usually exposed	Low V—mid/ high C	Low/mid	Legs, face, thorax
Sapromyophily	Carrion and dung flies	Day or night	Purple/red/brown, mottled	No	Strong, decaying meat or feces	Radial or bilateral ± deep with trap	None		Mid	Most of body
Psychophily	Butterflies	Day	Red, orange, yellow, mauve	Maybe	Slight to moderate, sweet	Small, long tube, often *en masse*	Concealed	Low V—low C	Low	Face, tongue, (± legs)
Phalaenophily	Most moths	Dusk, night	Cream, yellow, greenish	No	Fairly strong, sweet	Usually radial, moderate tube	Concealed	Low/mid V—low C	Low	Face, tongue
Sphingophily	Hawkmoths	Dusk, night	White, cream, pale green	No	Strong and sweet	Usually radial, long tube or spur	Concealed	Mid V—low/ mid C	Low	Face, tongue
Melittophily	Bees	Dawn, day	Pink/purple/blue, white, yellow	Yes	Moderate, usually sweet	Bilateral or radial, Exposed or short/ medium tube	Exposed or Concealed	Mid V—mid C	Mid	Head, dorsal, or ventral body
Ornithophily	Birds	Day	Red, orange	No	Usually none	Bilateral or radial, short/medium tube	Concealed	High V—low C	Low	Forehead, beak, throat
Chiropterophily	Bats	Dusk, night 1 night only	Dull white, dull beige/green	No	Strong, fruity or fermenting	Bilateral or radial, bowl or brush	Usually exposed	High V—low/ mid C	High	Face, head

Willmer 2011

Pollination syndromes

Are syndromes really a helpful way of approaching floral biology?

- Pollination syndromes represent an **oversimplification** of plant-pollinator interactions
- Continuum between specialization and generalization – with most **flowers being generalists** rather than specialists
- Pollinator selection of floral traits might be rather weak and constrained by **other ecological factors** (e.g. herbivores)
- ‘Adaptationist story-telling’ on flower-pollinator coevolution has been greatly **shaped in the past**

Willmer 2011, Waser et al. 1996, Herrera 1996

Specialized – Generalized continuum

Successful pollination by a small number of animal species

Ecological continuum

- *Yucca* species and yucca moths
- Fig-fig wasp interactions

a. *Bombus pascuorum*
b. *Anthophora* sp.

Specialized – Generalized continuum

A note on (the complex) terminology

Ecological specialization – referring to the number of pollinating species to a given plant species

Functional specialization – referring to the number of different groups of pollinators

Phenotypic specialization – referring to the specific adaptations for pollination by a functional group

Ollerton et al. 2007

Evolutionary specialization – when evolving towards more specialized relationships (genetic changes associated with increased specialization) (*a process*)

Functional group specialization – similar to 'Functional specialization'

Armbruster 2017

Generalist – specialist continuum

Ecological factors that **promote the evolution of specialization** in pollination systems

- **Pollinators as selective agents**
- **Requirements for specialization** under the most effective pollinator principle

Gómez and Zamora 2006

Stebbins' **most effective pollinator principle** states that when pollinators are not limiting, plants are expected to specialize and adapt to the most abundant and effective pollinator species available.

Requirements	Mechanisms
Pollinators exert actual selective pressure	
Pollinators must benefit fitness	The effect of a pollinator species on fitness is called the *importance* of that pollinator for a plant species and is a consequence of its abundance at flowers (namely the *quantity component* of the interaction) **and** its per-visit effectiveness (the *quality component* of the interaction).
and	
Pollinators must produce a significant covariance between fitness value and a given trait value	This pollinator-mediated fitness-trait covariation is considered a *pollinator-mediated phenotypic selection* and is a consequence of the pollinator ability to discriminate between different plant phenotypes (*pollinator preference*) **or** the pollinator ability to match to specific plant phenotypes (*pollinator mechanical fit*).
Each pollinator species represents a distinctive selective agent	
Variation among floral visitors in their effect on fitness	This among-pollinator variation permits the establishment of a ranking of different pollinators according to their service to the plants, and it occurs because pollinators consistently differ in per-visit effectiveness **or** abundance.
and	
Among-pollinator variation in the phenotypic selection that they originate	This pollinator-mediated trade-off in phenotypic selection is crucial for successful specialization and is produced by among-pollinator difference in preference **or** mechanical fit.

Generalist – specialist continuum

Factors supporting the **evolution of generalization** in pollination systems

- **Unpredictability of the most important pollinators** – spatio-temporal variability in pollinator assemblages
- **Similarity among pollinators** in selective role
- Real effect of pollinators on plant fitness – consequences of adopting a **life-cycle approach** to the study of plant-pollinator interactions
    - Complete estimates of pollinator importance
    - Conflicting pressures disrupting pollinator-mediated selection

Gómez and Zamora 2006

- Spatio-temporal variability in pollinator assemblages

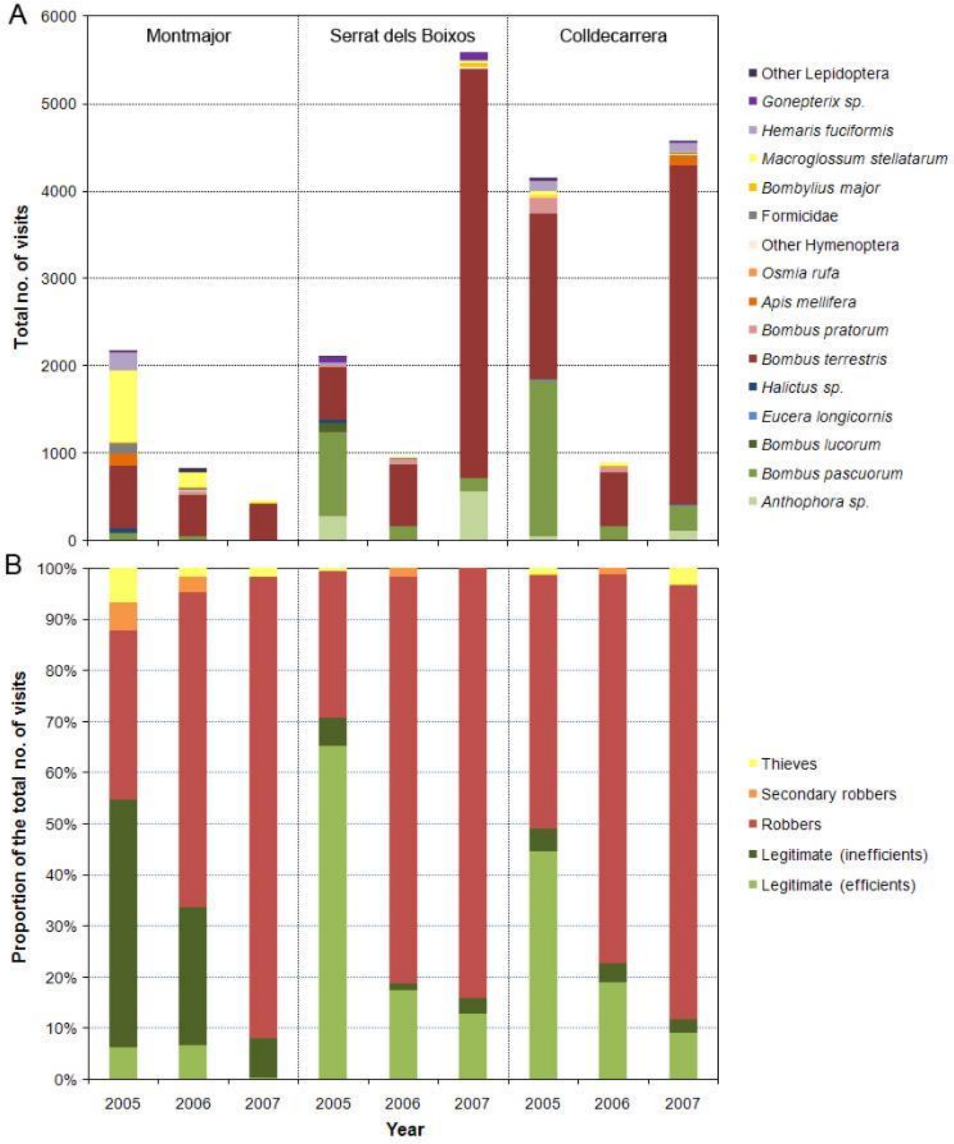
Polygala vayredae

Table 4.2.5 Probability of *Polygala vayredae* flowers to set fruits and seeds, and to receive efficient floral visits in a 15 min period along the three studied populations during 2005, 2006 and 2007.

Population	Year	Fruit set	Seed ovule ratio	Probability of efficient visit (%)
Montmajor	2005	7.4	4.8	0.6 ± 2.09
	2006	3.0	1.8	0.2 ± 0.78
	2007	1.9	0.9	0.01 ± 0.05
Serrat dels Boixos	2005	28.9	19.5	5.6 ± 8.69
	2006	22.3	16.7	0.7 ± 2.21
	2007	14.8	12.3	1.5 ± 2.86
Colldecarrera	2005	47.6	36.9	3.1 ± 8.20
	2006	21.0	15.3	1.1 ± 4.08
	2007	26.0	17.5	2.7 ± 7.51

a. *Bombus pascuorum*
b. *Anthophora* sp.

Castro et al. 2013



Generalist – specialist continuum

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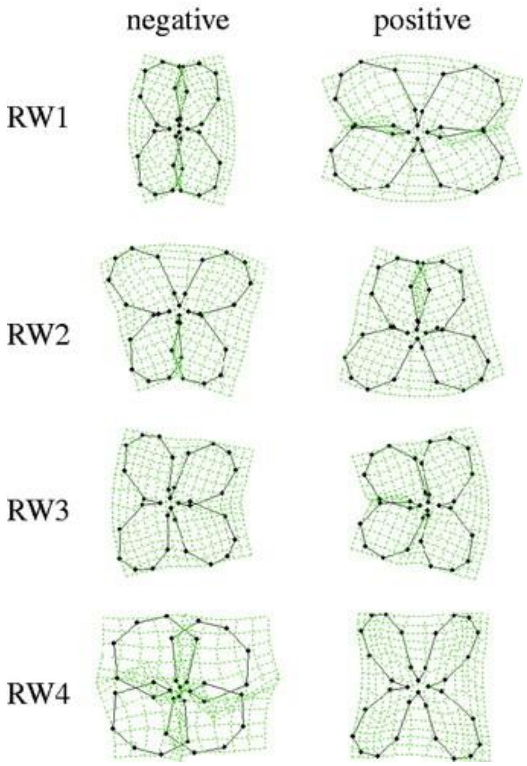
Gómez and Zamora 2006

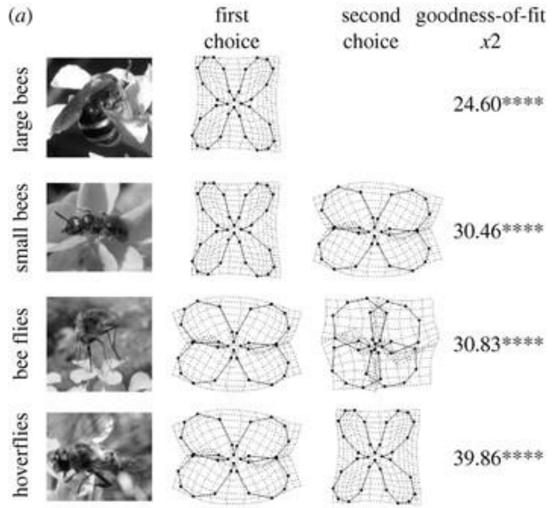
Generalist pollination systems

Identifying pollination niches of generalist flowers is a challenge

Generalist system *Erysimum* Goméz Lab

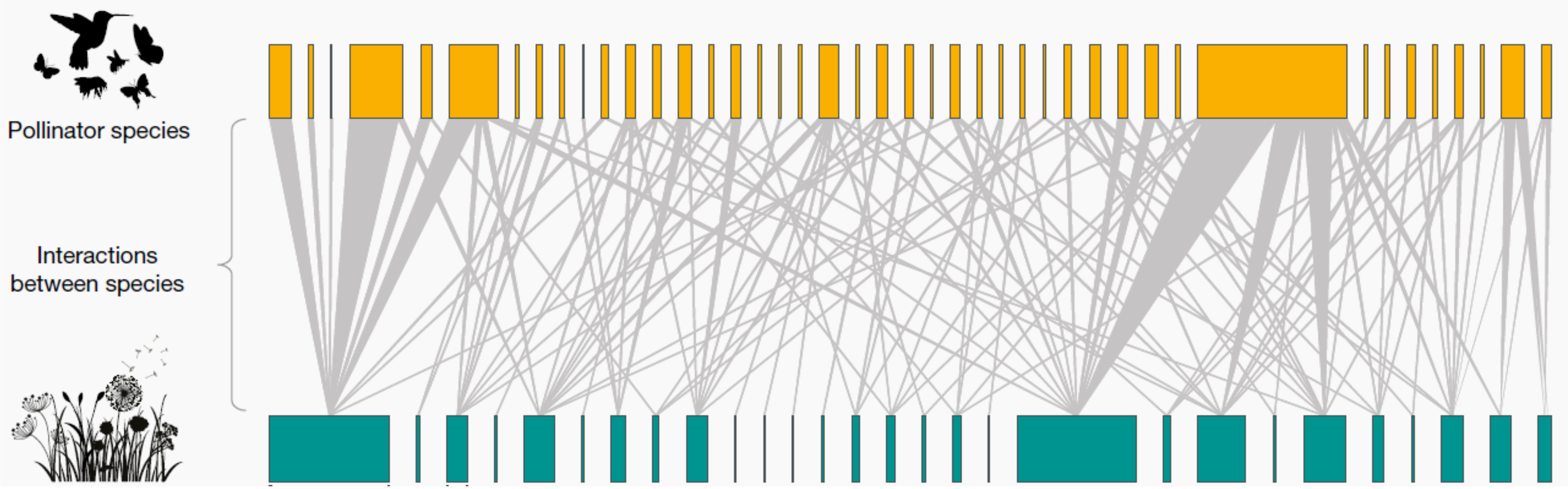
- Pollinator communities
- Trait selection in generalist system
- Evolution of pollinator niches



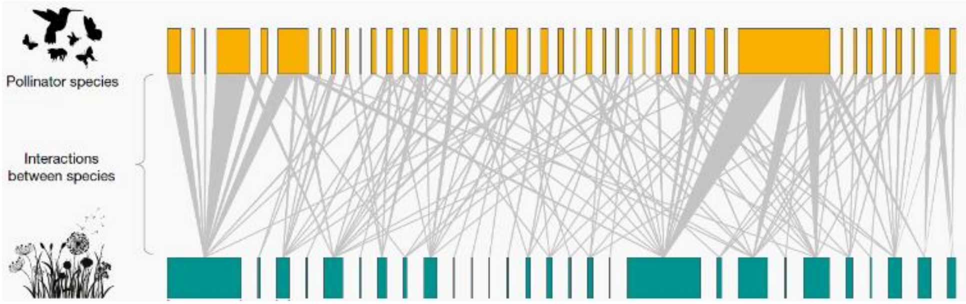


Plant-Pollinator networks

- Patterns of interactions between species
- Consequences for the functioning and stability of the communities
- Study the role of the different species within the network structure



Plant-Pollinator networks



Network parameters Examples

- Weighted connectance
- Weighted nestedness
- Interaction evenness
- Network specialization
- Plant niche overlap
- Pollinator niche overlap
- Plant robustness
- Pollinator robustness
- Generality
- Vulnerability

Network level descriptors

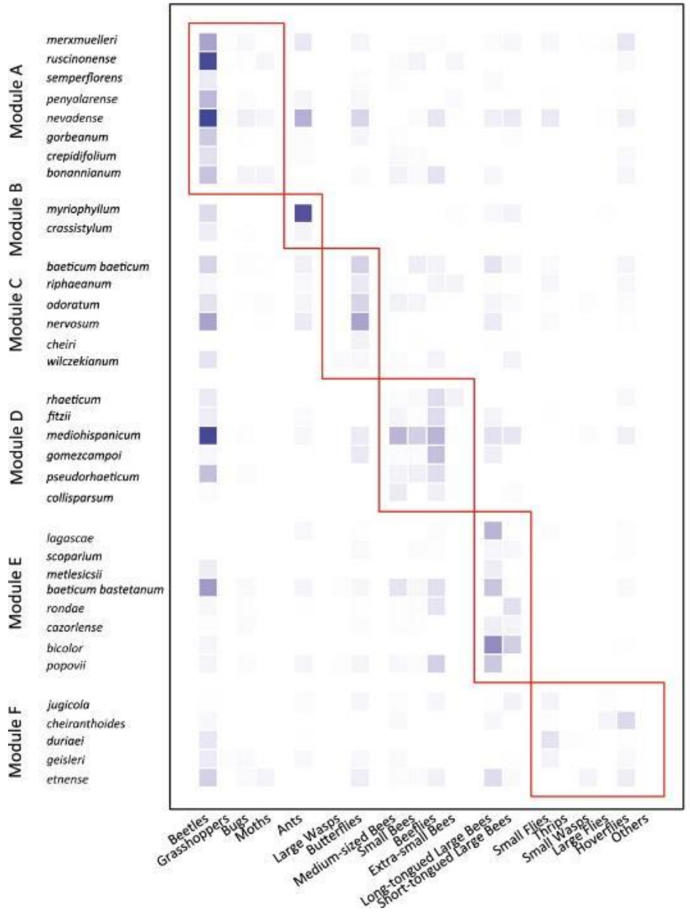
- **Normalised degree** for plants and for pollinators
- **Specialization (d')** for plants and for pollinators
- **Species strength** for plants and for pollinators

Species level descriptors

Plant-Pollinator networks

Erysimum Goméz et al. 2014a, 2014b

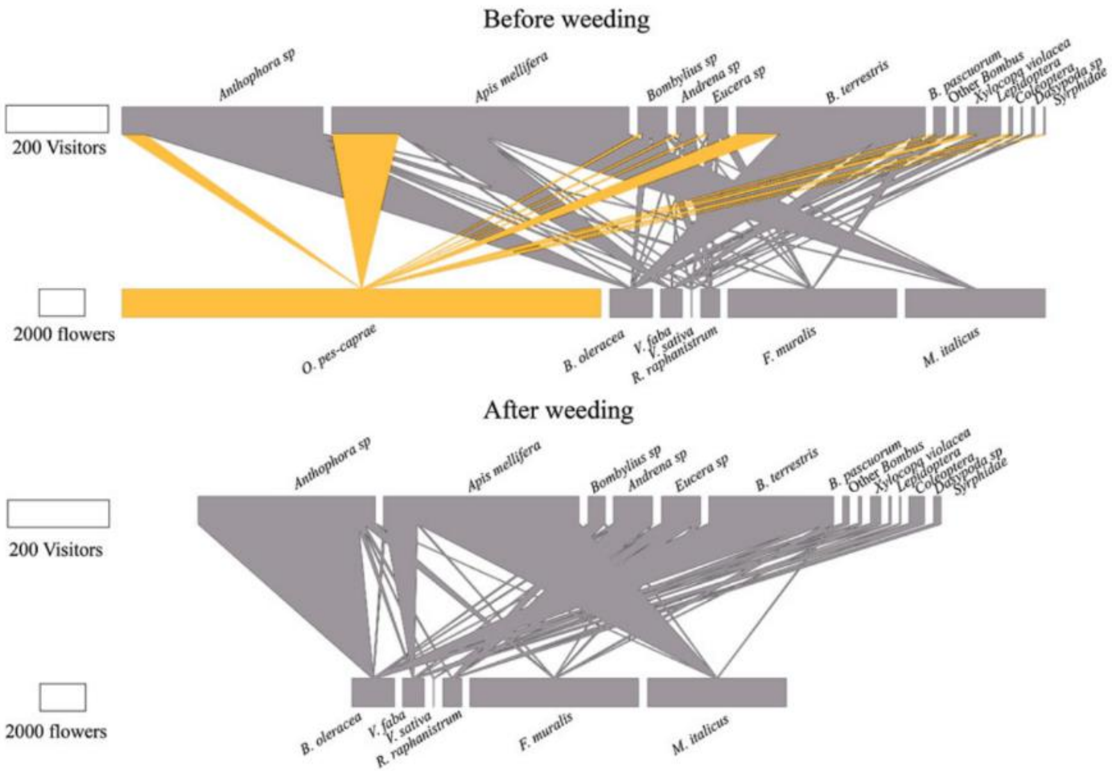
- *Erysimum* species group in multidimensional niches separated not by a shift of pollinators, but by **quantitative variation in relative abundances functional groups**



Plant-Pollinator networks

Oxalis pes-caprae Ferrero et al. 2013

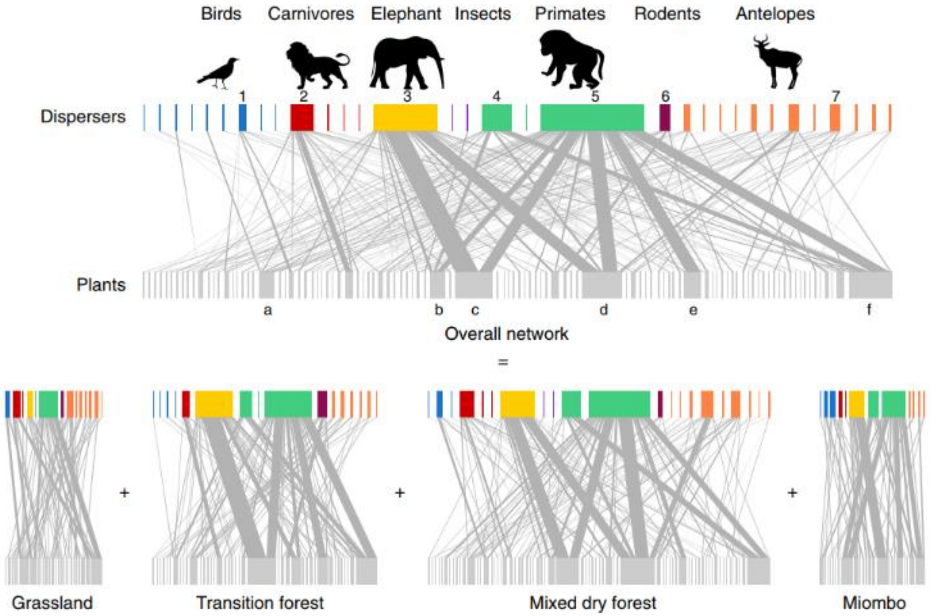
- Invader easily **established new interactions** with local pollinators
- Plant-pollinator **network was resilient** to the inclusion of the invader
- Some **facilitative effects** of the invader were observed



Plant-Pollinator networks

Multilayer networks Timóteo et al. 2013

- Plant-dispersal network is composed by spatially explicit communities of dispersers **spanning across habitats**, **functionally linking the landscape** mosaic



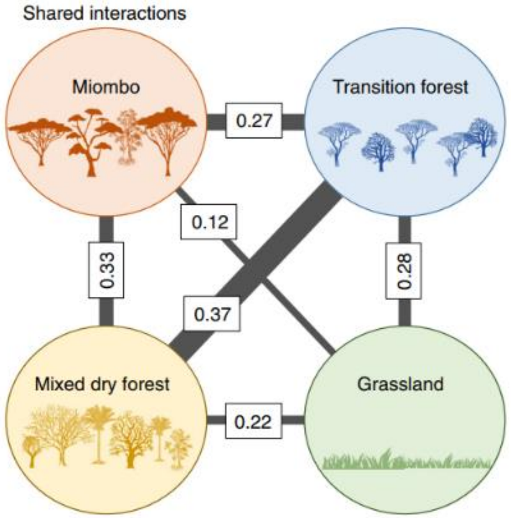
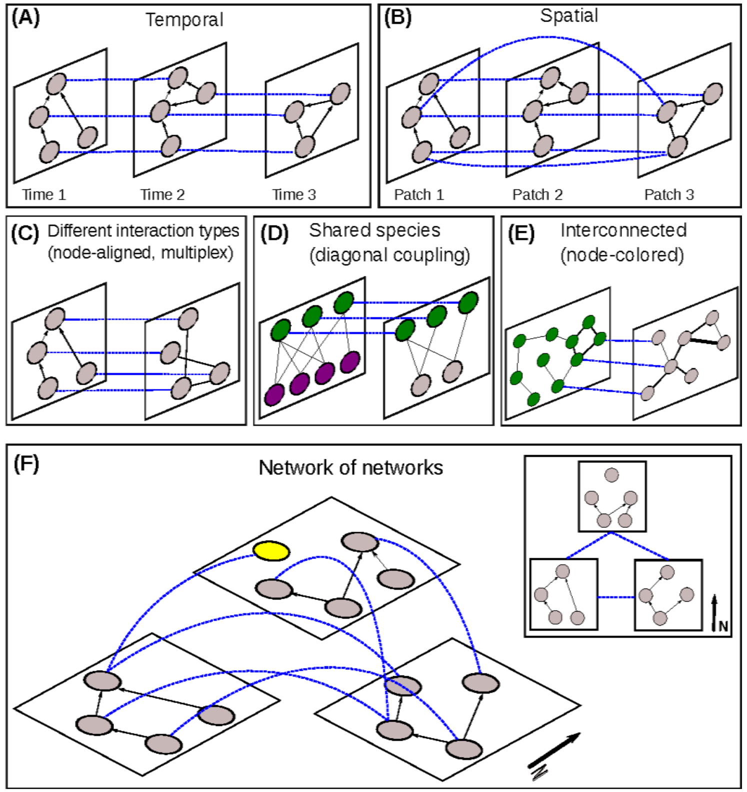


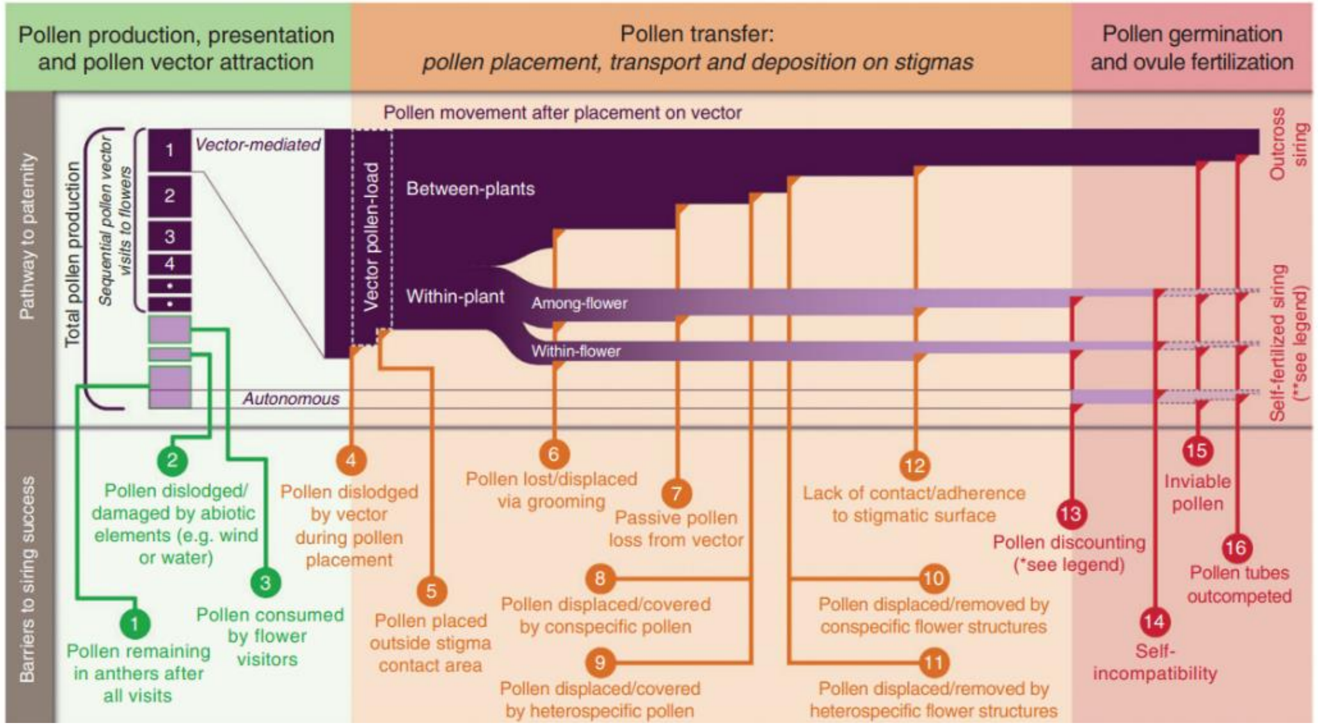
Fig. 6 Similarity in terms of shared interactions, between the habitat pairs of Gorongosa.



Pollination limitation

Consequences for plant conservation

- **Pollination limitation**, i.e. the inadequate **quantity** or **quality** of pollen for optimum seed set
- Pollen limitation is a **common** phenomenon in nature Knight et al. 2005



Minnaar et al. 2019; Inouye et al 1994

Pollination limitation
Consequences for plant conservation

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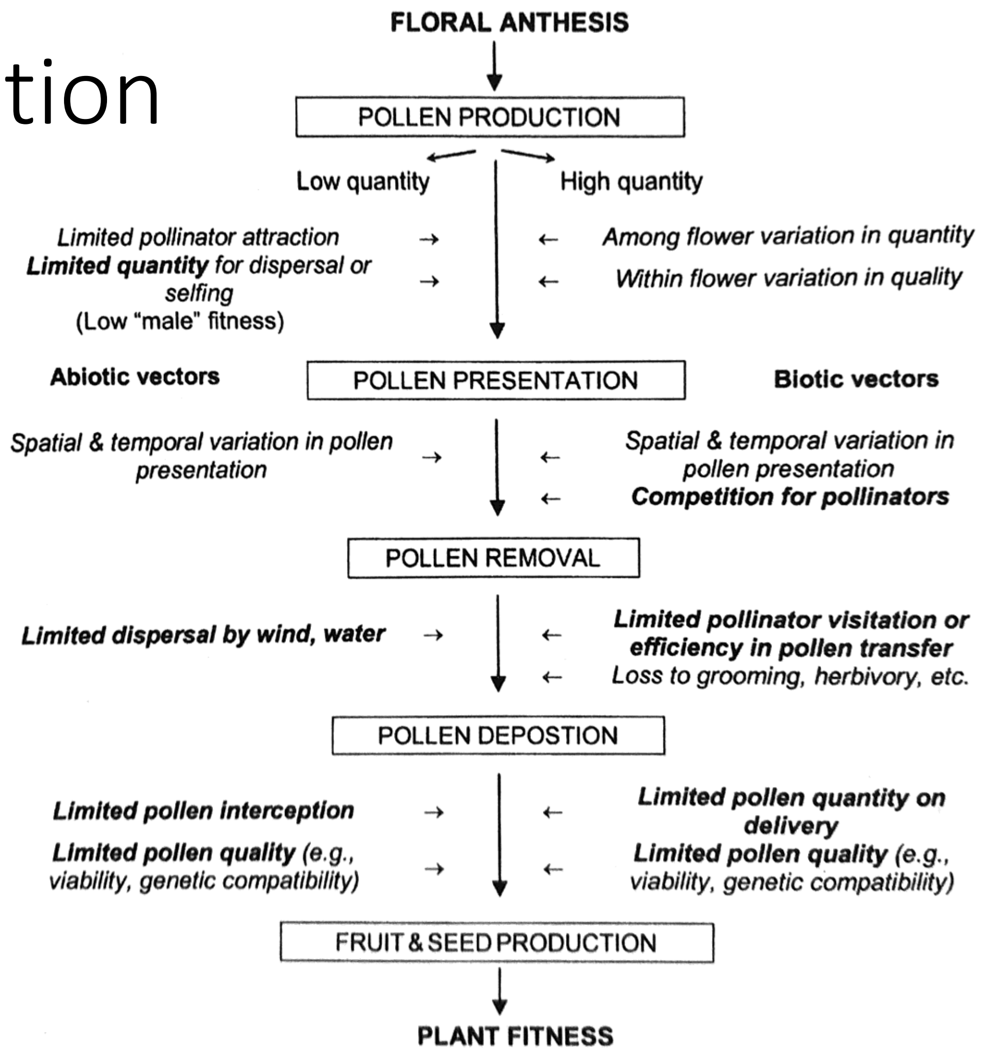


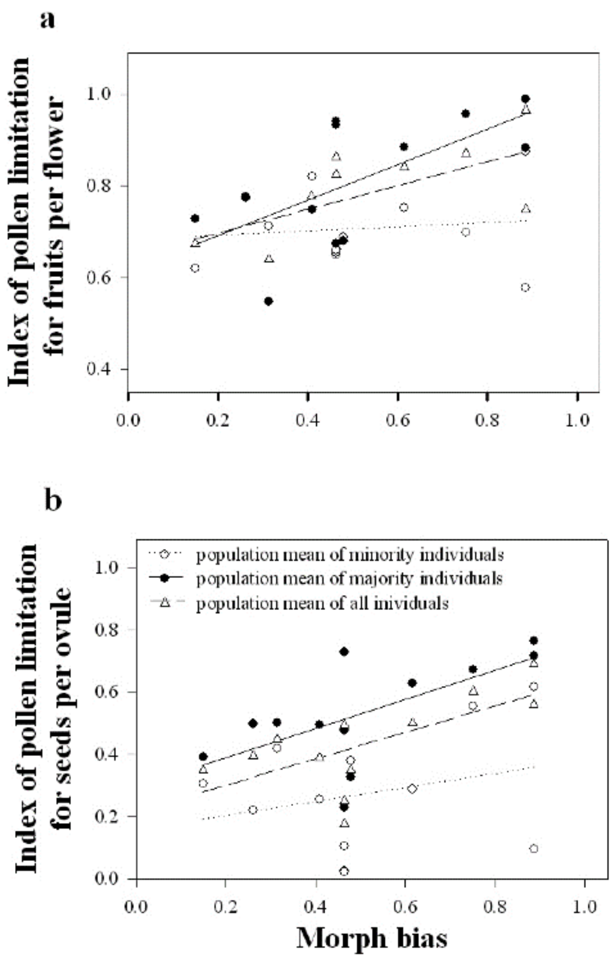
Dafni et al. 2005

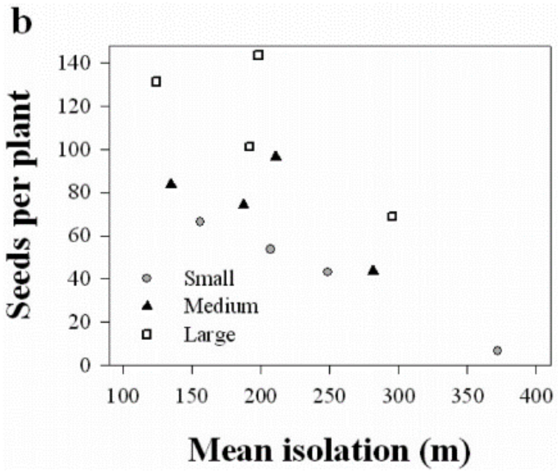
How much population dynamics is likely to suffer from a reduction in seed production caused by pollination limitation?

Pollination limitation
Consequences for plant conservation

Primula vulgaris Brys et al. 2008

- Decreasing population size significantly **reduced reproductive output**
- The impact was higher in **spatially isolated population**
- Skewed morph frequencies reduce reproductive success due to **lack of compatible pollen**

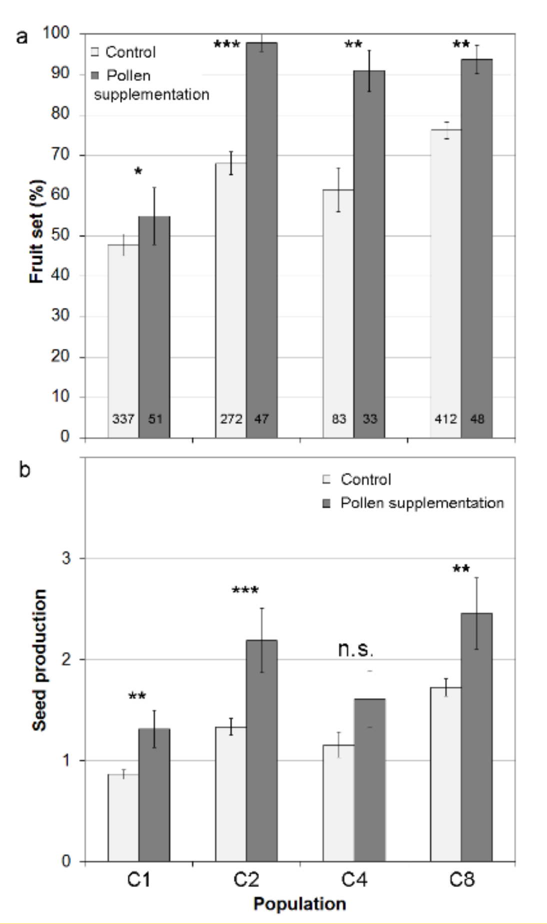


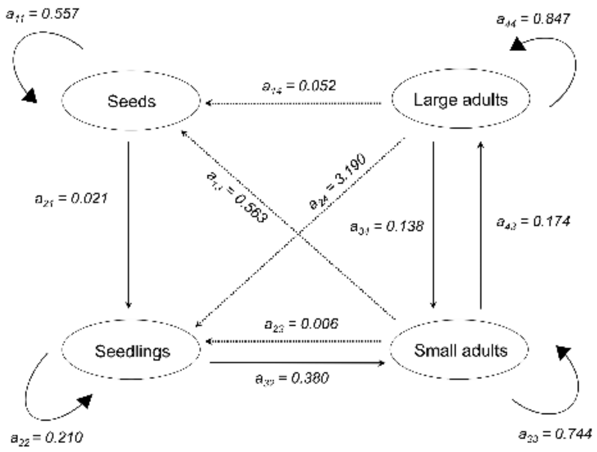


Qualitative component of pollination

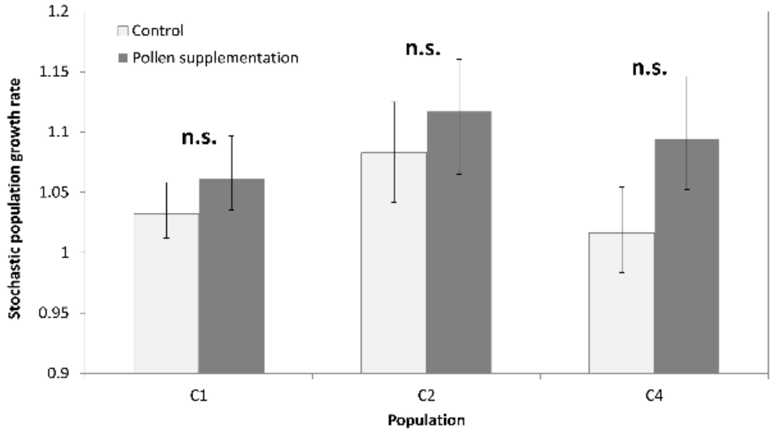
Pollination limitation
Consequences for plant conservation

Dracocephalum austriacum Castro et al. 2015





Limited pollination, but…



Castro et al. 2015

Pollination limitation
Consequences for plant conservation

- Multiple stressors are causing ongoing decreases in population numbers and sizes and may **exacerbate pollination limitation**

How much population dynamics is likely to suffer from a reduction in seed production caused by pollination limitation?

Questions

Pause