

Coevolución

- Qué es la coevolución
- Coevolución recíproca vs. difusa
- Mosaicos geográficos
- Ejemplos

Coevolución

- “Cambio evolutivo en un carácter de los individuos de una población en respuesta a un carácter de los individuos de una segunda población, seguido de una respuesta evolutiva de la segunda población al cambio en la primera” (DH Janzen, 1980, *Evolution* 34: 611-612).
- “Cambio evolutivo recíproco en especies interactuantes” (JN Thompson, 1994: 8, *The coevolutionary process*, U. of Chicago Press).

Importancia de la especialización recíproca para la evolución

“No podremos comprender la diversidad de especies a menos que también comprendamos la diversidad de las interacciones entre ellas. Estas dos mitades de la biología evolutiva están vinculadas mediante los procesos de especialización y coevolución. La especialización en las interacciones entre especies es la razón por la cual el mundo tiene millones de especies y no miles” (JN Thompson, 1994, *The Coevolutionary Process*).

Coevolución difusa

“La coevolución difusa ocurre cuando una o ambas poblaciones en la definición anterior están representadas por un conjunto de poblaciones que generan una presión de selección conjunta” (DH Janzen, 1980, *Evolution* 34: 611-612).

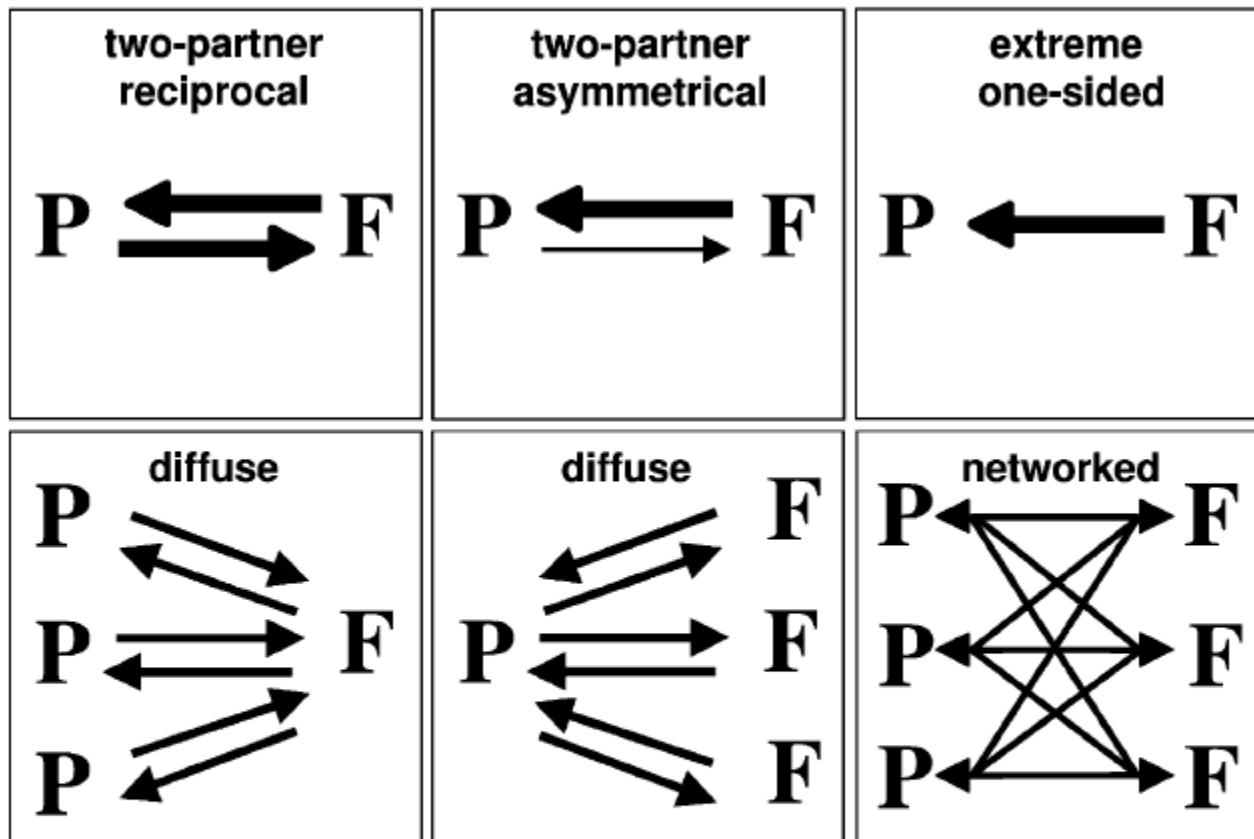
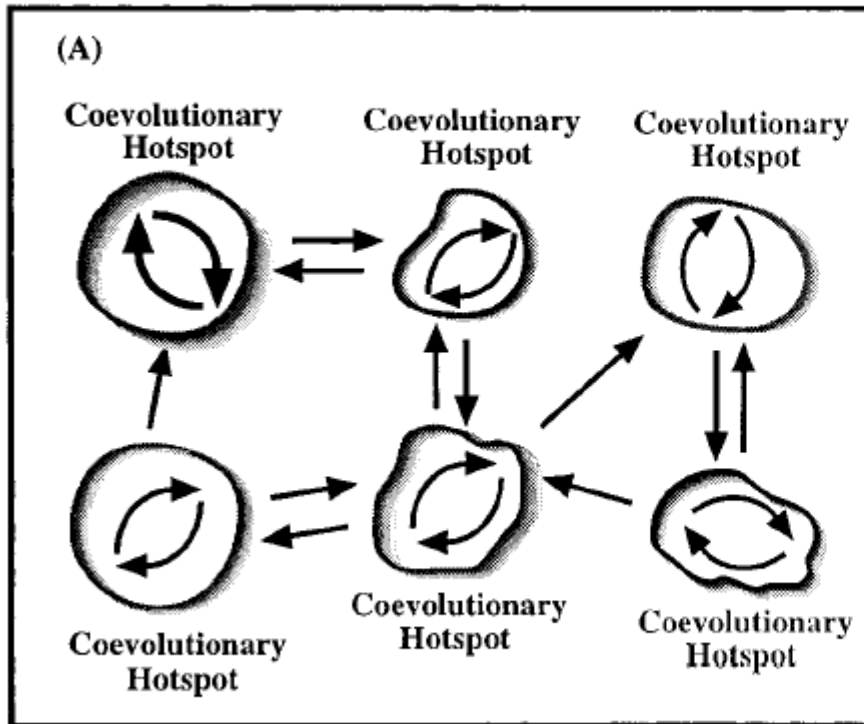


Fig. 1. Schemes of coevolutionary interactions between species. Arrows indicate strength and direction of selective forces on the evolution of coadaptations. F = flowering plant species, P = pollinator species.

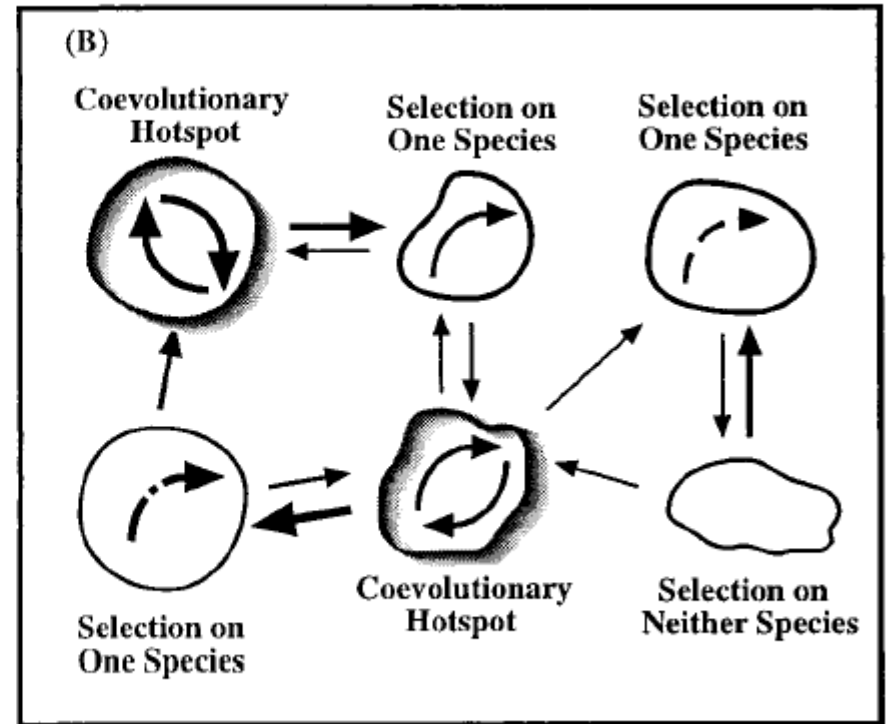
“Hemos creado caricaturas del proceso [de coevolución], a veces esperando que cada interacción local esté altamente coevolucionada [...]. Otras veces, la coevolución ha sido descartada como un evento raro [...], poco importante para la organización cotidiana de las comunidades, porque cada especie interactúa con muchas otras especies” (JN Thompson, 1999, *Am. Nat.* 153: S1-S14).



Universal hotspots



Complex mosaics



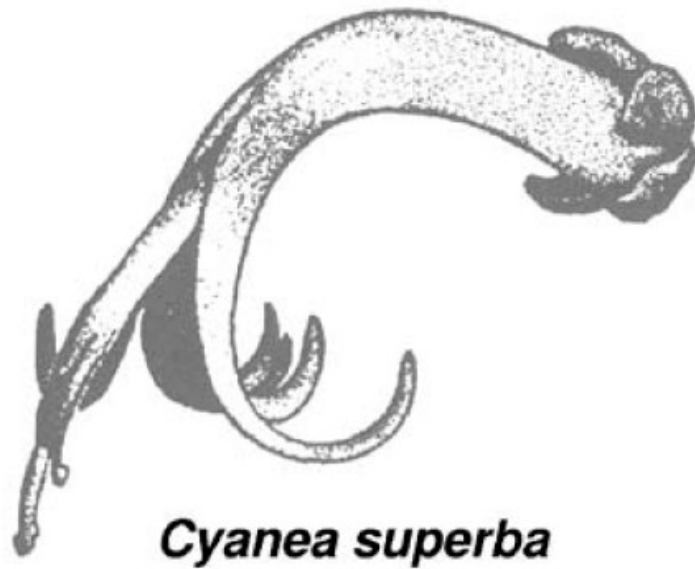


Fig. 2. Curvature as coadaptation: corolla tubes of *Cyanea fissa* and *C. superba*, heads and bills of *Drepanis pacifica*, *Vestiaria coccinea* and *Hemiatone sanguinea*. Modified and combined from Sedlag (1972) and Givnish et al. (1995).

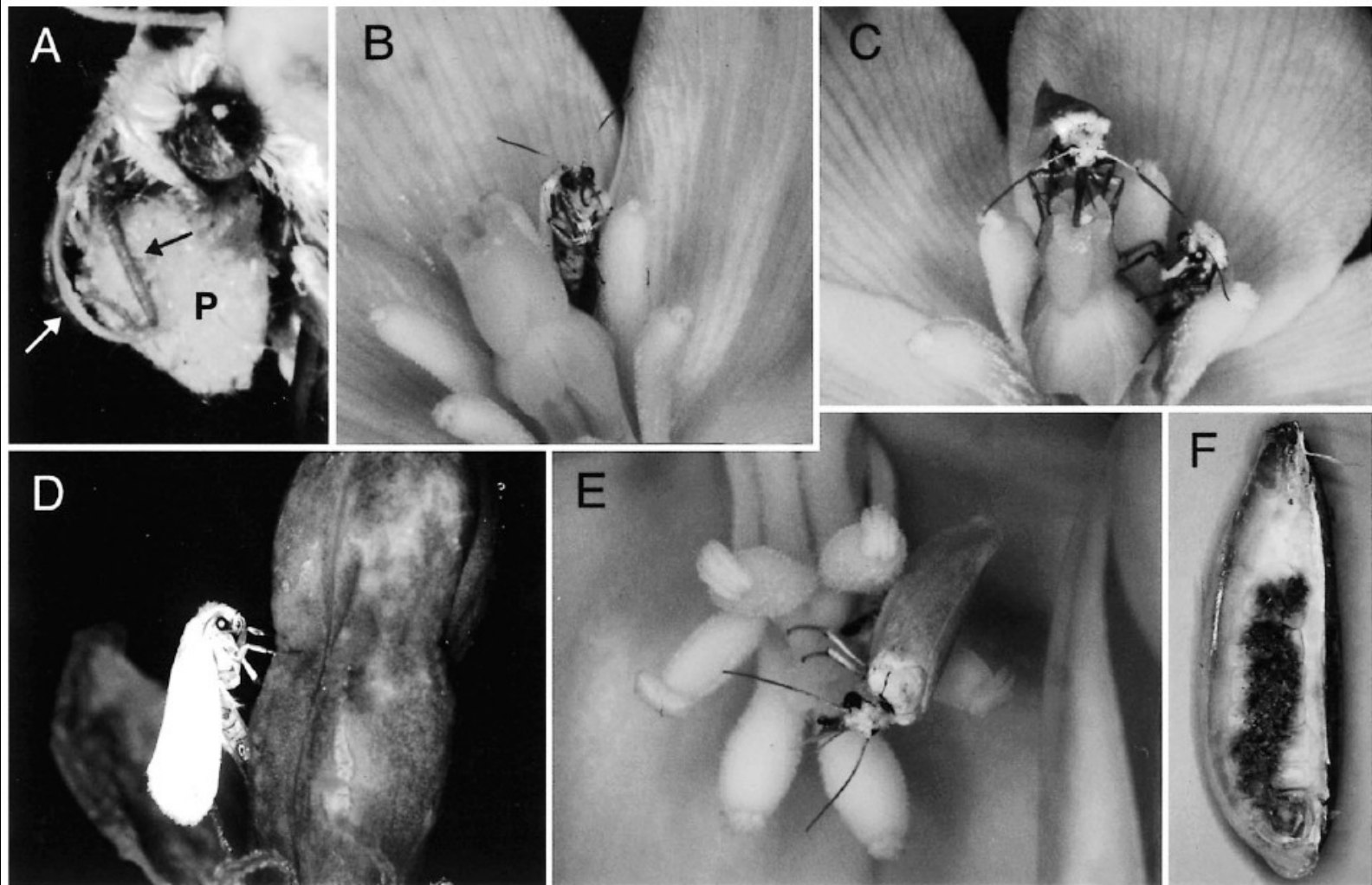
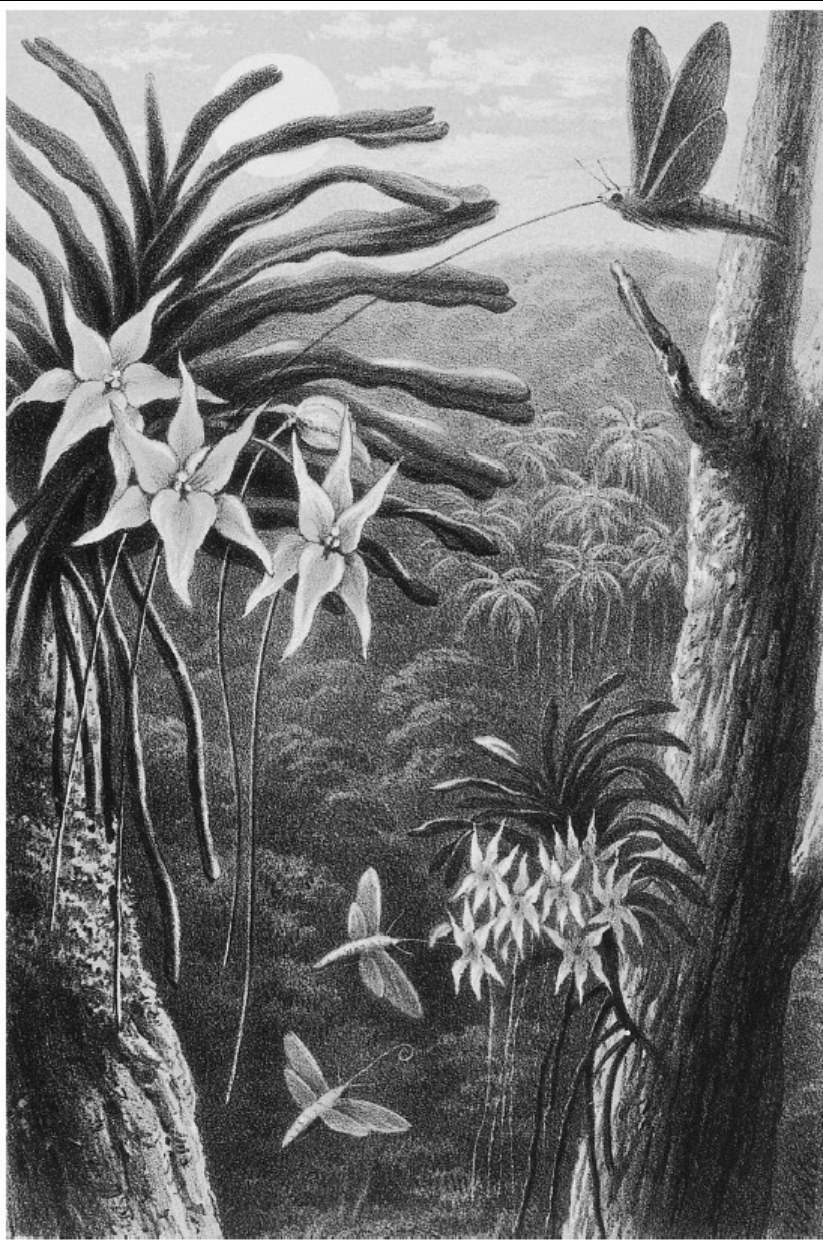


Figure 5. —A. Head of *Tegeticula carnerosanella* female. Large pollen load (P) held below the head, with left tentacle and proboscis indicated by black and white arrows. Cross section of tentacle 1.0 mm. —B. Female *T. yuccasella* compacting pollen just collected from a *Y. filamentosa* stamen. —C. Females of *T. yuccasella* pollinating (top) and ovipositing into (right) a *Y. filamentosa* ovary. —D. Female *T. intermedia* ovipositing into a ca. 8-day-old *Y. filamentosa* fruit; note constriction caused by *T. yuccasella* ovipositions. —E. *T. treculeanella* female pollinating *Y. treculeana* Carrière flower. Moth wing length in panels B–E 10–11 mm. —F. Longitudinal section through locule of mature *Y. carnerosana* (Trel.) McKelv. fruit, showing feeding path of *T. carnerosanella* larva that has destroyed seven seeds; fruit length 73 mm. For a set of color pictures of *T. yuccasella* behavior on *Y. filamentosa*, see Murawski (1997).

“Para determinar el papel histórico de la coevolución en la diversificación de una interacción [se requieren] grupos de plantas y polinizadores que hayan coexistido durante gran parte de su diversificación [para los que existan] filogenias bien resueltas, preferentemente con estimaciones de la longitud de las ramas. Este criterio no se cumple para la asociación entre las yucas y sus polillas, ni para ninguna otra asociación planta-polinizador similar.”



Fuente: Wallace AR (1867) *Quarterly Journal of Science* 4: 470-488



Fig. 2. Madagascar's *Xanthopan morgani praedicta*, the longest-tongued hawkmoth of the Old World. Photo by Börge Pettersson and L. Anders Nilsson.

Fuente: Nilsson LA (1998) *TREE* 13:259-260

“A medida que ciertas polillas malgaches aumentaron en tamaño mediante selección natural en relación a sus condiciones generales de vida [...] o a medida que su proboscis se alargó para obtener néctar de *Angraecum* y otras flores tubulares profundas, los individuos de *Angraecum* con los nectarios más largos [...] y que, en consecuencia, obligaron a las polillas a insertar la proboscis hasta su base, fueron las mejor fertilizadas. Esas plantas producirían el mayor rendimiento de semillas, y las plántulas heredarían en general nectarios largos; y así sucedería en sucesivas generaciones de la planta y de la polilla.”

Fuente: Darwin C (1862) *On the various contrivances by which British and foreign orchids are fertilised by insects*. Murray.

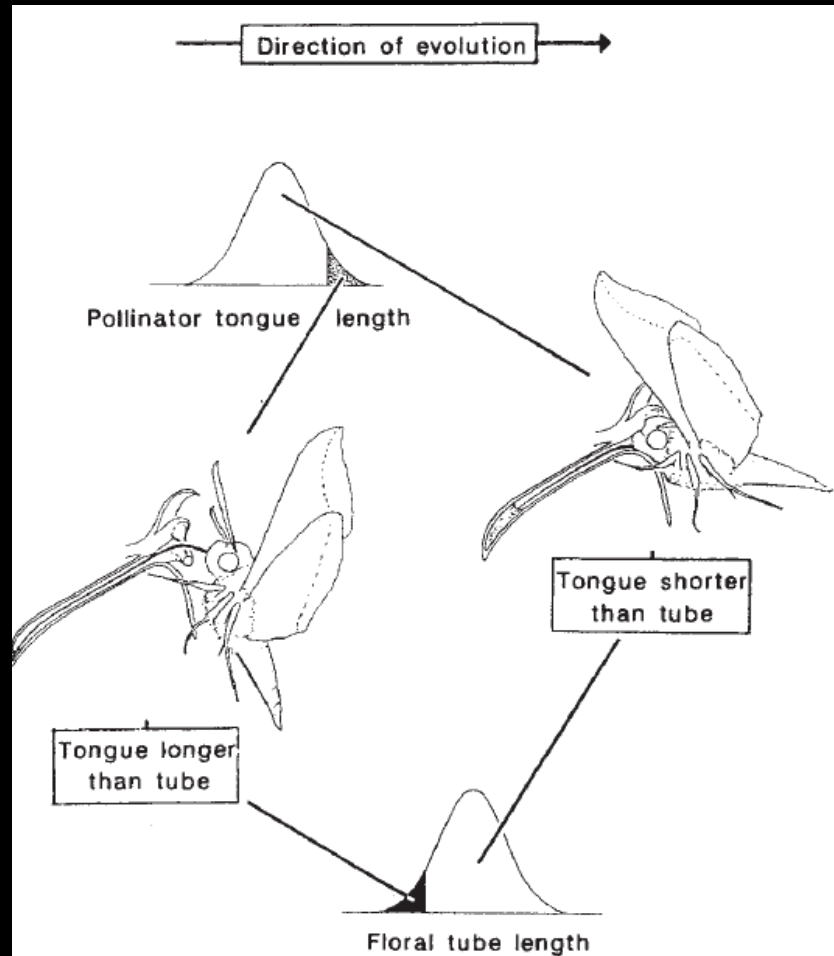


Fig. 1 Modified version of Darwin's hypothesis on the evolution of deep flowers in plants. Long-tongued pollinator individuals are not compelled to contact the floral sexual organs in short-tubed plant individuals, which therefore receive fewer pollinations than the long-tubed individuals that pollinate freely with each other via the pollinators.

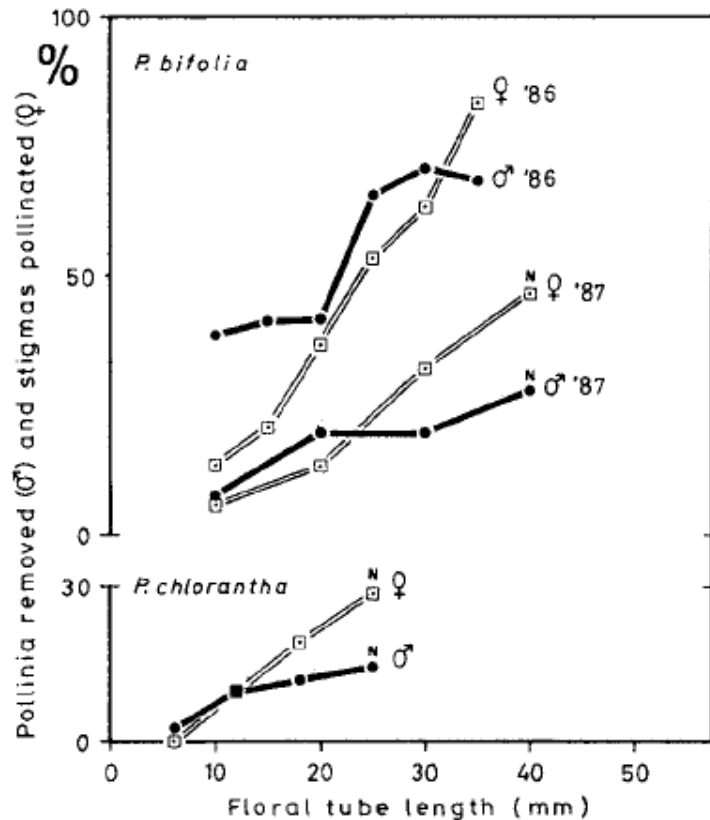


Fig. 2 Experimental shortening of floral tube has a strong negative effect on male (pollinia removal, black bars) and female (stigma pollen receipt, open bars) components of fitness in *P. bifolia* (top) and *P. chlorantha* (bottom). Experiments were performed with series of tube lengths, for *P. bifolia* in 1986; 10, 15, 20, 25, 30 and 35 mm ($n = 30$ per length) (180 flowers) and in 1987; 10, 20, 30 and 40 (natural length) ($n = 59$ per length) (236 flowers) and for *P. chlorantha* in 1987; 6, 12, 18 and 25 (natural length) mm, ($n = 42$ per length) (168 flowers). Three fresh, unvisited flowers per inflorescence were manipulated using tape (1986) or cotton thread (1987). The within-spike positions were alternated. In 1986, the often low nectar-content in shortened spurs was not compensated, but in 1987 the nectar was squeezed up, above the constriction. Patterns in reduction of fitness, however, were similar. Flowers were exposed 10 (*P. bifolia* 1987), 8 (*P. bifolia* 1987) and 6 (*P. chlorantha* 1987) nights to natural pollinators (moths). χ^2 homogeneity tests on data for each sex function and experiment indicate significant effects ($P < 0.025$) of treatment in all cases.

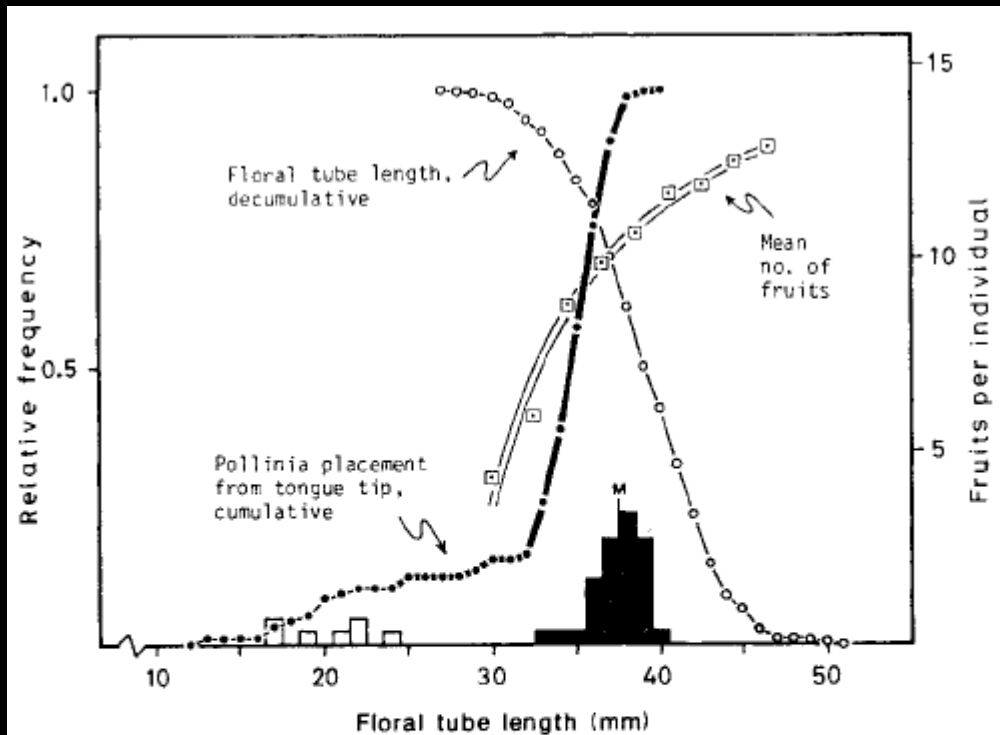


Fig. 3 Floral tube length and pollinia placement pattern on pollen vectors affect differential production of fruit in a population of *P. bifolia* (central forest area on Öland, South Sweden). Heavy black line denotes the contribution from pollinia placement on *Sphinx ligustri*. Effective tongue length (total length minus portion obstructed by palpi) of visiting moths is shown by bars, those representing *S. ligustri* being filled black (*M* = mean length in this hawk-moth). Data obtained 1972–1986. Sample sizes: 349 plants, and 42 moths with a total of 245 pollinia.

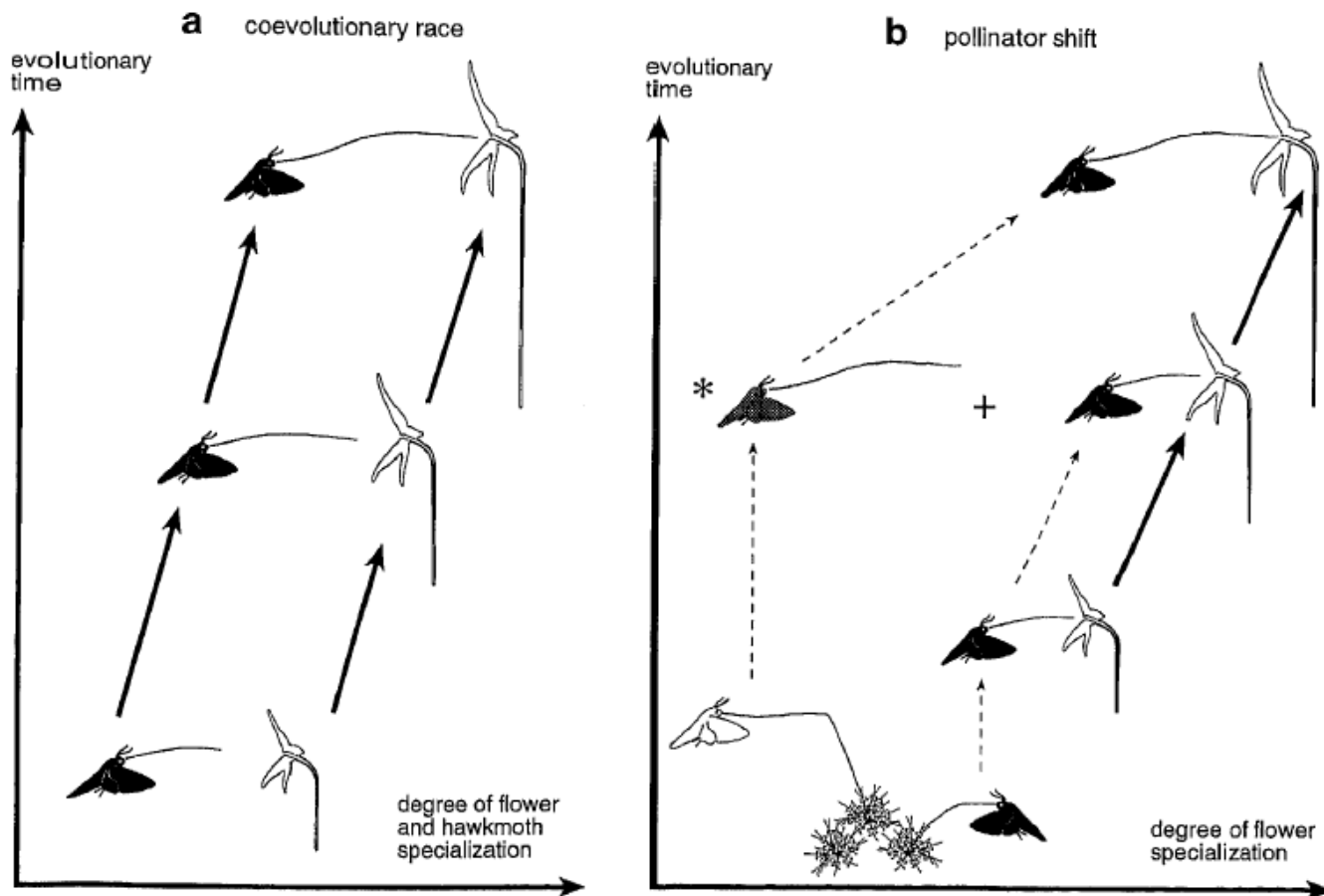


Fig. 12 Comparison of the "coevolution" model of Darwin 1862 (a) and the "pollinator shift" model (b) in orchid spur evolution. **a)** Evolutionary race between increasing spur length and increasing tongue length. **b)** Recruitment of generalist feeders with preadapted tongues of different lengths as pollinators by long-spurred angraecoid orchids and their gradual substitution. When spur enlargement driven by the primary visitor exceeds a certain diameter, the flower can be exploited by a longer-tongued illegitimate visitor (asterisk): Such a situation has recently been represented by the interaction of *X. morgani* and *C. solani* with *A. compactum*. The occurrence of the long-tongued species exerts an increase of

selective pressure towards spur elongation on the orchid. When the spur size of the flower has reached a dimension so that the nectar column is out of reach for the primary pollinator, the flower may still be pollinated by this species but now acts as a deceptive flower. If an increase of overall dimension leads to pollinaria wastage by the shorter-tongued visitor, the selection favours further changes in the proportions of the flower's sexual organs so that pollinaria cannot be extracted by the shorter-tongued visitor. This is the case in *A. sesquipedale* and *A. sororium*. Black signature: orchid pollinator; grey: non-pollinating orchid visitor; white: moth incapable of exploiting orchid.

“La evidencia a favor de la hipótesis del escape de los predadores no es inequívoca. En particular, no existen reportes de datos cuantitativos demostrando que existe depredación sistemática sobre las polillas al visitar las flores. [...] Por lo tanto, parece más probable que la proboscis larga de *praedicta* se haya originado por una carrera coevolutiva” (Nilsson, 1998, *TREE* 13: 259-260).

“El efecto recíproco en el modelo de la carrera coevolutiva que postula que las proboscis largas evolucionaron como una adaptación para explotar nectarios largos [...] nunca ha sido confirmado” (Wasserthal, 1998, *TREE* 13: 459-460).

“El argumento de Nilsson [...] es una especulación que necesitaría estudios de campo detallados [...]. La hipótesis de Wasserthal [...] también necesita más evidencia. Por lo tanto, actualmente no hay ninguna explicación convincente del significado adaptativo del largo de la lengua de *X. m. praedicta*, si es que hay alguno” (Jermy, 1999, *TREE* 14: 34).

Condiciones para demostrar coevolución

1. Variación fenotípica (presencia de caracteres polimórficos discretos en poblaciones naturales).
2. Evidencia de base genética de esta variación.
3. Medidas de aptitud darwiniana (“fitness”).
4. Estudios comparativos entre poblaciones.

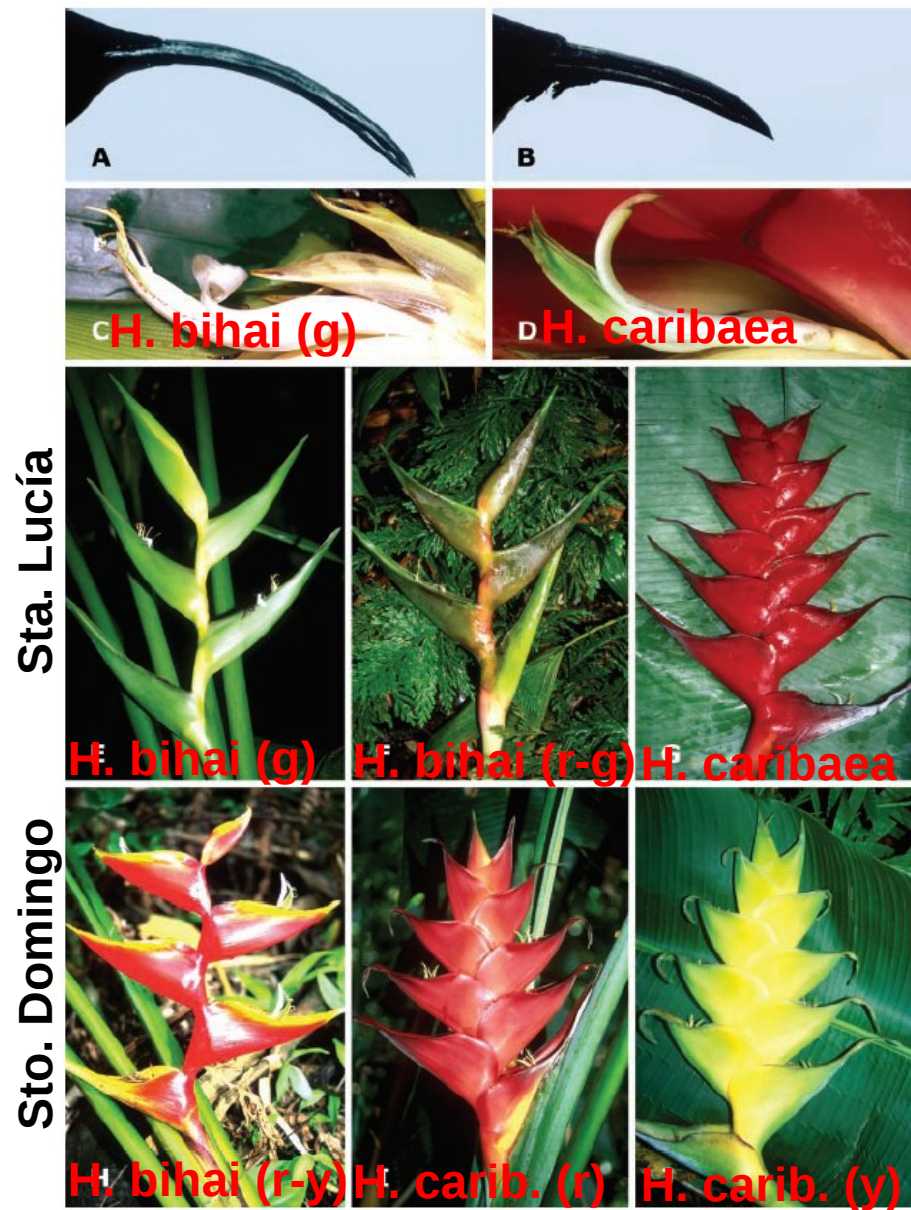
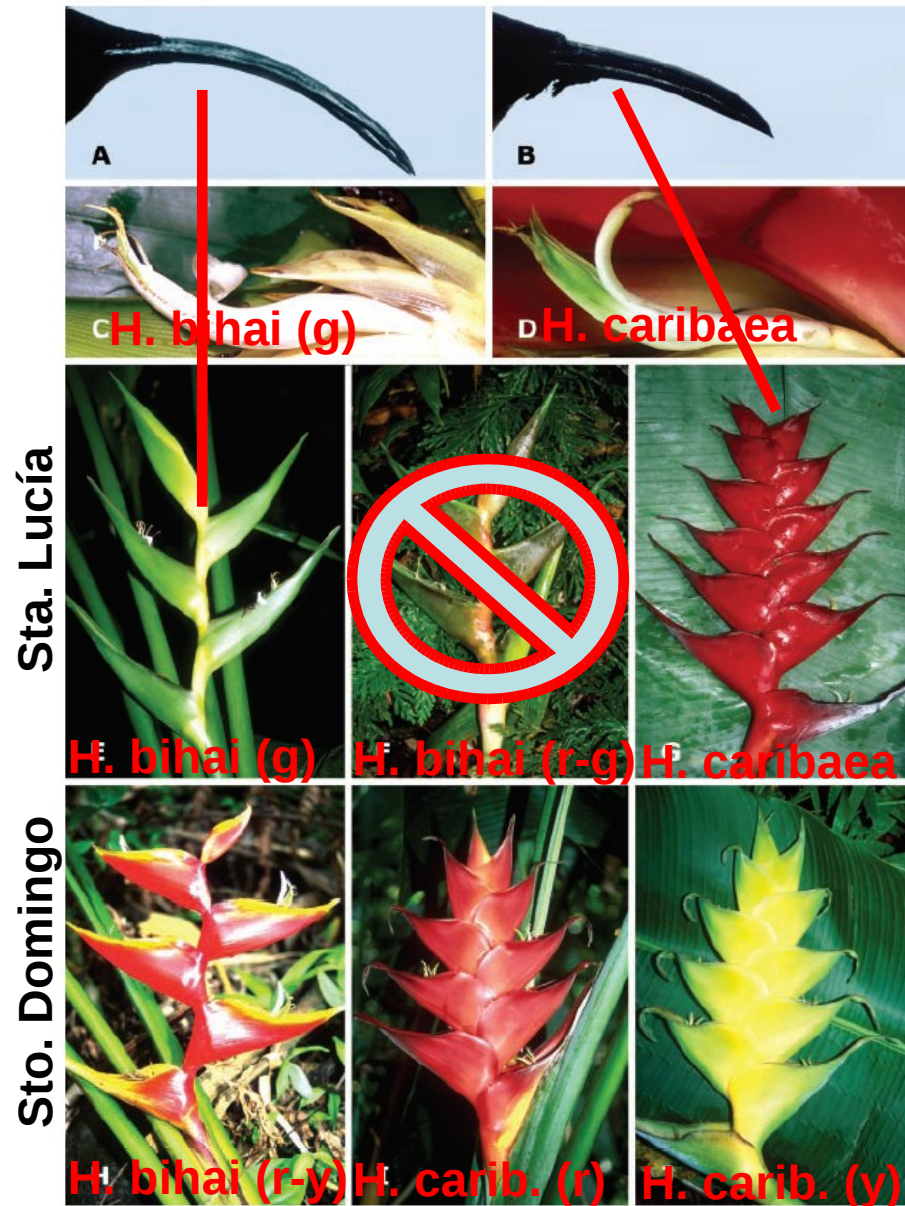


Fig. 1. Polymorphisms in bills of *E. jugularis* (A and B) and in flowers (C and D) and inflorescences (E to J) of *Heliconia* species on St. Lucia (E to G) and Dominica (C to D and H to J), West Indies. (A) *E. jugularis*, female bill. (B) *E. jugularis*, male bill. (C) *H. bihai*, flower. (D) *H. caribaea*, flower. (E) *H. bihai*, green inflorescence morph, St. Lucia. (F) *H. bihai*, red-green inflorescence morph, St. Lucia. (G) *H. caribaea*, inflorescence, St. Lucia. (H) *H. bihai*, red-and-yellow-striped inflorescence, Dominica. (I) *H. caribaea*, red inflorescence morph, Dominica. (J) *H. caribaea*, yellow inflorescence morph, Dominica.

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Fuente: Temeles EJ y Kress WJ
(2003) *Science* 300: 630-633

Santa Lucía:

Dentro de las reservas

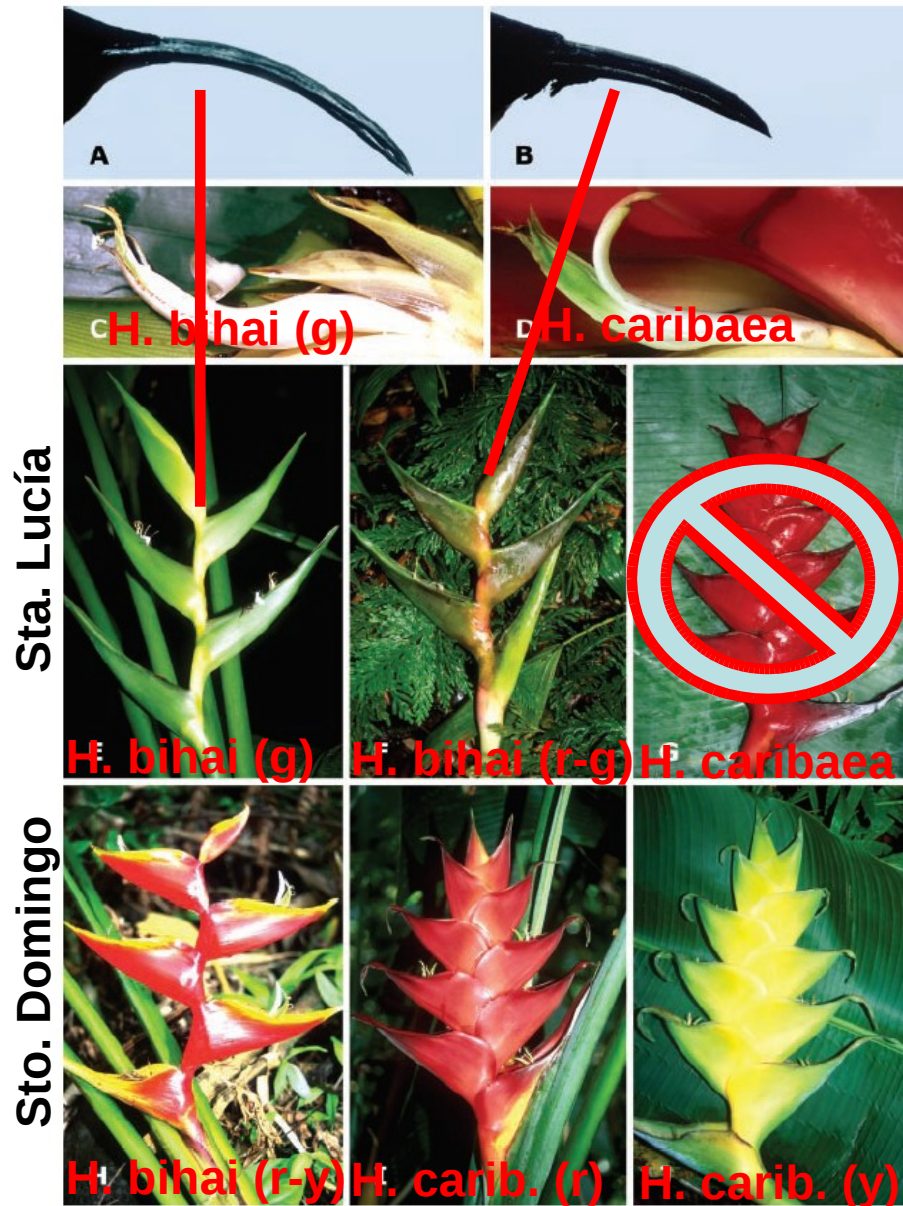
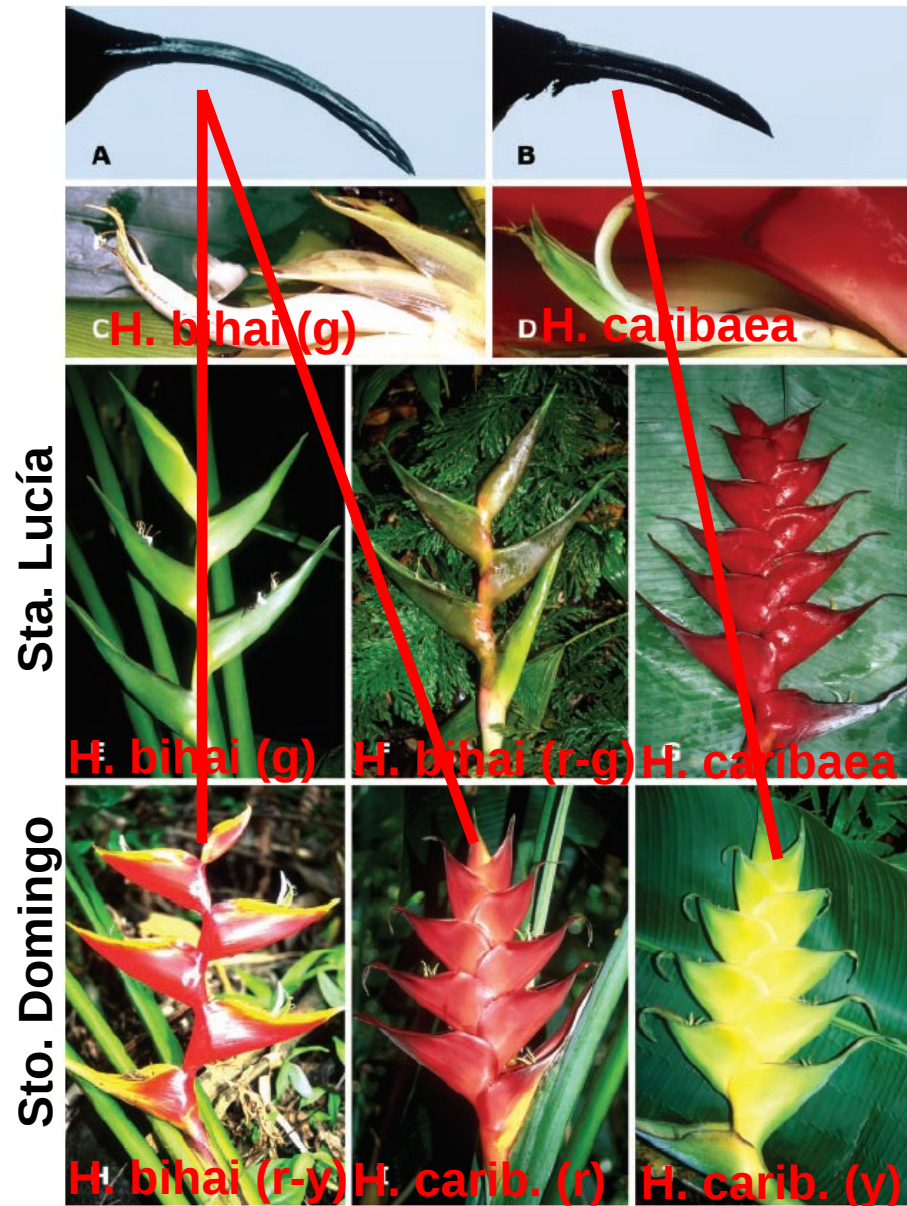


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Santo Domingo



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Santo Domingo

Table 1. Flower lengths and curvatures [mean \pm SE (n , where n is the number of flowers)] of *H. bihai* and the red and yellow morphs of *H. caribaea* along six transects in Dominica, West Indies.

Transect	<i>H. bihai</i>	Red <i>H. caribaea</i>	Yellow <i>H. caribaea</i>
		<i>Flower length (mm)</i>	
Salisbury Loop	47.6 \pm 0.3 (16)	39.7 \pm 0.4 (23)	36.2 \pm 0.3 (15)
Mt. Diablotin	47.2 \pm 1.2 (8)	40.0 \pm 0.4 (20)	37.2 \pm 0.2 (15)
Freshwater Lake	48.5 \pm 0.4 (25)	38.3 \pm 0.3 (14)	36.6 \pm 0.4 (17)
Morne Trois Pitons	48.9 \pm 0.7 (13)	38.1 \pm 0.2 (16)	35.4 \pm 0.3 (9)
Layou River	Absent	36.4 \pm 0.2 (19)	35.8 \pm 0.2 (15)
Central Forest	Absent	36.2 \pm 0.4 (16)	36.4 \pm 0.4 (12)
		<i>Flower curvature (degrees)</i>	
Salisbury Loop	28.8 \pm 0.5 (16)	24.0 \pm 0.7 (12)	20.2 \pm 0.4 (13)
Mt. Diablotin	30.0 \pm 0.4 (8)	22.6 \pm 0.6 (15)	19.4 \pm 0.7 (12)
Freshwater Lake	29.7 \pm 0.5 (12)	24.9 \pm 0.6 (12)	18.4 \pm 0.6 (10)
Morne Trois Pitons	31.3 \pm 0.9 (13)	23.9 \pm 0.6 (16)	20.7 \pm 0.5 (9)
Layou River	Absent	20.0 \pm 0.3 (19)	19.2 \pm 0.3 (15)
Central Forest	Absent	20.8 \pm 0.4 (7)	20.4 \pm 0.5 (7)

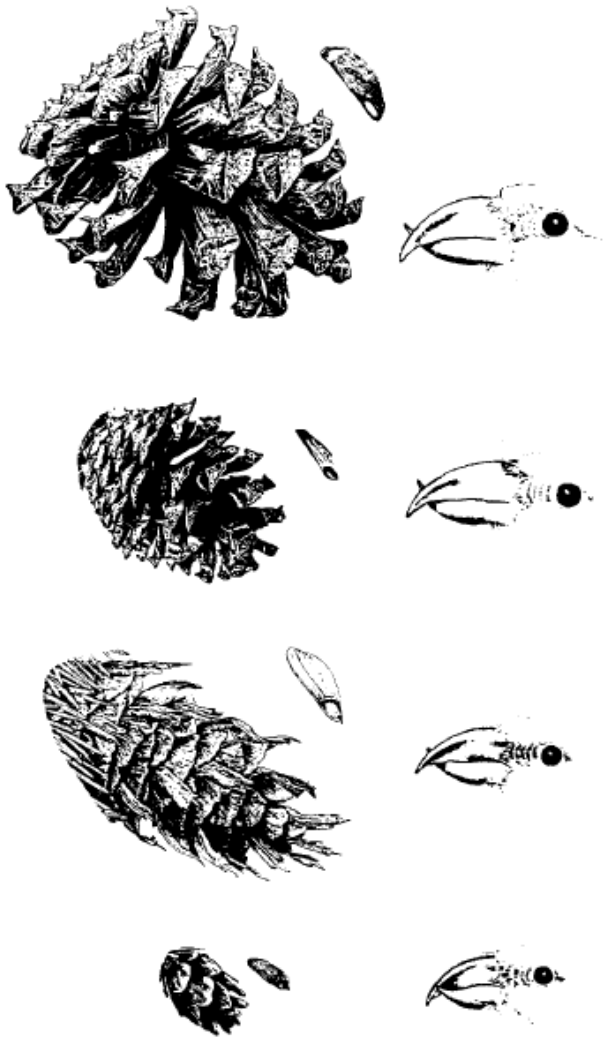
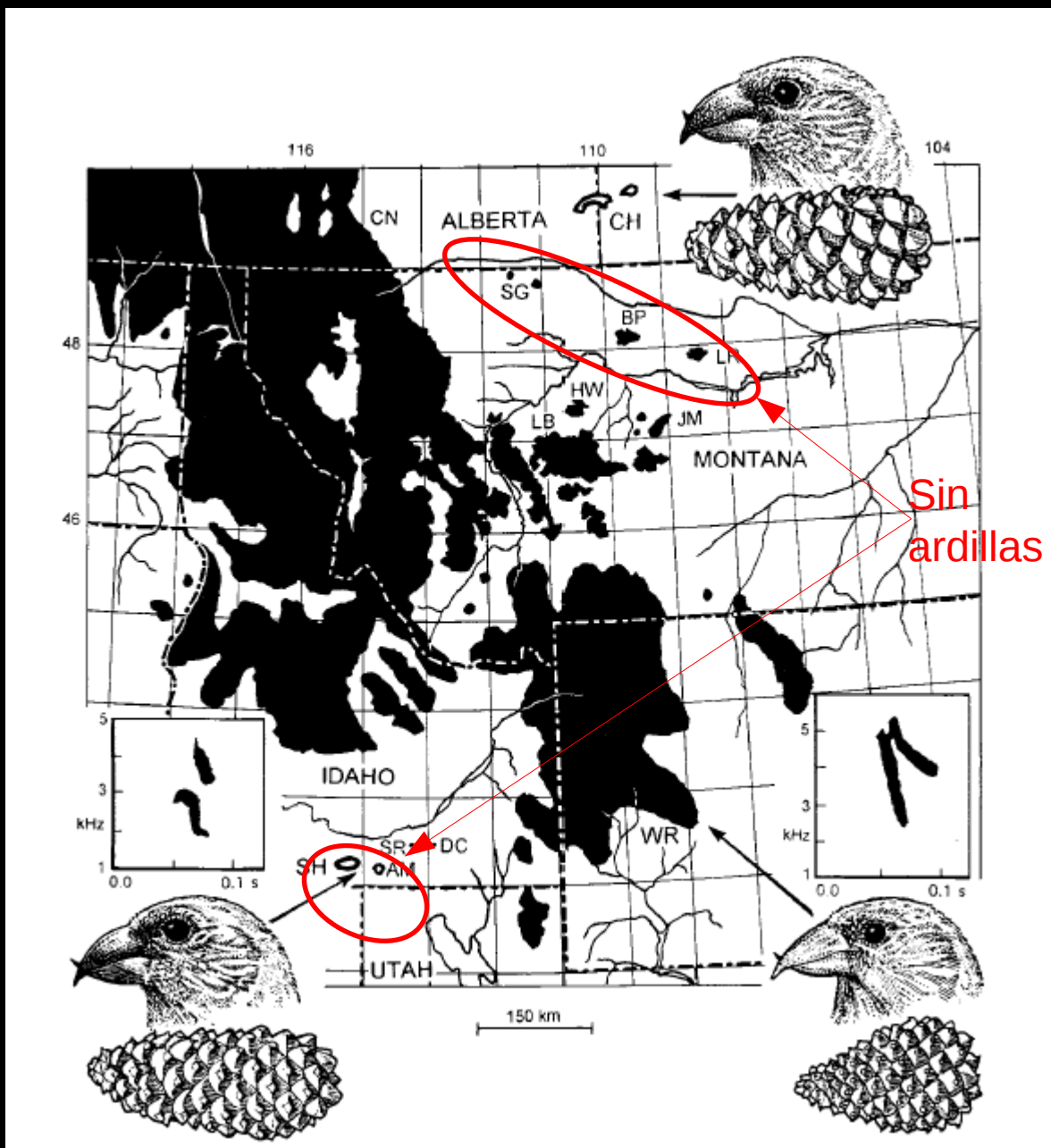


Figure 1: A schematic of four different forms or call types of red crossbills (Groth 1993) and the cones on which each crossbill specializes (from top to bottom: ponderosa pine *Pinus ponderosa* ssp. *scopulorum*, lodgepole pine *Pinus contorta* ssp. *latifolia*, Douglas-fir *Pseudotsuga menziesii* ssp. *menziesii*, western hemlock *Tsuga heterophylla* [reproduced from Sudworth 1917, 1967]). The bills are drawn to relative scale and so are the cones, but bills are drawn about 1.5 times larger compared with the cones.



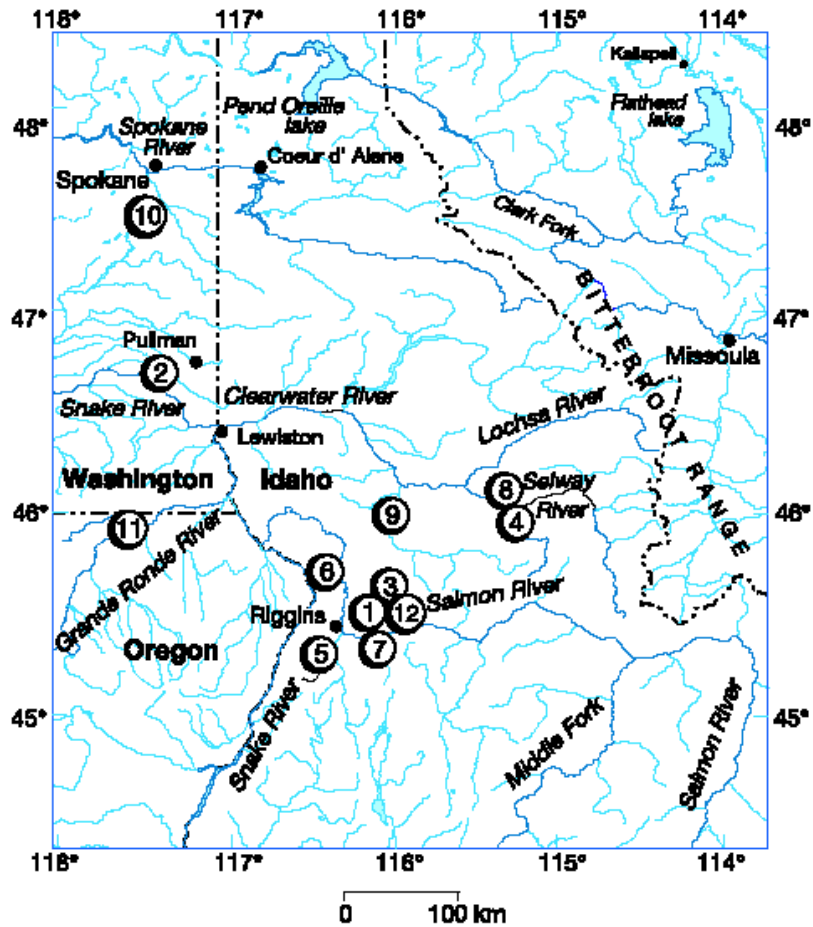


Table 2 Effect of moth oviposition on probability of floral development in *L. parviflorum*

Population	Effect of <i>Greya</i> oviposition on floral development		
	1997	1998	1999
Mutualistic effect of <i>Greya</i>			
Berg	1.1	3.0	1.8
Meadow	–	2.4	1.6
Saddle	0.8	20.5	9.2
Turnbull	1.0	1.0	2.4
Antagonistic effect of <i>Greya</i>			
Rapid	0.5	0.9	1.3
Salmon	–	0.4	–
South Fork	–	0.6	0.4
Wenaha	2.1	0.4	1.6
No effect of <i>Greya</i>			
Granite	0.5	1.1	1.0
Keating	1.1	1.1	1.2
Selway	–	0.9	–
Wind	–	0.7	1.0

Results are shown as the ratio of the percentage of developed capsules containing eggs to the percentage of aborted capsules containing eggs. Significant effects ($P < 0.05$) determined by χ^2 tests are shown in bold. Values significantly >1 indicate selective development of capsules containing eggs. Values significantly <1 indicate selective abortion of capsules containing eggs. The number of dissected capsules for each analysis averaged 678 (s.d. = 89.5, range = 386–898). Populations indicated with a dash were either not studied in that year or had too few aborted capsules for statistical analysis. Analyses were restricted to floral positions 2–4 on each plant.

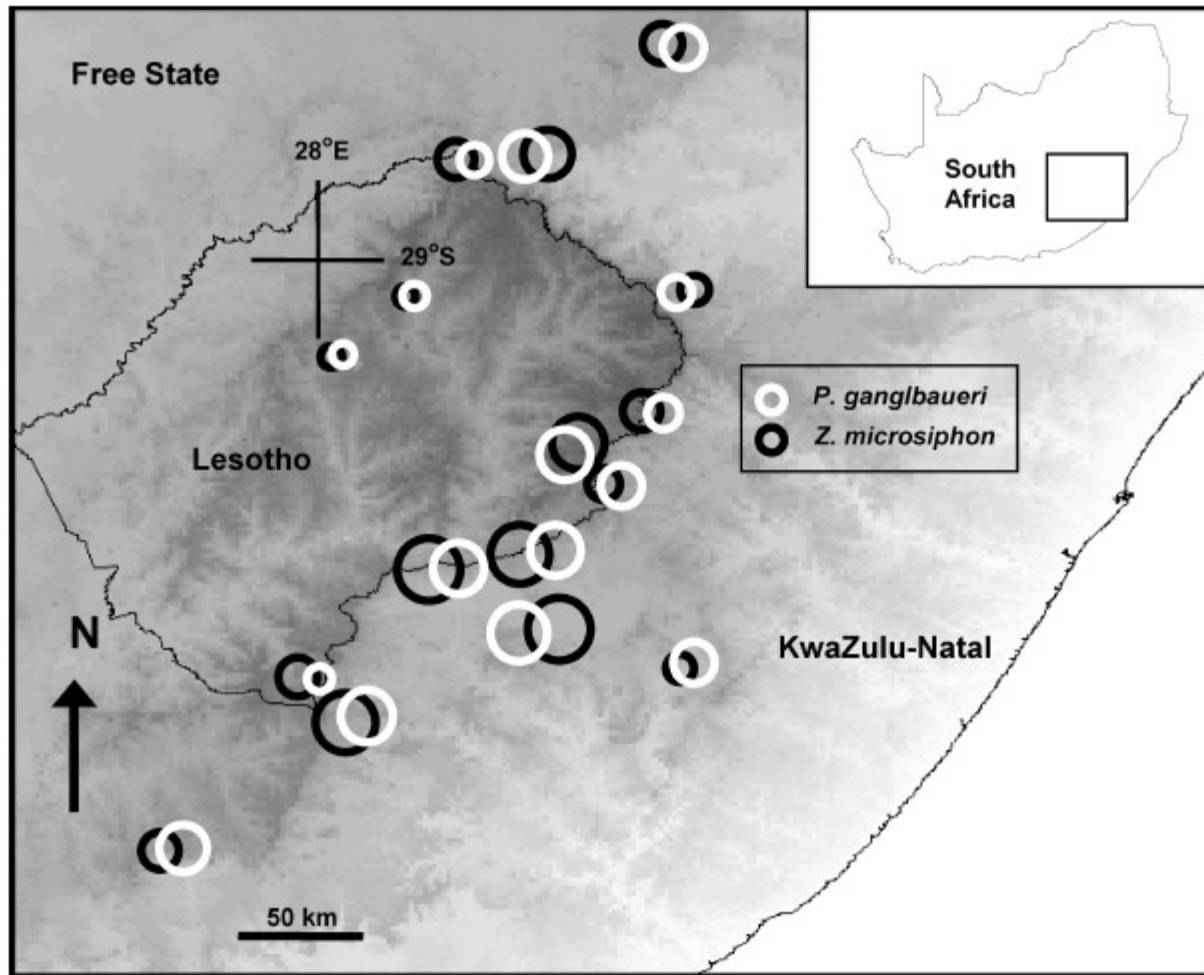


Figure 1. Variation in the functional proboscis length of *P. ganglbaueri* and the corolla length of its main food plant (*Z. microsiphon*) in 16 populations. Length of these traits are proportional to the diameter of the circles. The diameter of the circle in the boxed legend represents 25 mm.

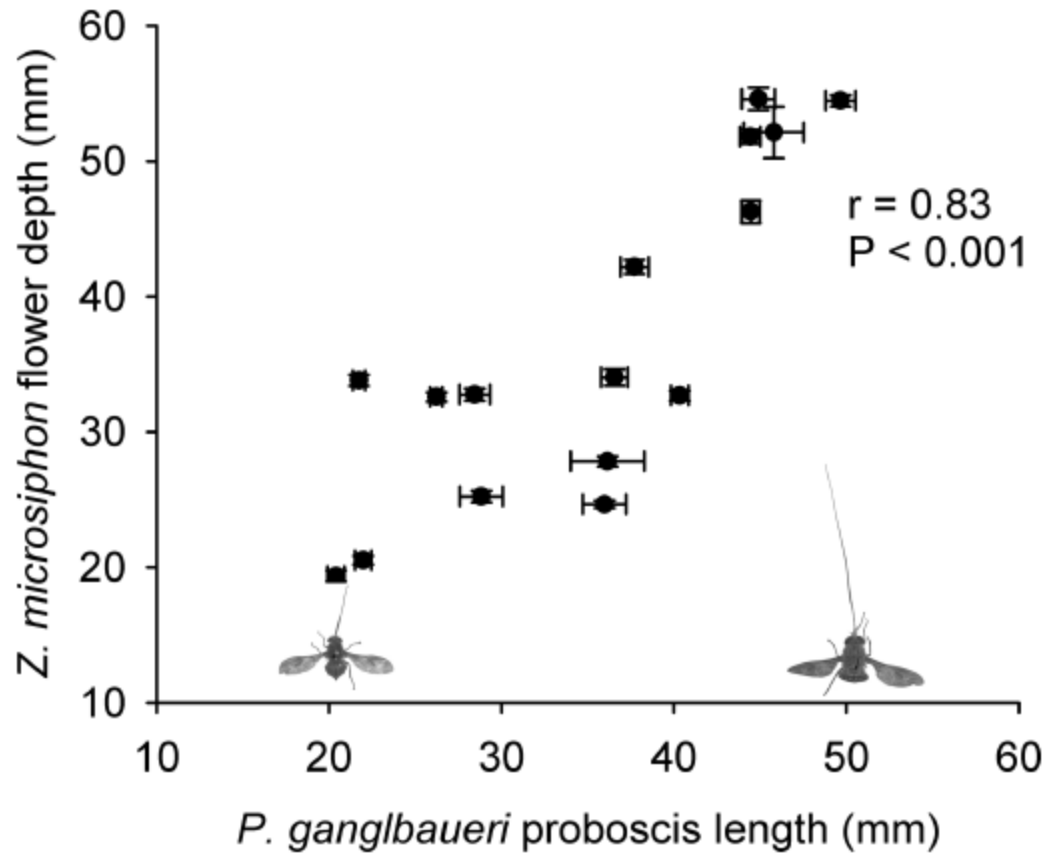


Figure 2. The relationship between proboscis length *P. ganglbaueri* flies and the depth of *Z. microshiphon* flowers in 16 populations. Each symbol represents the mean trait value (se) per population. A fly from the shortest tongued and longest tongued population are included to show the magnitude of variation in the system.

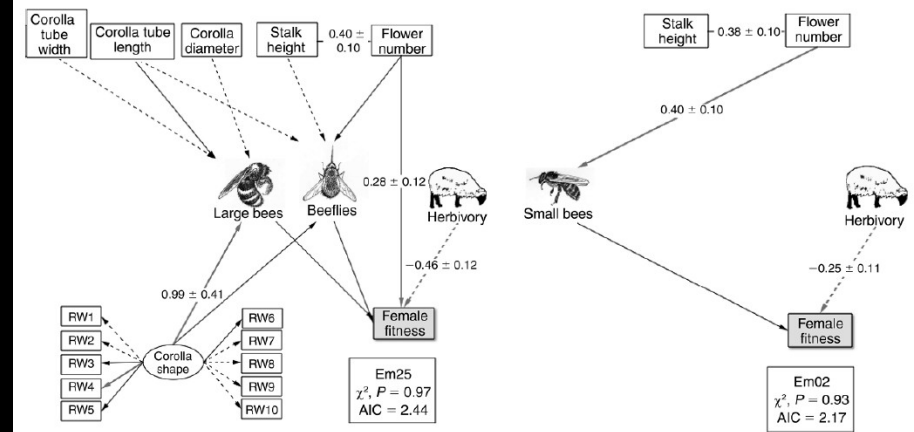
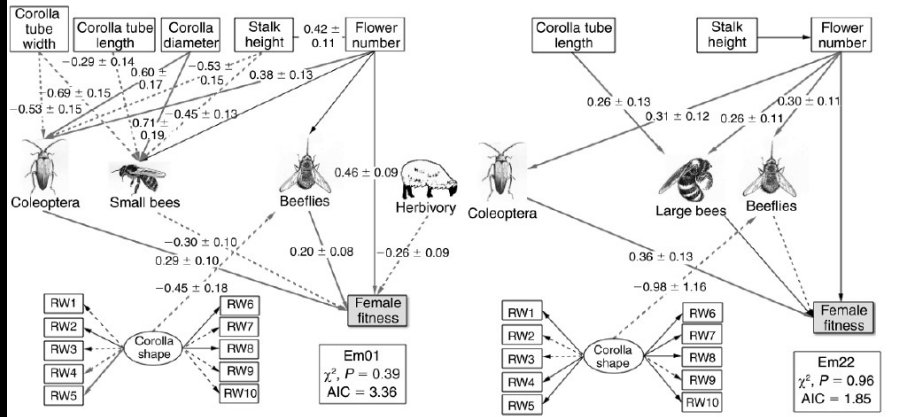
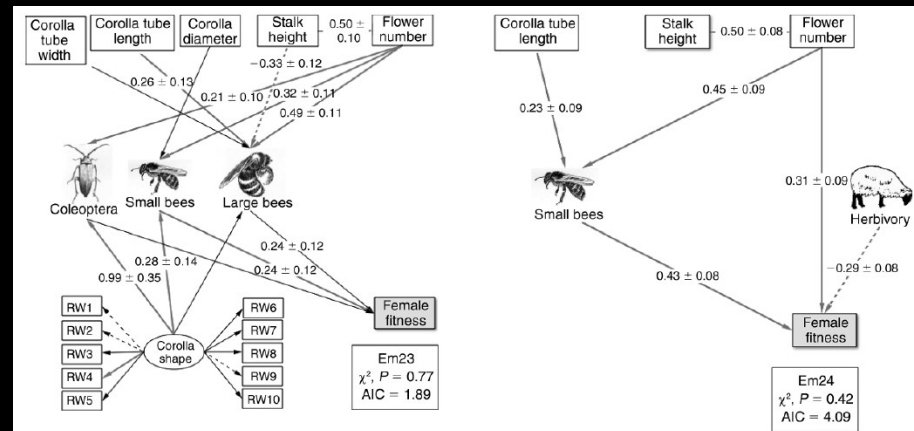
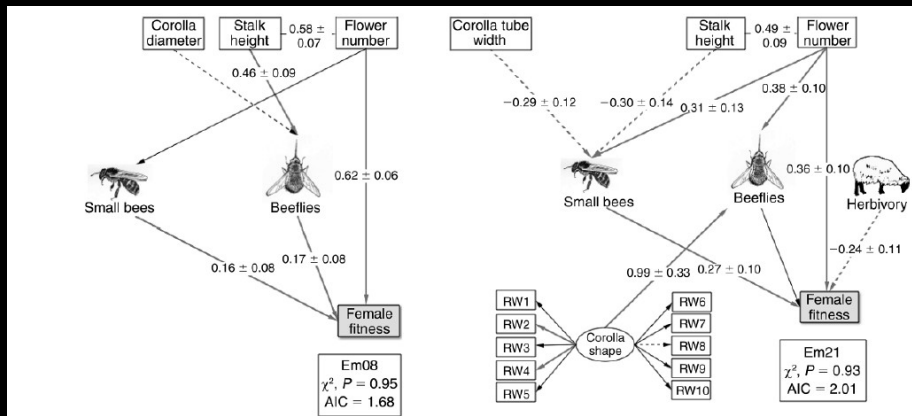


FIG. 4. The best structural equation model (EM) for each population, showing the causal relationships between the set of indicator variables (boxes), the latent variable (sphere), the main pollinators, and the female fitness estimates (see Fig. 1 for the saturated model). Only the values of the path coefficients (mean \pm SE) that were significant in the best models are shown. Positive effects are indicated by solid lines, and negative effects by broken lines. RW1–RW10 refer to the first 10 relative warps in the geometric morphometric analysis of flower shape.

FIG. 4. Continued.

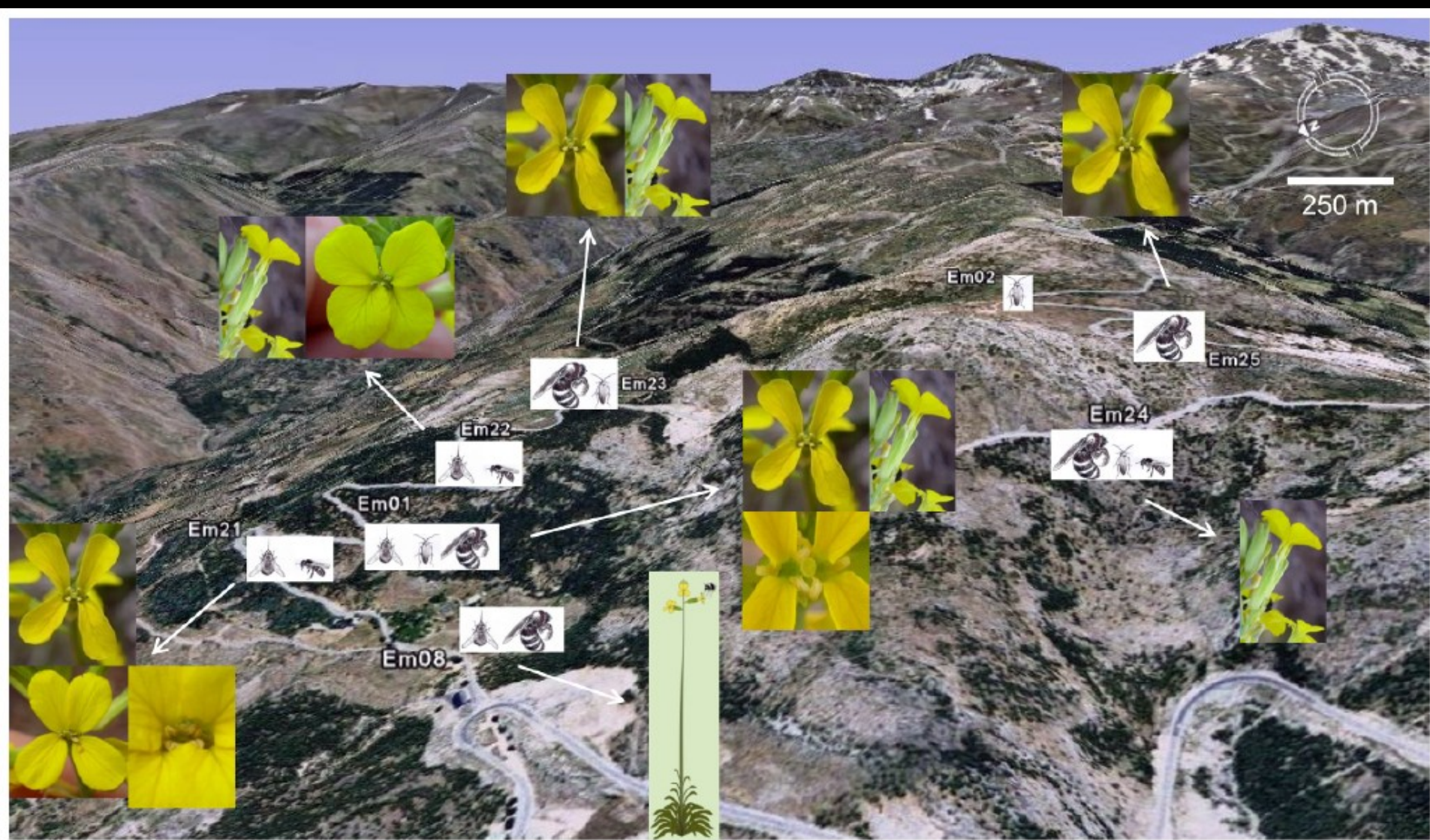


FIG. 6. Geographically varying selective landscape in *E. mediohispanicum*, indicating the spatial distribution of the pollinator-mediated selective hotspots for plant traits across the landscape. The pictures show the fit floral phenotype in each population, according to our geographic selection study. Only pollinators representing >20% of the visits in a given population are shown (see Fig. 1). Photos by J. M. Gómez; drawings by D. Nesbitt.

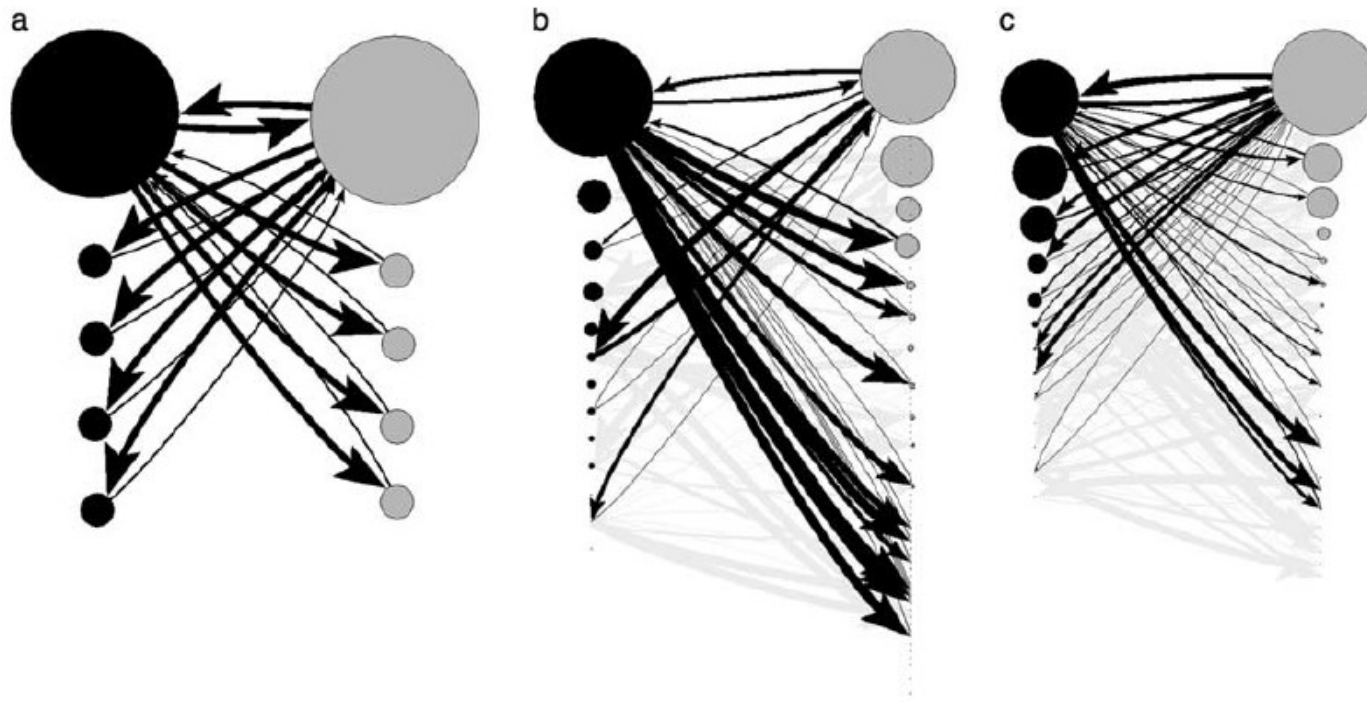


Fig. 1. Graphical representation of quantitative interaction networks to illustrate the abundance–asymmetry hypothesis. Under this hypothesis, abundant species (large circles) are dominant in terms of number of interactions (arrows) and the strength of those interactions for other species (arrow width). Conversely, rare species (small circles) have few interactions and have a minimal effect on abundant species (thin arrows). This model predicts asymmetric effects between rare and abundant species, and symmetric, reciprocally strong effects between abundant species, (a) Simple simulated network; (b) mutualistic network of plants (black circles) and insect pollinators (grey circles) from Llo Llo Municipal Reserve, Bariloche, Argentina (dataset 1, Appendix 1); (c) antagonistic network of mammals (black circles) and fleas (grey circles) from Volovské Vrchy mountains, Slovakia (dataset 39, Appendix 1). For clarity, in (b) and (c) only interactions involving the most abundant species are shown in black; other interactions are shown in light gray.