Floral rewards (pollen, nectar) in the Mediterranean under conditions of climate change

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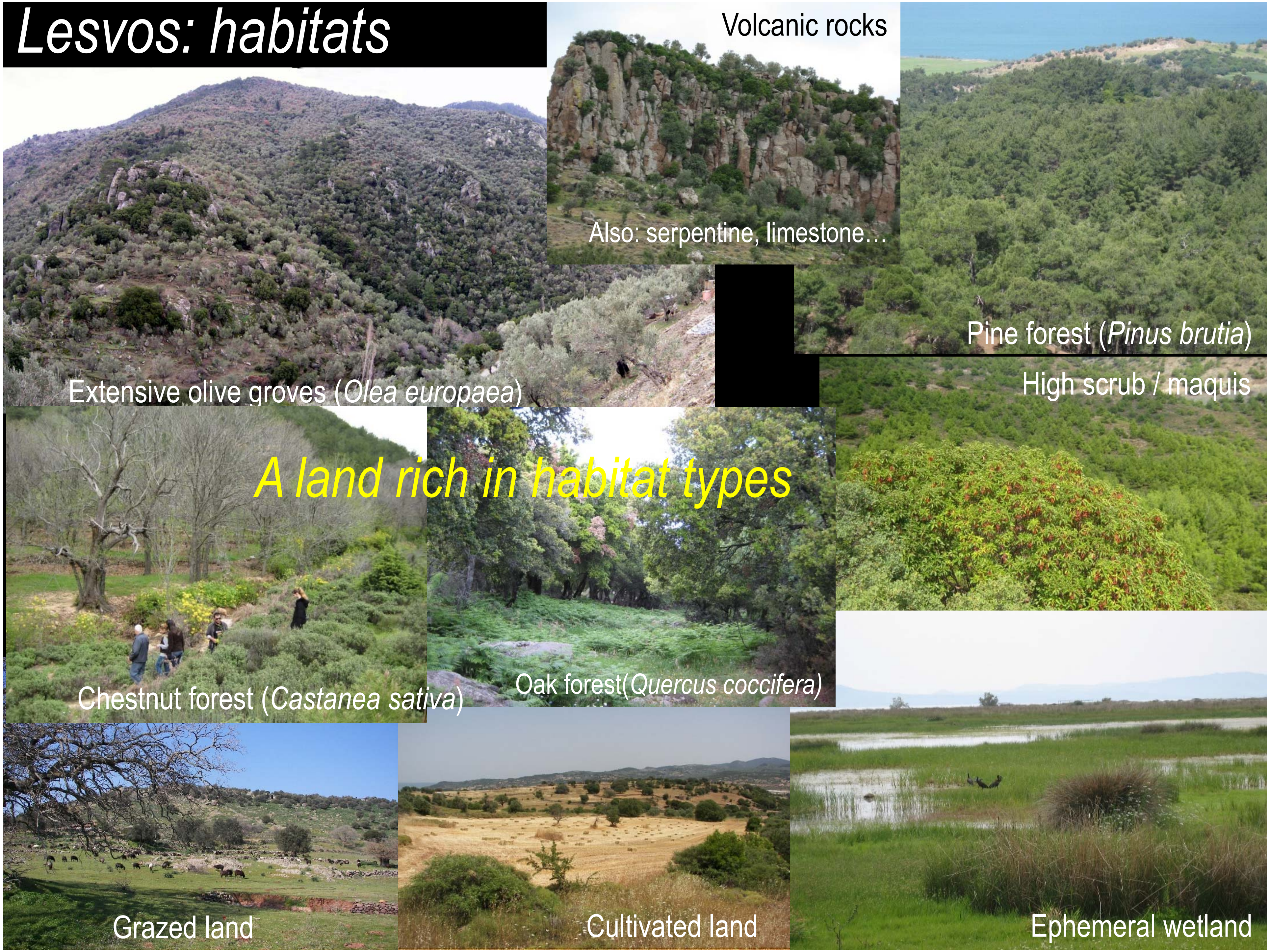
VIII Mediterranean Bee-keeping Forum, 22-23 November, Chefchaouen, Morocco

Lesvos

Lesvos: habitats



Lesvos: plants



Land of flowers: 1607 flowering plant species



Lesvos: bees

Land of bees: > 500 bee species!

Research in the Laboratory of Biogeography & Ecology

1. Ecogeography: Mediterranean landscapes

Terraces for agriculture

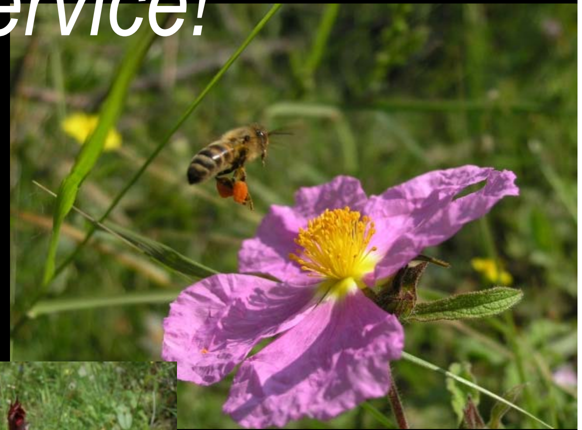
Salinas for salt making

Research in the Laboratory of Biogeography & Ecology

2. Ecology – Biogeography: partnership between flowers and pollinators

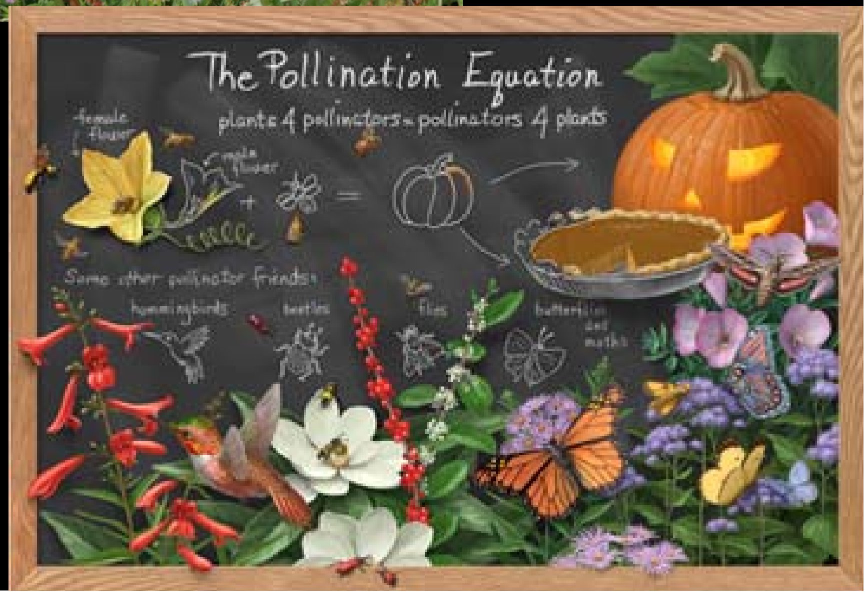
1. Diversity (plants, pollinators – mainly bees & hoverflies)
2. Architecture of the mutual relationships at community level (plant–pollinator networks)
3. Ecophysiology of the floral traits:
   - Primary (rewards) & secondary attractants….
4. Landscape ecology: which habitats for pollinator guilds & their interactions?
5. Threats to p–p partnership in the Aegean/Mediterranean?
   - … unconcern/ ignorance
   - Grazing
   - Fires
   - Telephony antennas
   - Excessive bee-keeping
   - Climate change
   - Invasive species

Pollination: an important ecosystem service!



1. decisive and important first step for sexual reproduction … species evolution

2. an invaluable ecosystem service … wild life & landscape preservation



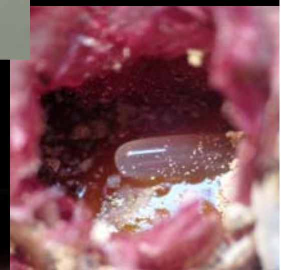
3. pivotal keystone process in almost all productive terrestrial systems

The Mediterranean: a land for flowers…

Driving factors for high plant diversity

1. Biogeography (neighbors, Pleistocene)
2. Geology (history, volcanic activity)
3. Ecology (niche/habitat diversity)
4. Human presence and history

The Mediterranean: a land for flowers… and bees



Driving factors for high bee diversity

1. Dryness and hotness
2. Diversity of flowering plants
3. Availability of bare ground, diversity of nesting sites & materials
4. Seasonality of vegetation
5. Frequent events of disturbance (e.g. fires)
6. Traditional management (grazing, surface ploughing every 2-3 y)

The Mediterranean: a land for flowers… and bees

Nests of *Chalicodoma parietina nestorea*

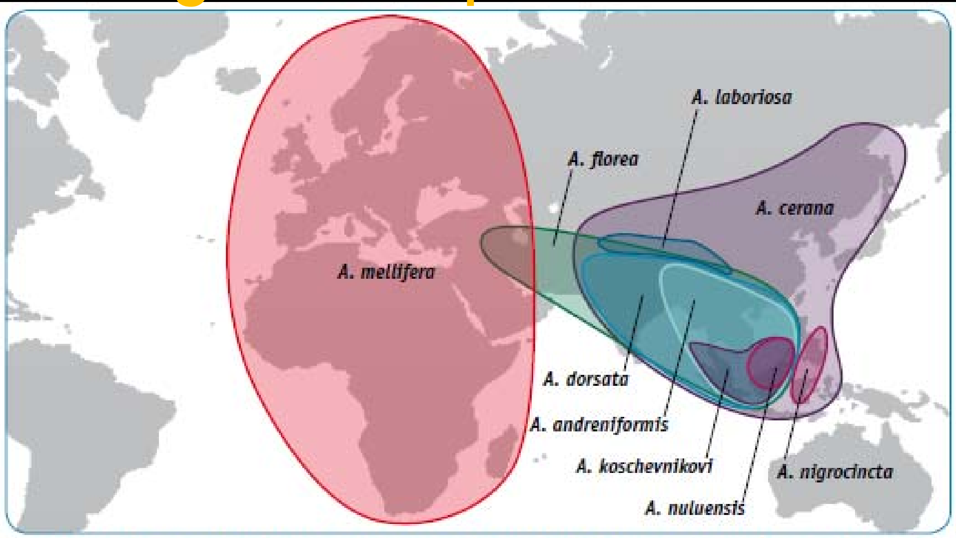
Photo: Nico Vereecken

…*including homes for people*

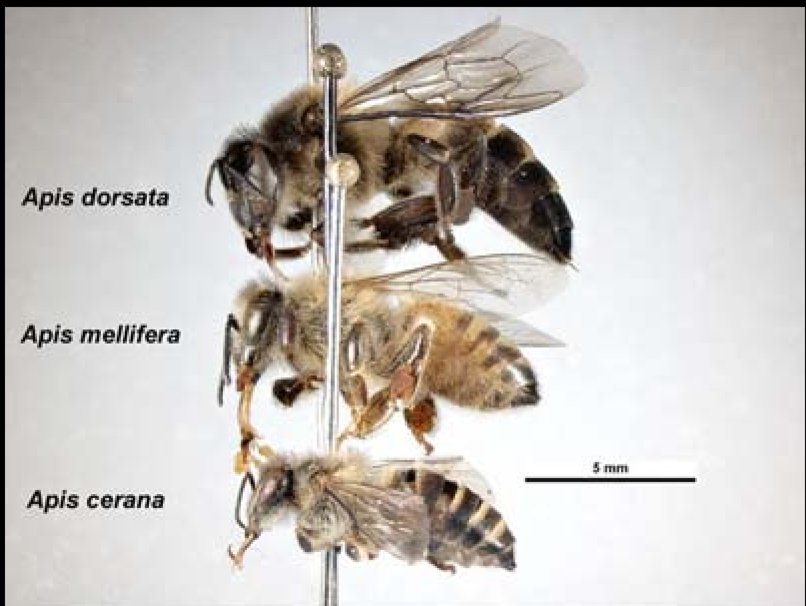
Wild bees

Bee family	#species
Andrenidae	125
Anthophoridae	175
Apidae	3
Colletidae	36
Halictidae	114
Megachilidae	160
Melittidae	5

The genus Apis



Source: Franck *et al.* 2000; Le Conte and Navajas 2008. Figure printed with permission from P. Franck (Franck 1999).



MAIN GEOGRAPHIC RACES OF *APIS MELLIFERA*.

A, M, C and O are the four evolutionary branches.

THE NATURAL RANGE OF *APIS MELLIFERA*.

The natural range of *Apis mellifera mellifera* coincides with the 15-20° zone (July average temperatures).

Nectar: a floral primary attractant par excellence!

1/2 primary attractants (= floral rewards) to bees/hbs

Solution of sugars in water

- glucose, fructose, sucrose + >20 other rel. simple sugars
- sugar content: 15 – 45 …75% (w/w sucrose)
- high variability

other constituents

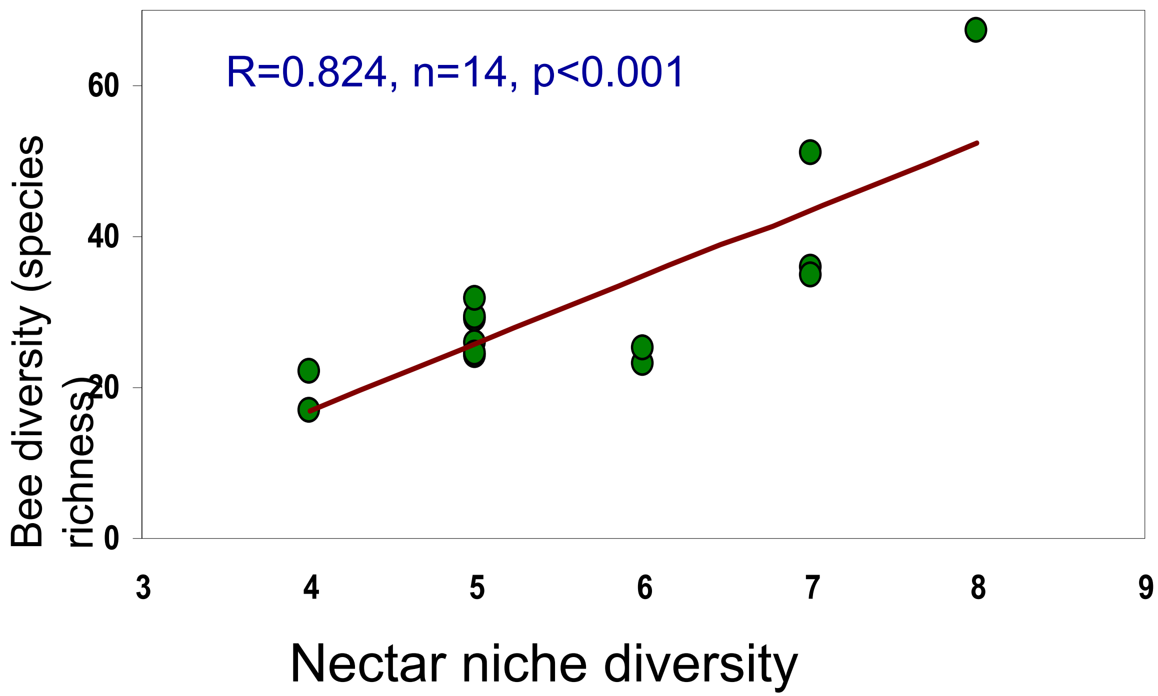
- amino acids, minerals, pectines, phenols, fats, proteins, antioxidants, antibiotics, alkaloids

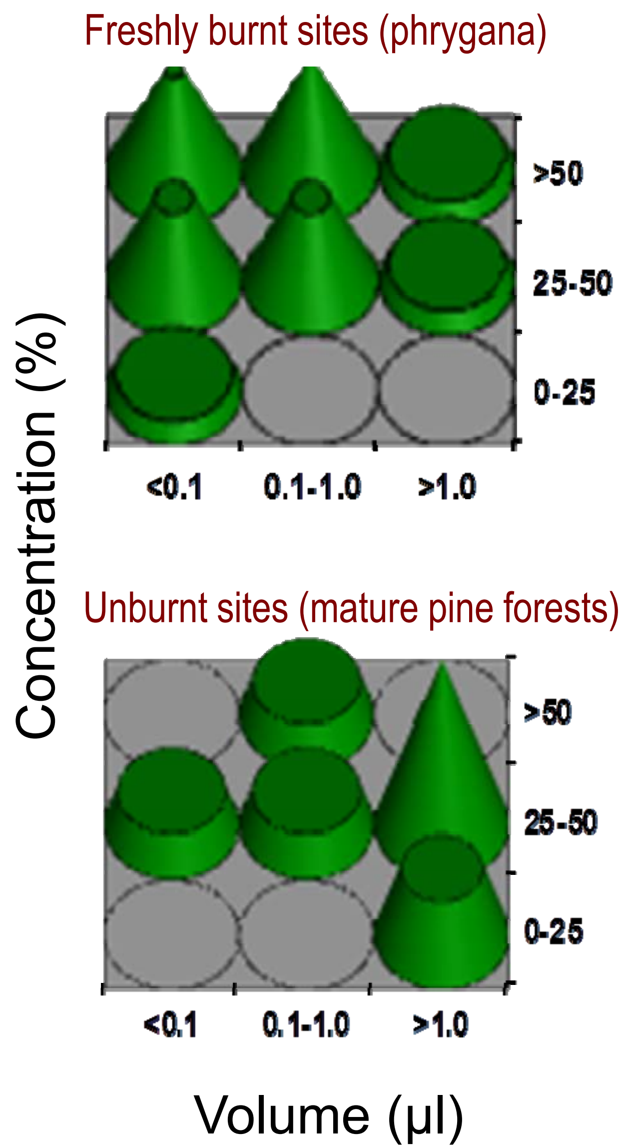
Provides: fuel (high calorific value!), water

Secretion rate

- depends on the plant, age, ecological factors (T, RH, light, water regime etc)

Nectar niche diversity shapes bee diversity





Potts et al. (2004). Ent Exp Appl 113: 103-107

Nectar: sugars, but also amino acids!

Amino acids	Mean quantity (pmoles/flower)	SE	% of total amino acids
Arginine	78	17.4	2.8
Asparagine	152	43.8	5.6
Aspartic acid	234	140.0	8.6
Glutamic acid	66	16.7	2.4
Glycine + threonine	218	35.3	8.0
Histidine + glutamine	231	61.6	8.5
Isoleucine	33	6.6	1.2
Leucine	52	10.1	1.9
Lysine	68	11.9	2.5
Methionine	55	23.8	2.0
Ornithine	101	17.5	3.7
Phenylalanine	715	229.5	26.2
Serine	166	26.2	6.1
Tryptophan	43	11.2	1.6
Tyrosine + alanine	250	40.2	9.2
Unknown	71	21.5	2.6
Valine	119	18.7	4.4
H-serine	2	2.1	0.1
β-Alanine	3	1.9	0.1
GABA (γ-aminobutyric acid)	75	24.6	2.7
Total amino acids	***2731***	***469.1***	***100.0***

Amino acids in the floral nectars of phrygana by HPLC analysis

Essential (indispensable) amino acids for bees

Phagostimulatory effects

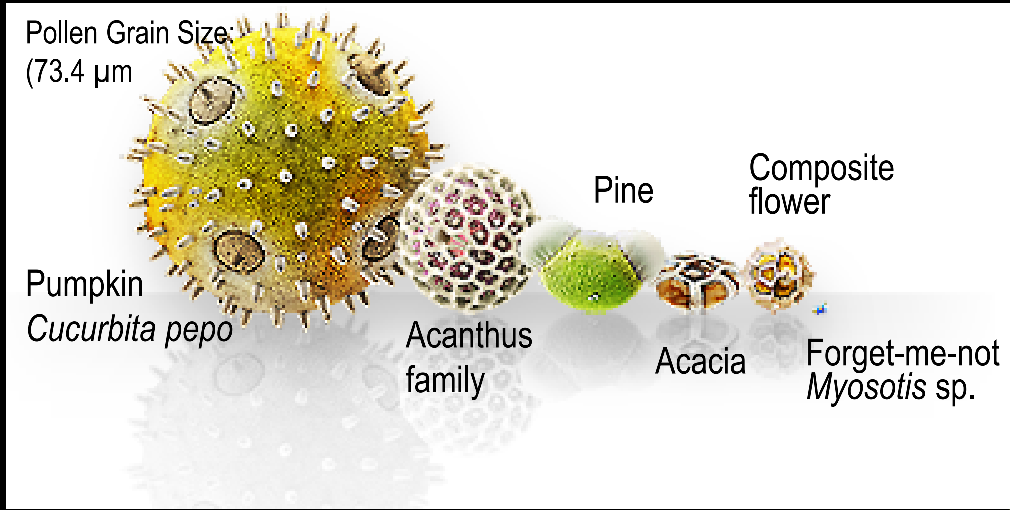
Nectar: sugars vs. amino acids

Table 5. Relationship of pollinator guilds and families to different nectar parameters of the floral nectars of the phryganic plants visited by each pollinator group. We give multiple regression results (adjusted overal R^2 and partial coefficients) of flower visitors (numbers of visitor species of a certain insect guild visiting a plant species) over the total nectar volume, total AA content and total sugar content (glucose + fructose + sucrose) contained in the nectars of the plant species visited. All data were transformed ($x' = \ln(x+1)$). No significance was found for: total sugars and the insect guilds and families missing from the table. *: $P < 0.05$, **: $0.05 < P < 0.01$, ***: $0.01 < P < 0.001$.

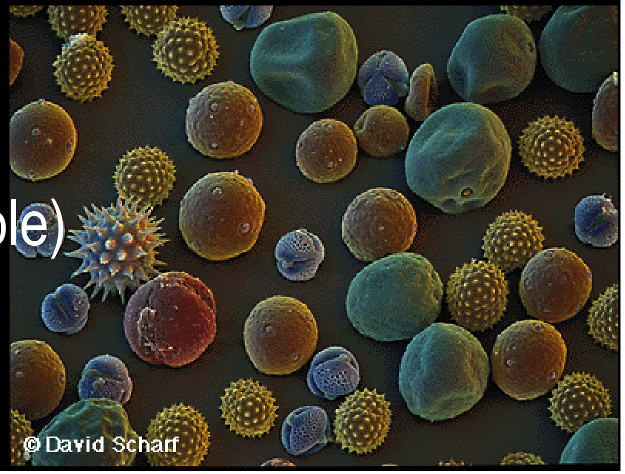
Nectar traits	LT bees		Anthophoridae		Megachilidae		Apidae		Other Diptera		Syrphidae		Wasps	
	$R^2 = 13.4$, 65 df		$R^2 = 21.6$, 65 df		$R^2 = 4.3$, 65 df		$R^2 = 8.2$, 65 df		$R^2 = 12.0$, 65 df		$R^2 = 6.8$, 65 df		$R^2 = 4.3$, 65 df	
	b	P	b	P	b	P	b	P	b	P	b	P	b	P
Volume									−0.522	**	−0.393	*	−0.330	0.052
Total AAs	0.326	**	0.368	***	0.174	0.052	0.084	*						
Total sugars														

Nectar traits	Coleoptera		Hemiptera		Long-tongued bees (excl. Apidae)		Other Diptera		Short-tongued bees		Syrphidae		wasps		Andrenidae		Anthophoridae		Colletidae		Megachilidae	
Overall coefficients																						
	$R^2 = 34.9$, 63 df		$R^2 = 4.4$, 65 df		$R^2 = 38.1$, 61 df		$R^2 = 41.2$, 62 df		$R^2 = 11.4$, 64 df		$R^2 = 32.6$, 61 df		$R^2 = 33.6$, 63 df		$R^2 = 8.8$, 64 df		$R^2 = 33.4$, 62 df		$R^2 = 8.8$, 65 df		$R^2 = 32.3$, 63 df	
Partial coefficients																						
	b	P	b	P	b	P	b	P	b	P	b	P	b	P	b	P	b	P	b	P	b	P
Volume							−0.484	***					−0.282	*								
Glucose													−0.490	**								
Fructose	0.391	**					0.421	***	0.310	*	0.443	***	0.613	***								
Sucrose					0.168	*																
Asn	−0.516	***	−0.124	*			−0.342	**	−0.286	*			−0.330	**					−0.158	**	−0.271	*
Gaba					0.371	**	0.302	**			0.269	*			0.251	*	0.331	**				
Trp	0.363	*			−0.468	**					0.320	*					−0.558	***				
Met															−0.270	*						
Val																	−0.289	*				
Phe					0.189	*															0.183	*
Leu																					−0.551	*
H-Ser					−0.962	**											−0.786					

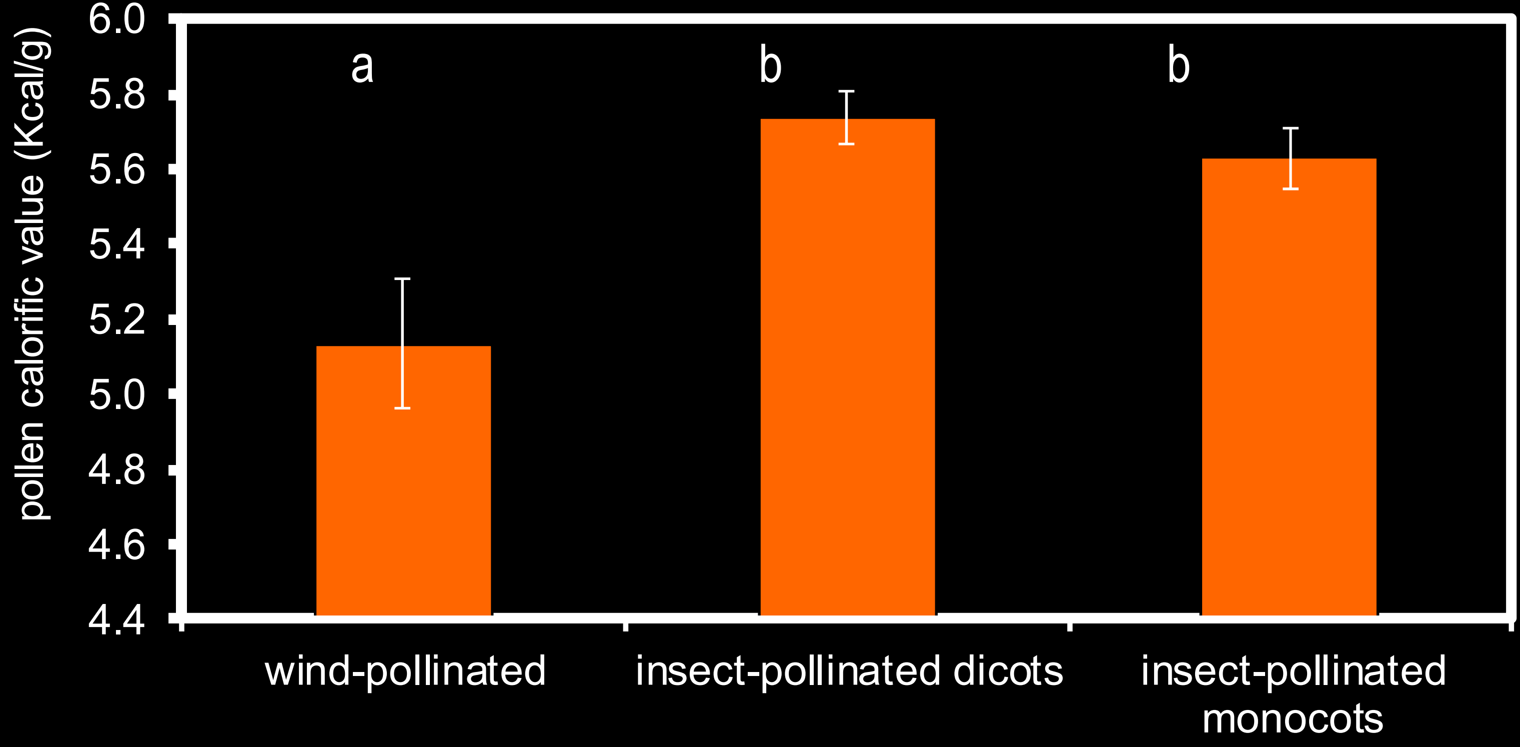
Pollen: a floral primary attractant



- 1/2 primary attractants (= floral rewards) to bees/hbs
- 16-30% proteins, 1-7% starch, 0-15% sugars, 3-10% fats
- starchy (anemophiles) vs. lipid-rich pollen (entomophilous plant spp.)
- rich in nitrogen (N_2)
- different strata: exine (non digestible), entine (digestible)
- pollen producers: *Cistus, Papaver, Paeonia* etc.
- Highly nutritive: proteins, lipids, vitamins etc.



Pollen: nutritional & energy-supplying resource!



Petanidou & Vokou (1990). Am J Bot 77: 986-992

Pollen as reward in the Mediterranean: dual role

Pollen: a floral primary attractant

- Pollen in the Mediterranean: higher calorific value of entomophilous plants vs. anemophiles
- Not in continental systems
- Pollen more important in the arid Mediterranean as an extra fuel resulting from nectar scarcity
- Selection favors increased pollen attractiveness

TABLE 2. *Mean pollen caloric content, number of pollinators, and median date of flowering of plant species occurring in a Mediterranean-type ecosystem, as numbered in Table 1. Energy contents are based on three or four samples per species*

Plant species	Mean (± S.E.) pollen caloric content (kcal g^{-1} ash-free d.w.)	% Difference of max to min value	Number of pollinators; Lepidoptera in parentheses	Median date of flowering period (from 1 January)
Wind-pollinated plants				
1	4.4068 ± 0.0539	2.99	0	60
2	5.4324 ± 0.0671	4.36	0	58
3	5.6075 ± 0.0677		0	90
4	5.1099 ± 0.0316		0	100
5	5.2584 ± 0.0584		0	118
6	4.9901 ± 0.0790	1.98	0	80
	$\bar{x}$ = 5.1342 ± 0.1711			
	Range: 4.4068–5.6075			
Insect-pollinated dicots				
7	5.9372 ± 0.2713	15.80	18	189
8	5.7476 ± 0.0585		50 (3)	131
9	5.6450 ± 0.0278		39 (1)	104
10	5.4965 ± 0.1459		36 (1)	137
11	5.8894 ± 0.0006		70 (1)	128
12	5.8086 ± 0.0882		32 (5)	136
13	6.2576 ± 0.1000		65 (5)	115
14	5.8942 ± 0.0310	1.42	39 (3)	105
15	6.0035 ± 0.0469	2.10	10	116
16	5.7613 ± 0.0957		16 (2)	134
17	5.5156 ± 0.0912		21 (3)	86
18	5.6774 ± 0.0185		8	118
19	5.1555 ± 0.0439	0.67	14 (1)	111
20	5.4559 ± 0.0885	9.64	18	272
21	5.5787 ± 0.0426	5.42	5	97
22	6.2954 ± 0.0441	3.98	18 (8)	25
23	6.0730 ± 0.0055		29 (1)	169
24	5.1810 ± 0.0932	8.27	27	99
25	5.8315 ± 0.0965		44 (3)	105
26	5.5688 ± 0.0109		1	79
	$\bar{x}$ = 5.7387 ± 0.0682			
	Range: 5.1555–6.2954			
Insect-pollinated monocots				
27	5.6834 ± 0.0692	7.57	10 (1)	295
28	5.4057 ± 0.0476	1.97	3	26
29	5.8668 ± 0.0472	1.47	14 (1)	295
30	6.0489 ± 0.0032		10	325
31	5.7289 ± 0.0694	3.20	4	83
32	5.8757 ± 0.1161	8.94	53 (5)	83
33	5.4981 ± 0.1100	6.16	2	86
34	6.1099 ± 0.0717		28 (1)	49
35	5.2792 ± 0.0709		18	100
36	5.7309 ± 0.0265	4.92	37 (3)	70
37	5.8125 ± 0.0262	1.33	31 (4)	259
38	5.3975 ± 0.0896	7.23	9	84
39	5.1912 ± 0.0398	0.16	9	108
40	5.2123 ± 0.0473		9	86
	$\bar{x}$ = 5.6315 ± 0.0809			
	Range: 5.1912–6.2954			
	Overall $\bar{x}$ = 5.6105 ± 0.0588			

POL-AEGIS (2012–2015)

The POLlinators of the AEGean archipelago: dIversity & ThreatS

Aegis = shield

Basis for improving our understanding on what, where, role of & threats to pollinators aiming at their conservation

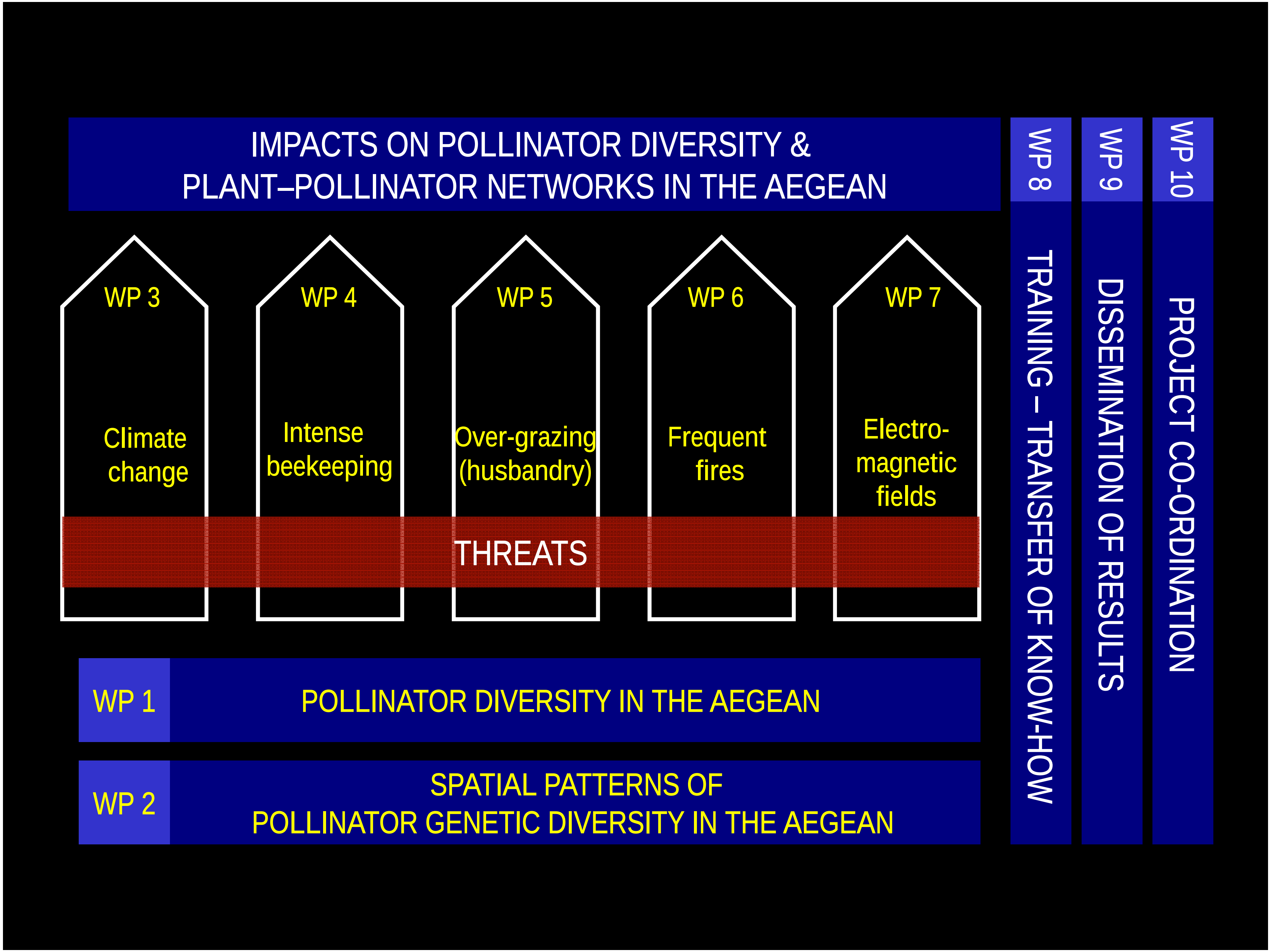
POL-AEGIS

The pollinators of the Aegean: diversity & threats

αἰγίς, ἴδος, ἡ:
goatskin, worn as a dress; esp. the skin **shield** of Zeus, lent by him to Athena; later, with fringe of snakes and Gorgon's head, the **aegis of Athena**

L-S-J Lexicon

NSRF 2007-2013
programme for development


IMPACTS ON POLLINATOR DIVERSITY &
PLANT–POLLINATOR NETWORKS IN THE AEGEAN
WP 3
Climate change
WP 4
Intense beekeeping
WP 5
Over-grazing (husbandry)
WP 6
Frequent fires
WP 7
Electro-magnetic fields
THREATS
WP 1
POLLINATOR DIVERSITY IN THE AEGEAN
WP 2
SPATIAL PATTERNS OF
POLLINATOR GENETIC DIVERSITY IN THE AEGEAN
WP 8
TRAINING – TRANSFER OF KNOW-HOW
WP 9
DISSEMINATION OF RESULTS
WP 10
PROJECT CO-ORDINATION

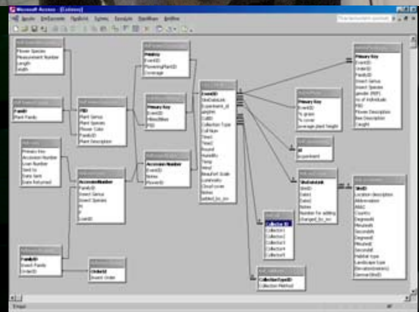
Direct goals:

1. Knowledge on the pollinating fauna of the Aegean
2. Knowledge on the threats to apply pollinator-friendly management
3. Creation of infrastructures and tools for the future (*Melissotheque of the Aegean, Taxonomic human capital & keys*)
4. Data base for future monitoring

Long-term goal:

Safeguard wild pollinators in the Aegean

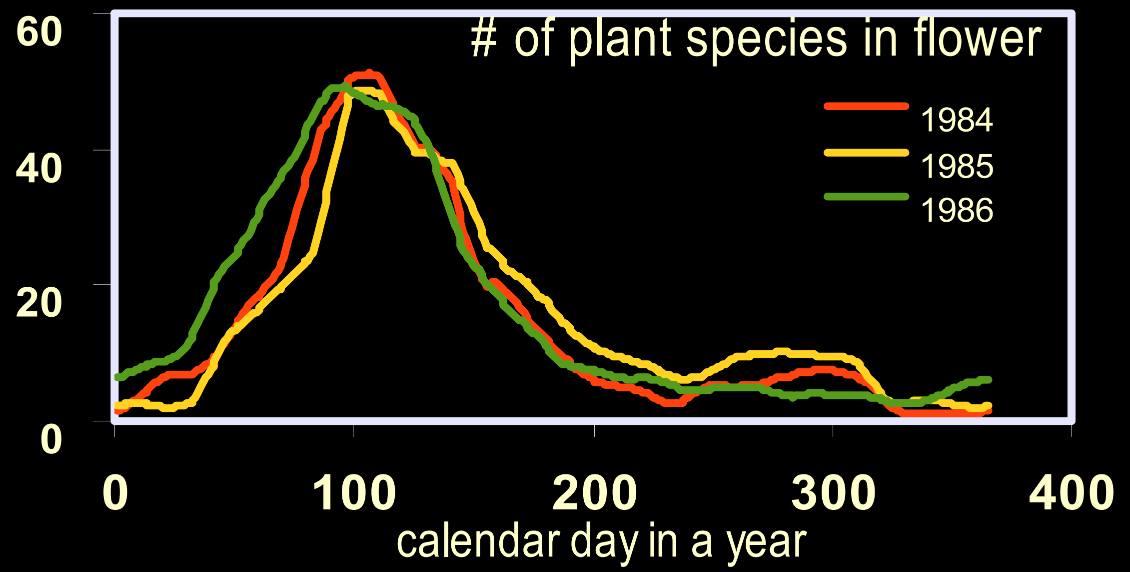
The Melissotheque of the Aegean



- Collection of bees a.o. pollinators from the Aegean
- Fully databased
- Total of ca. 250,000 specimens + records (≈80% ided)
  - >850 bee species
  - >600 hoverfly, bee fly, a.o. species
  - > 30 species new for science

Will climate change challenge nectar secretion?

Inter-annual changes in flowering phenology

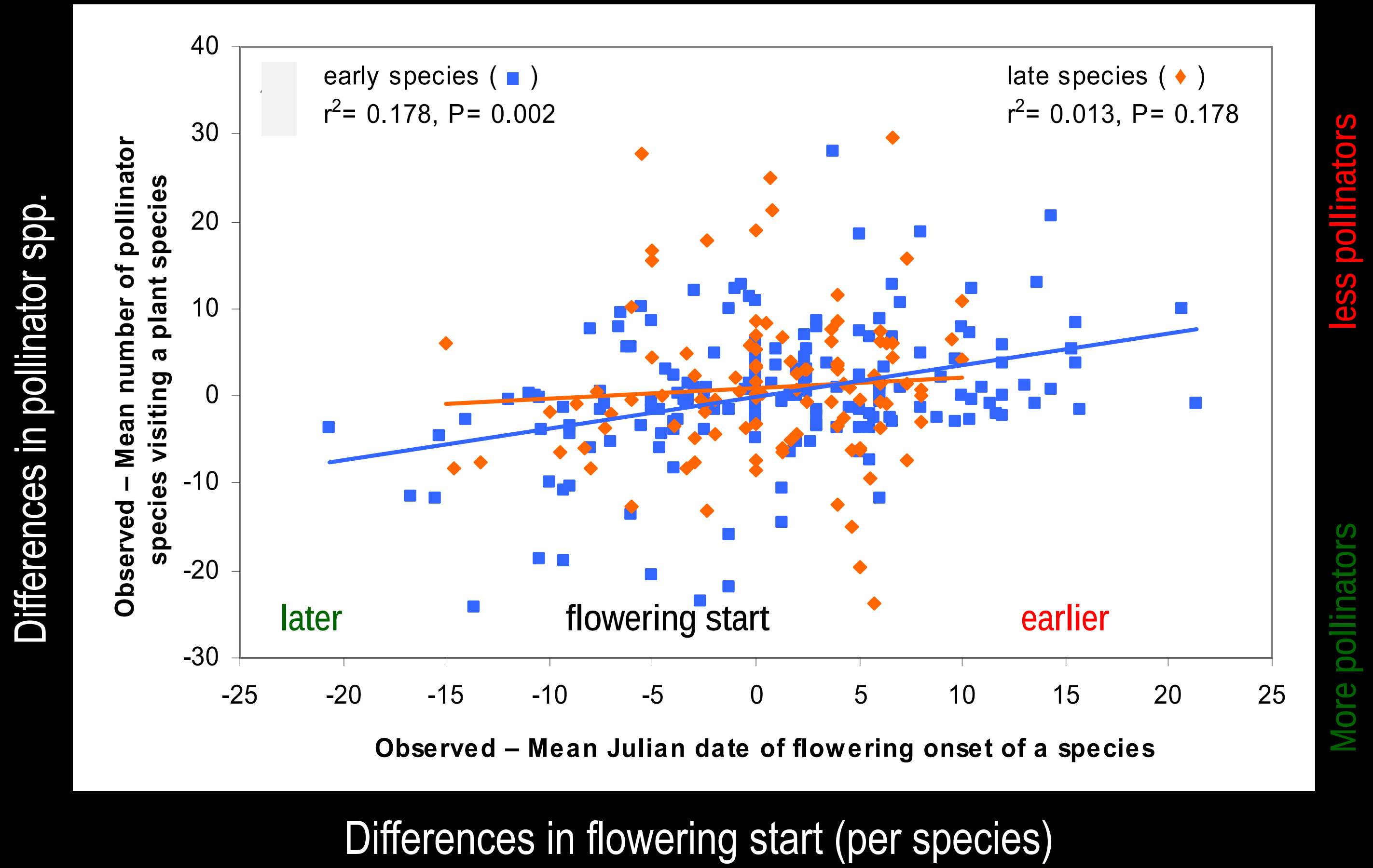


Petanidou et al. (1995). Am J Bot 82: 607-620

surplus (= actual – long term average) of	*P (multiple regression)*	
	Start of flowering	End of flowering
T of previous month	0.000	ns
monthly T	ns	ns
rainfall of previous month	ns	ns
monthly rainfall	ns	ns

- *Seasonality*
- *Significant shift in the start of flowering between years*
- *Flowering onset is T-dependent*

Inter-annual changes in flower-bee interactions



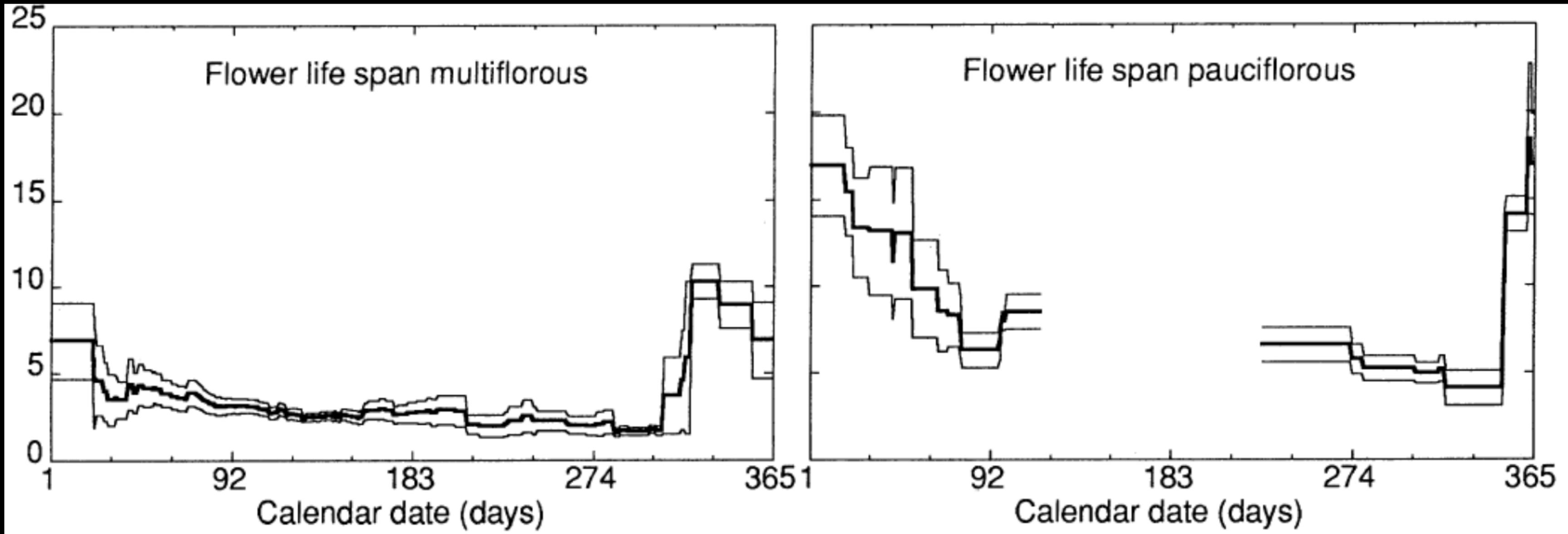
Climate change?

Petanidou et al. (2014). Acta Oecol 59: 104–111

Flowering earlier: Fewer pollinators available

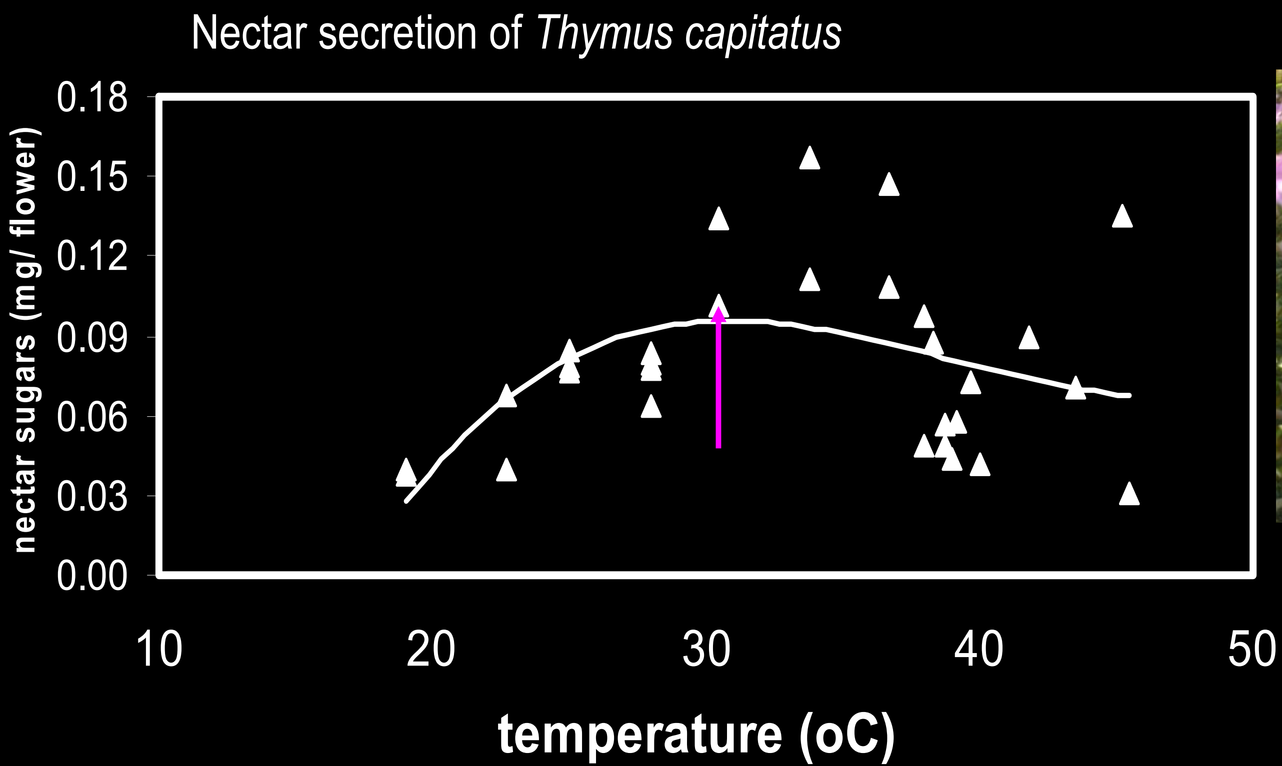
Seasonal variations of flower-life span & flowering duration

		DF		Flower life span	
	N	Mean (days)	SE	Mean (days)	SE
All species	133	55.1	2.25	3.5	0.30
Main flowering period	88	51.5	2.11	3.2	0.30
Between main and secondary	20	66.6	8.92	2.6	0.52
Secondary flowering period	10	46.9	6.79	2.7	0.61
Winter	15	66.4	8.10	7.1	1.60



Flower life-span & flowering duration lower in summer vs. winter

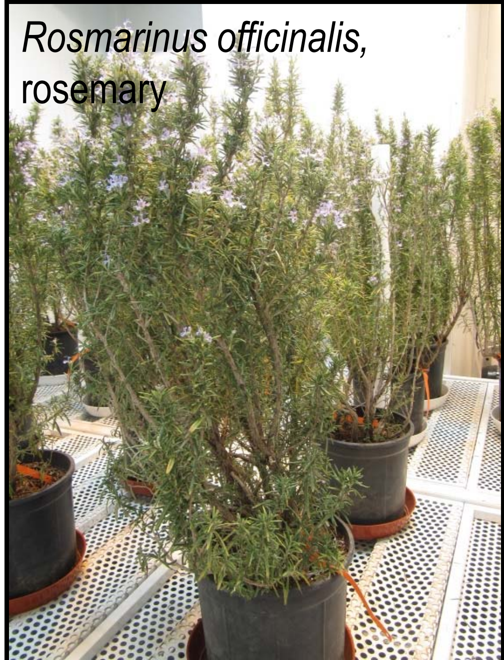
Nectar secretion decreases with temperature

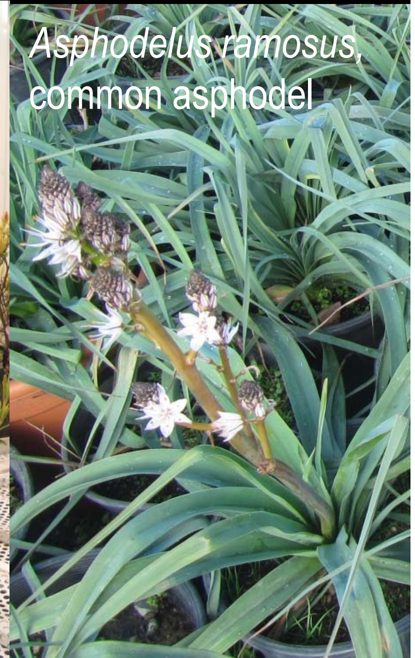


Petanidou & Smets (1996). New Phytol 133: 513–518

- *Typical summer flowering species; well adapted to drought*
- *Nectar secretion decreases after 30°C*

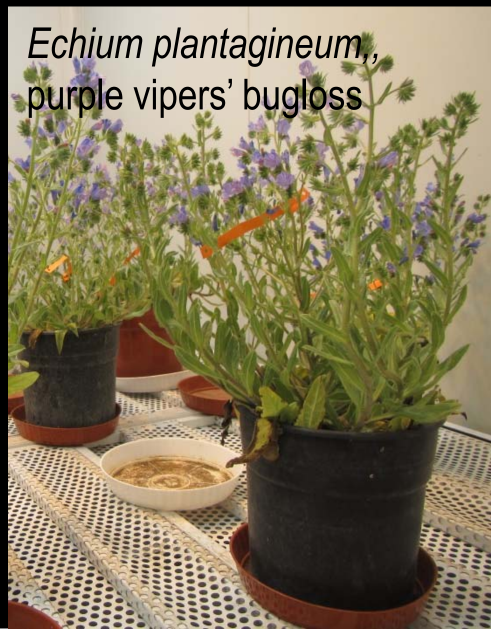
Study plants, 2013–2015





Perennials

Annuals



Experimental setting

- climate chamber: controlled T, RH
- outdoors (natural conditions: standardize for the effect of flowering stress/span)
- Plants not water-stressed

Measurements:

- Nectar volume/ fl; concentration/ fl
- Nectar sugars/ fl
- # flowers/ plant

Development of experimental plants collected in nature

Echium plantagineum
(βοϊδόγλωσσο)

Raising of experimental plants collected in nature

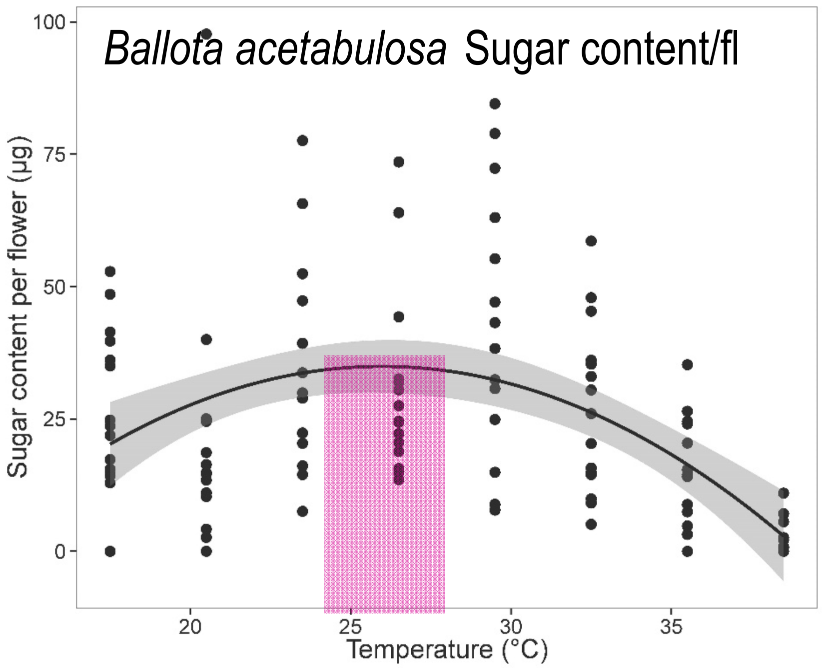
Raised from seeds

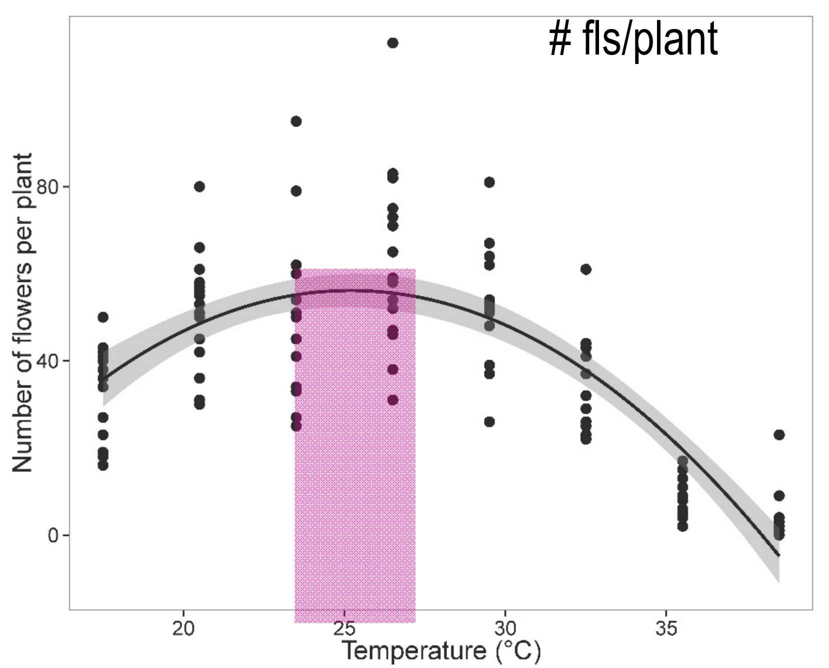
- *Echium plantagineum*
- *Brassica napus*
- *Ballota acetabulosa*

Collected as mature plants

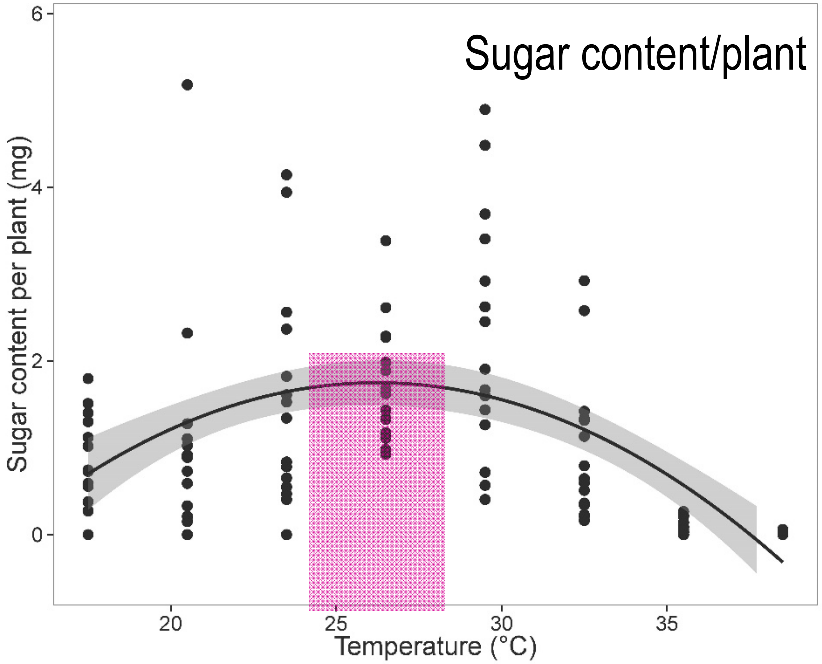
- *Asphodelus ramosus*
- *Rosmarinus officinalis*
- *Lavandula stoechas*
- *Teucrium divaricatum*

Does nectar secretion follow temperature increase?





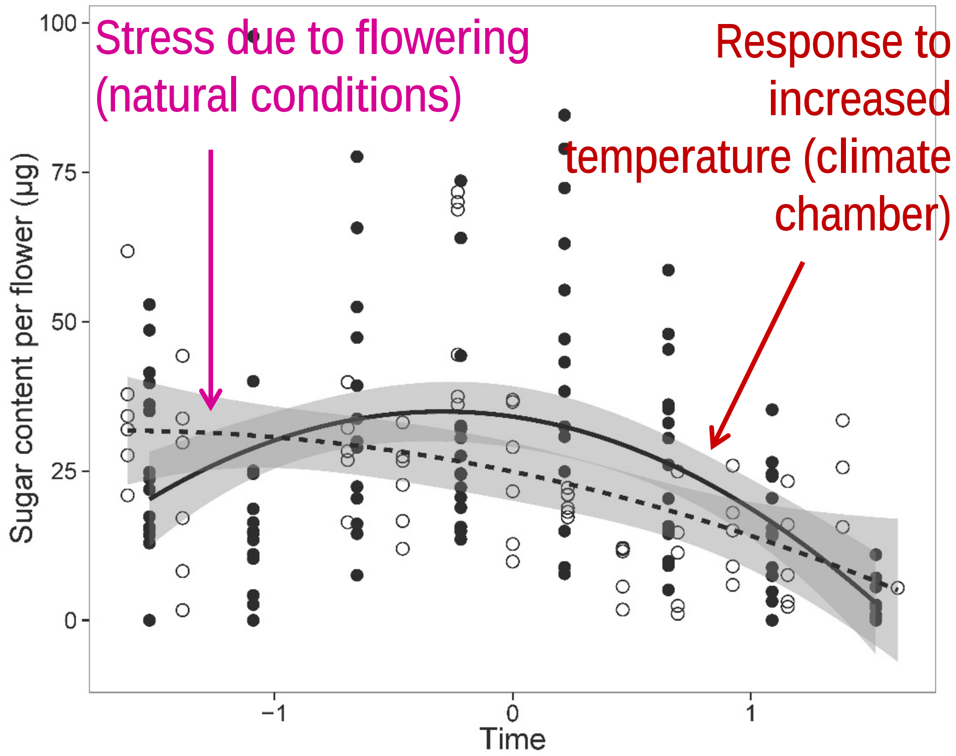
Takkis et al. (2015). AoB Plants 1-13

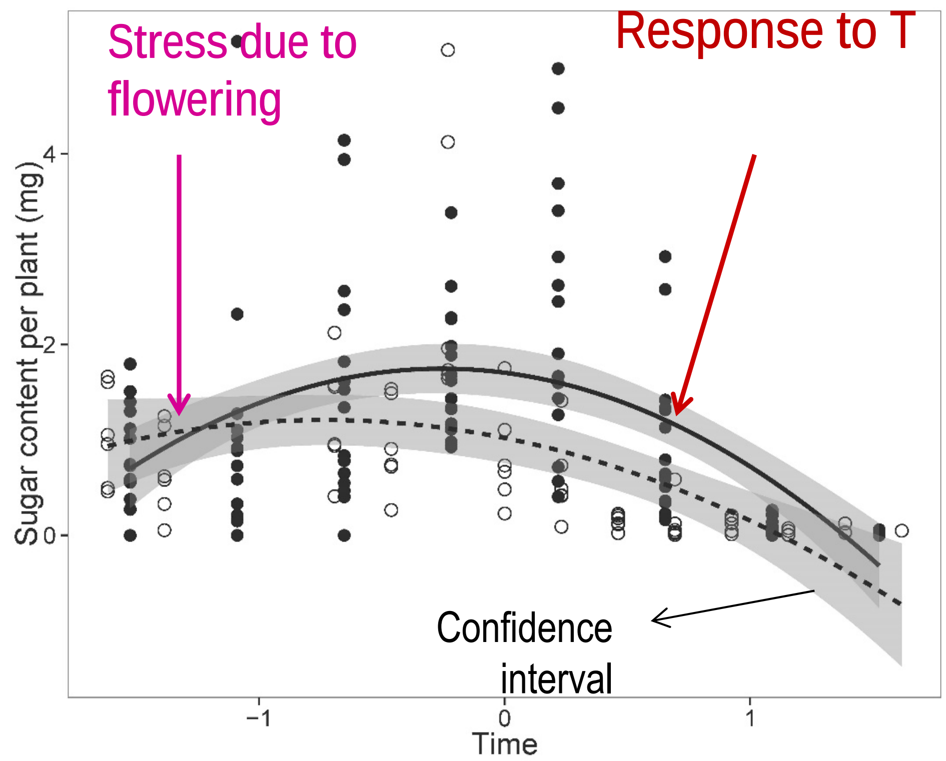


- Higher secretion
- Maximal sugar secretion: 24–27°C
- Thereafter, dramatic decrease

In all experiments we considered the stress from flowering duration

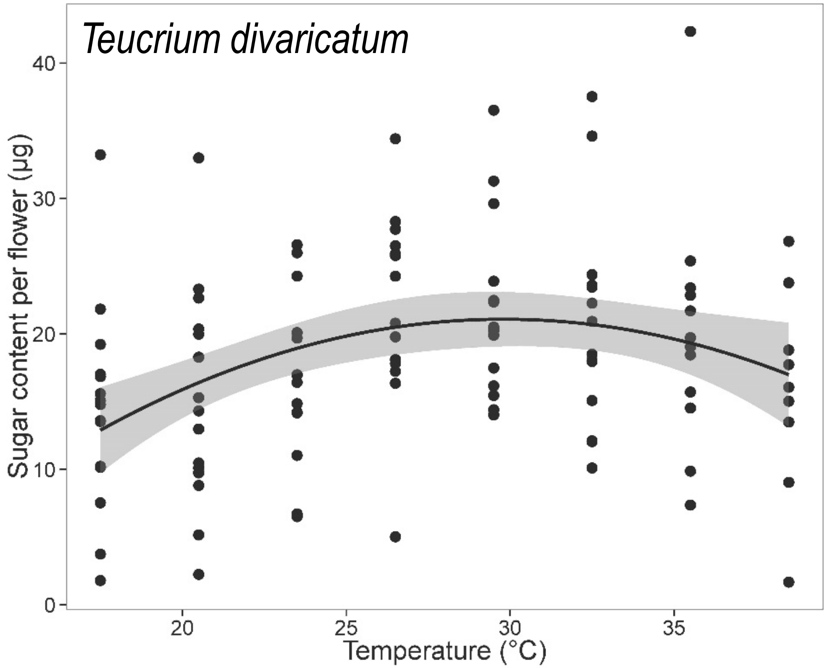
Experiments on Ballota acetabulosa *: sugars contained in the nectar*

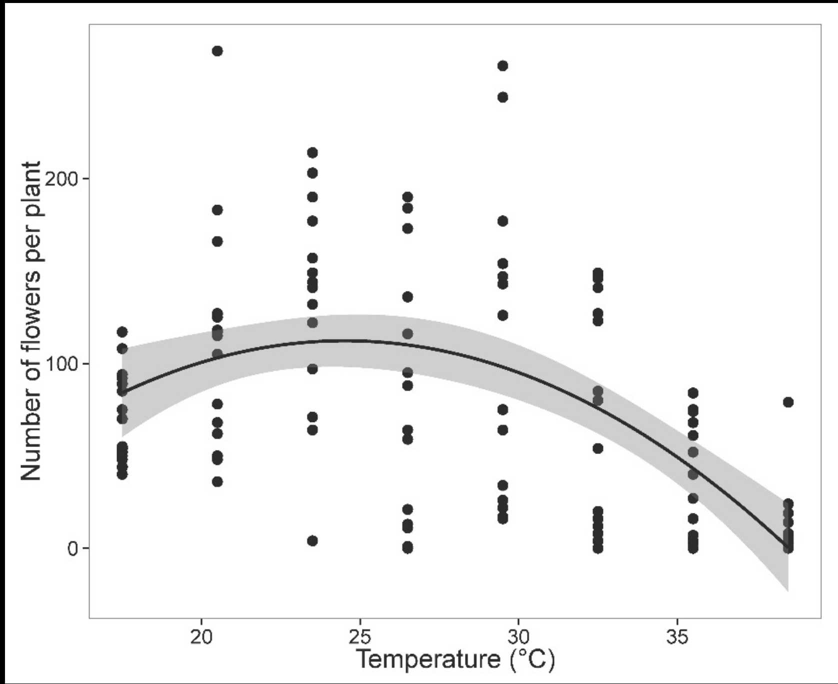


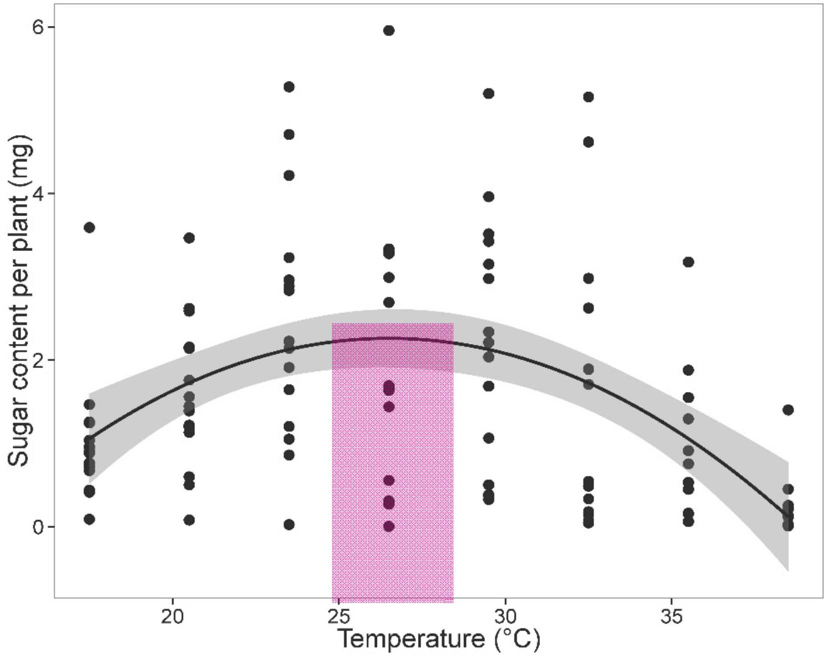


Takkis et al. (2015). AoB Plants 1-13

Does nectar secretion follow temperature increase?

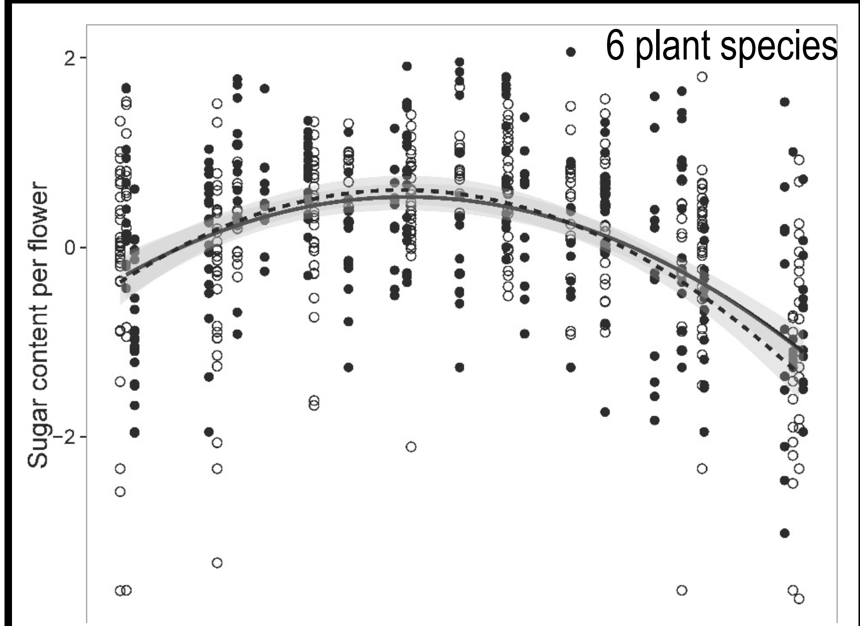


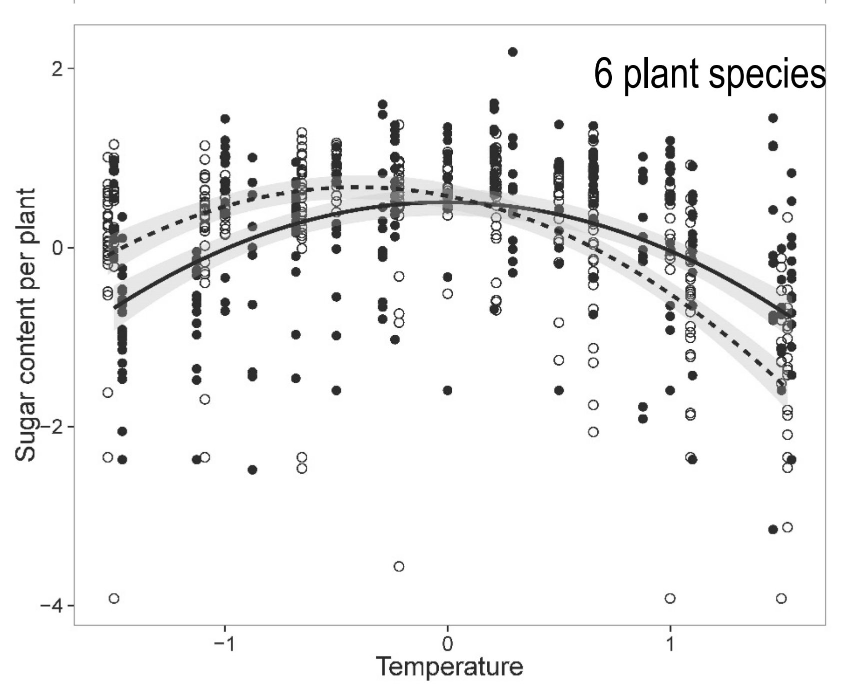


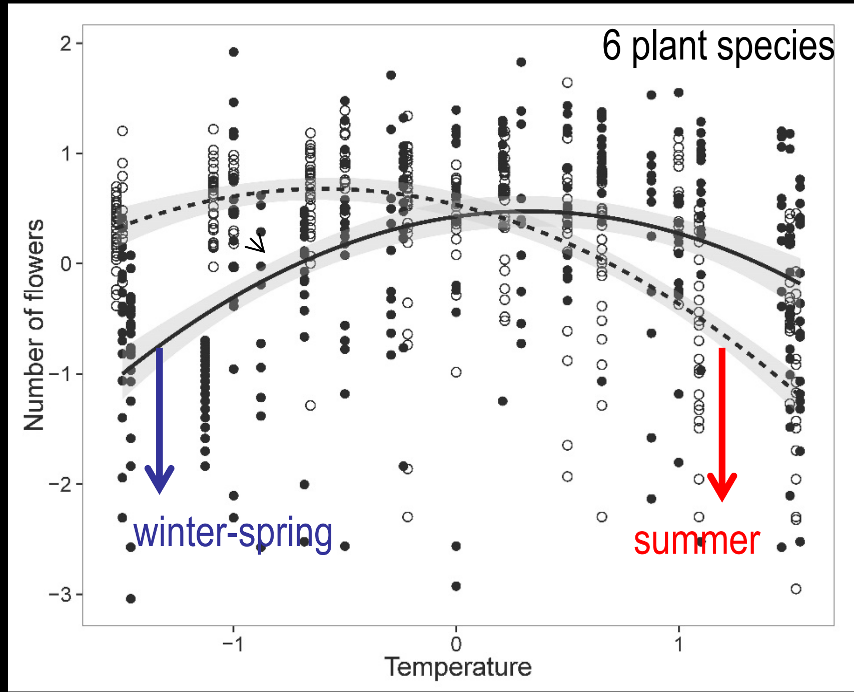


- Higher secretion
- Maximal sugar secretion: 25–28°C
- Thereafter, dramatic decrease

Does nectar secretion follow temperature increase?







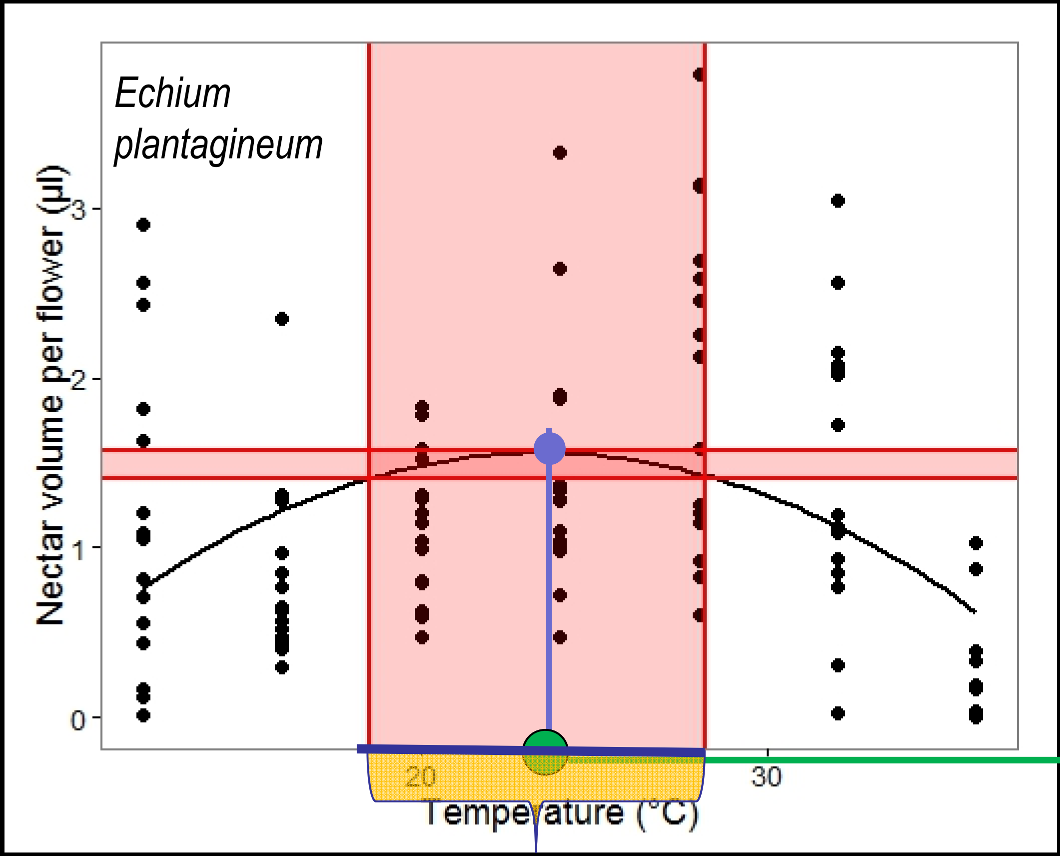
With temperature increase:

- *summer-flowering species suffer decreased nectar secretion*
- *winter-spring are benefited*

Which plant species will be more affected by climate change?

For all nectar traits & plant species, calculation of:

- optimal temperature
- optimal temperature range

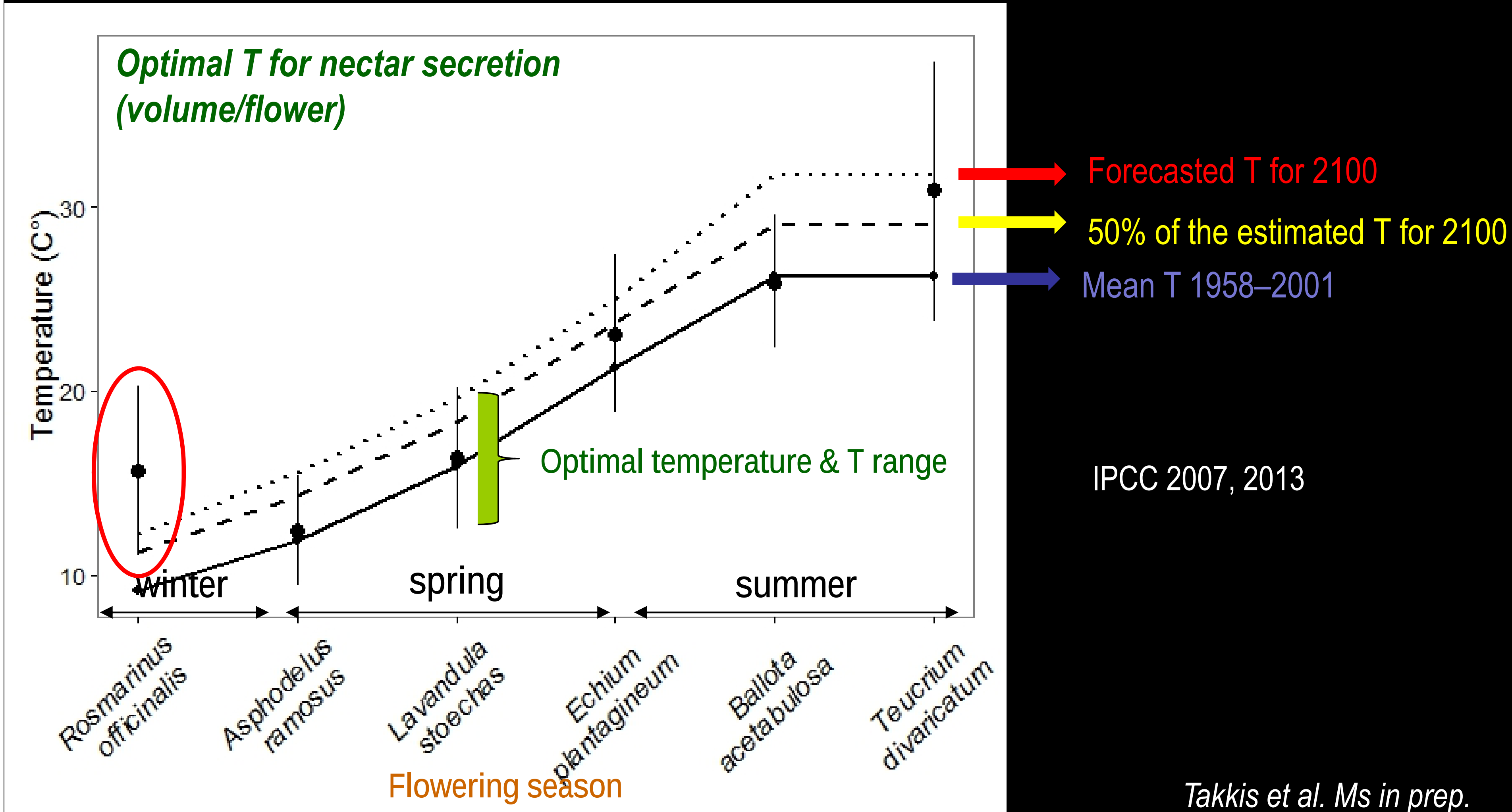


| the highest 5% of the trait values

optimal temperature

optimal temperature range

Which plant species will be more affected by climate change?

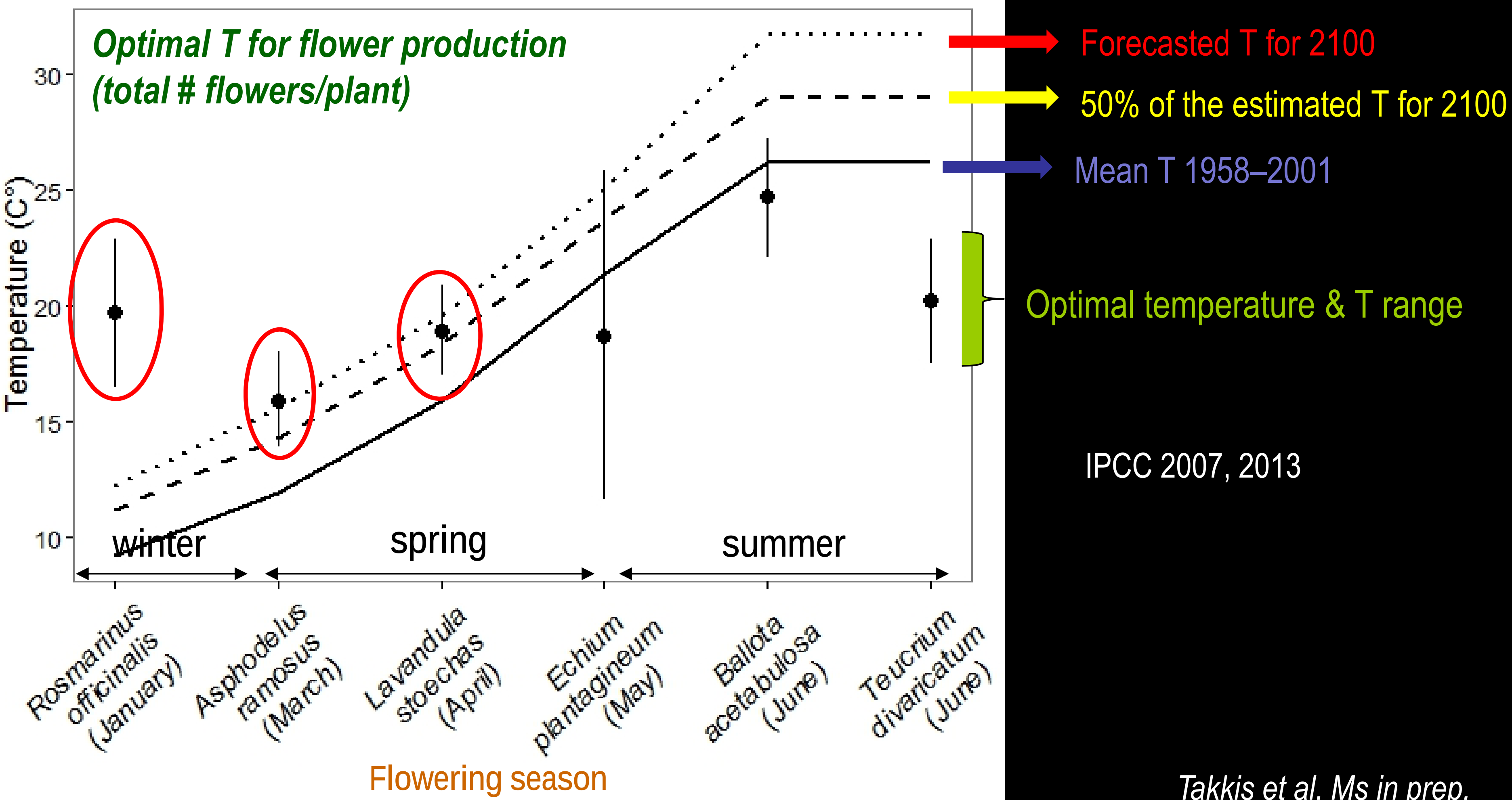


IPCC 2007, 2013

Takkis et al. Ms in prep.

Few flowering plants (e.g. winter-)will be benefitted as to volume/flower secretion
Bees have to work more between plants for water uptake (sub-optimal foraging)

Which plant species will be more affected by climate change?

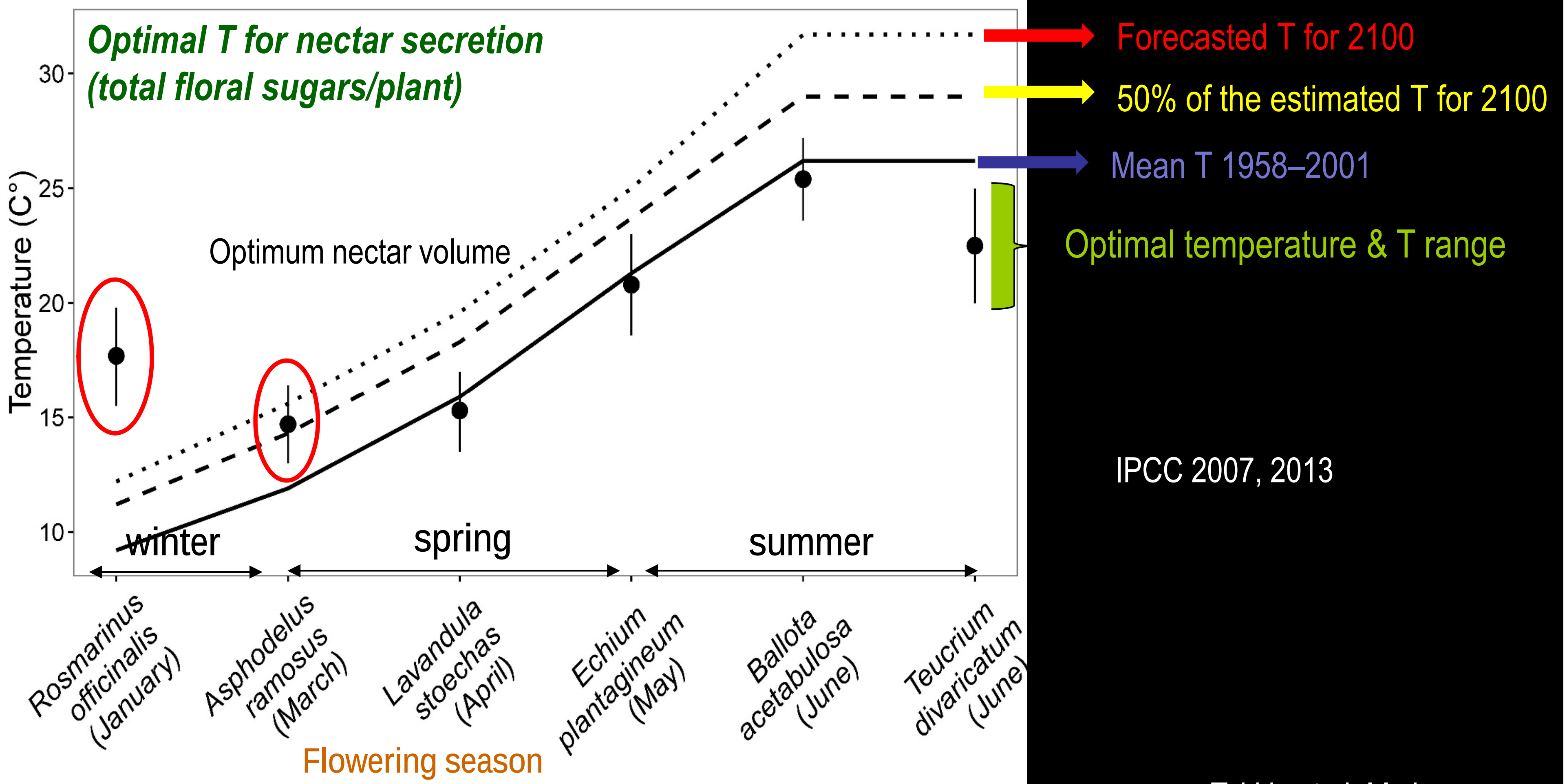


IPCC 2007, 2013

Takkis et al. Ms in prep.

Winter- & spring flowering plants will be benefitted as to flower production

Which plant species will be more affected by climate change?

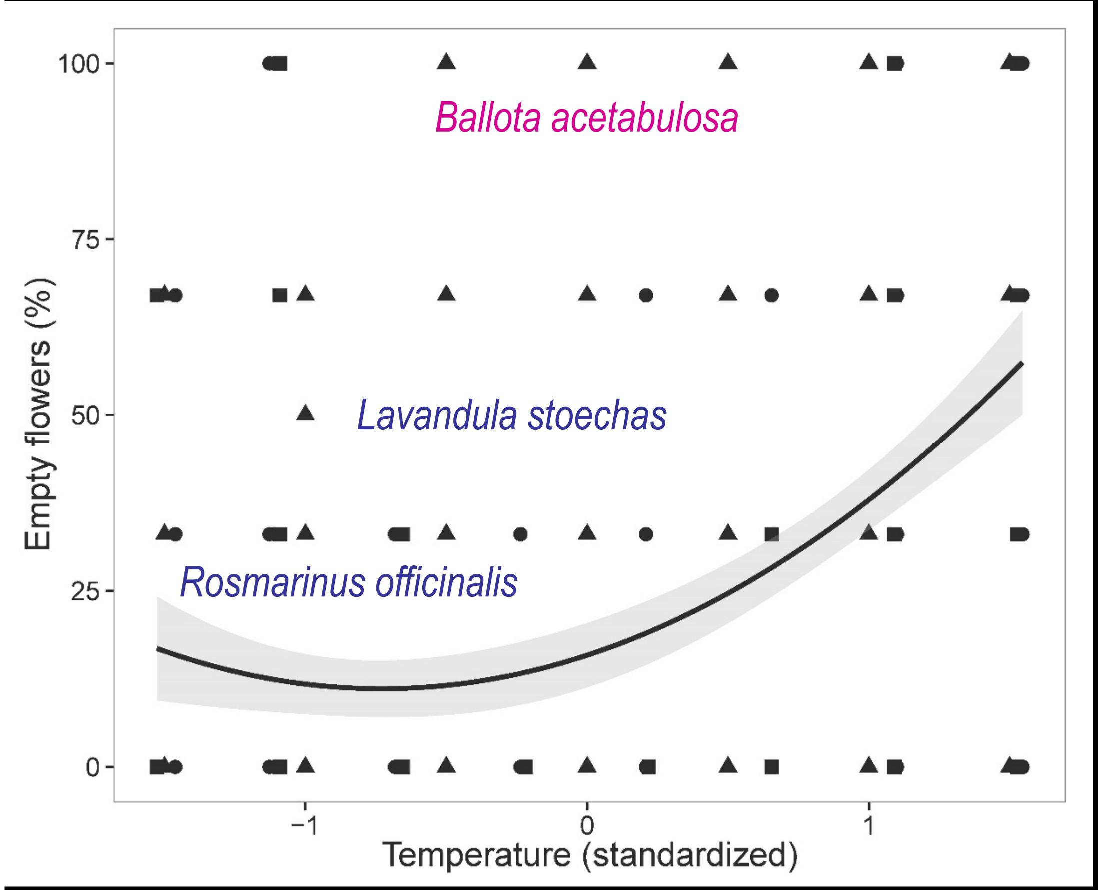


Takkis et al. Ms in prep.

Estimated nectar sugars/plant towards the end of the century

- *summer- & spring-flowering plants will be dramatically stressed*
- *winter & early-spring flowering plants will be benefited*

Another effect temperature increase: empty flowers!



3 species with many empty flowers!

Most of them Lamiaceae (¾)

T increases emptiness

Foreseen:
impacts on honeybee behavior

Conclusions I: effects on flowering plants

Flowering time

- Shift towards winter, especially the spring-flowering plants

Nectar secretion

- Unstable weather conditions (low T):
  - longer flower span, larger duration
  - but less nectar/flower, maybe smaller flowers
- Better performance of winter flowering plants (e.g. rosemary)

Pollen-flower plants

- May take over vs. nectar-flower plants

Conclusions II: imminent effects on bee-keeping

Direct effects on honeybees

- Sub-optimal foraging in summer, but also in spring!
- Low-foraging summer period will be more critical both for hive sustenance (food provision by bee-keeper) and breeding
- Higher hb competition (intra-, hetero-specific) for nectar in spring

Quantity and quality of honey yield

- Topmost nectar/honey yields will be confined in winter, and (less) in early spring & autumn
- More difficult to obtain unmixed yields (i.e. one-plant honey)
- Significant honey labels may be challenged (e.g. thyme)

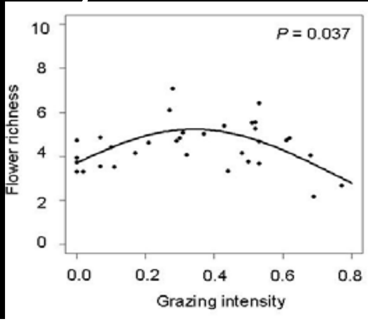
Conclusions III: adaptive actions in the Mediterranean

Bees

- Need to sustain bees for longer periods or move them more drastically in new forage areas (higher latitudes/elevations)

Foraging flora

- Create/conserve natural honeybee gardens enriched with nectariferous plants
- Combine with pollination of existing orchards
- Combine bee-keeping with plantations of aromatic plants
- Encourage the creation of flowering gardens vs. lawns
- Control overgrazing; keep the mosaic in Mediterranean systems



Business

- Create new products (e.g. rosemary honey?)
- Combine with pollination?

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