ESPECIAÇÃO e EXTINÇÃO

**Importância da especiação na Biogeografia
é que se trata de um processo evolutivo de ramificação:**

**Linhas evolutivas separam-se e adaptam-se
a diferentes ambientes, ocupando novas áreas.**
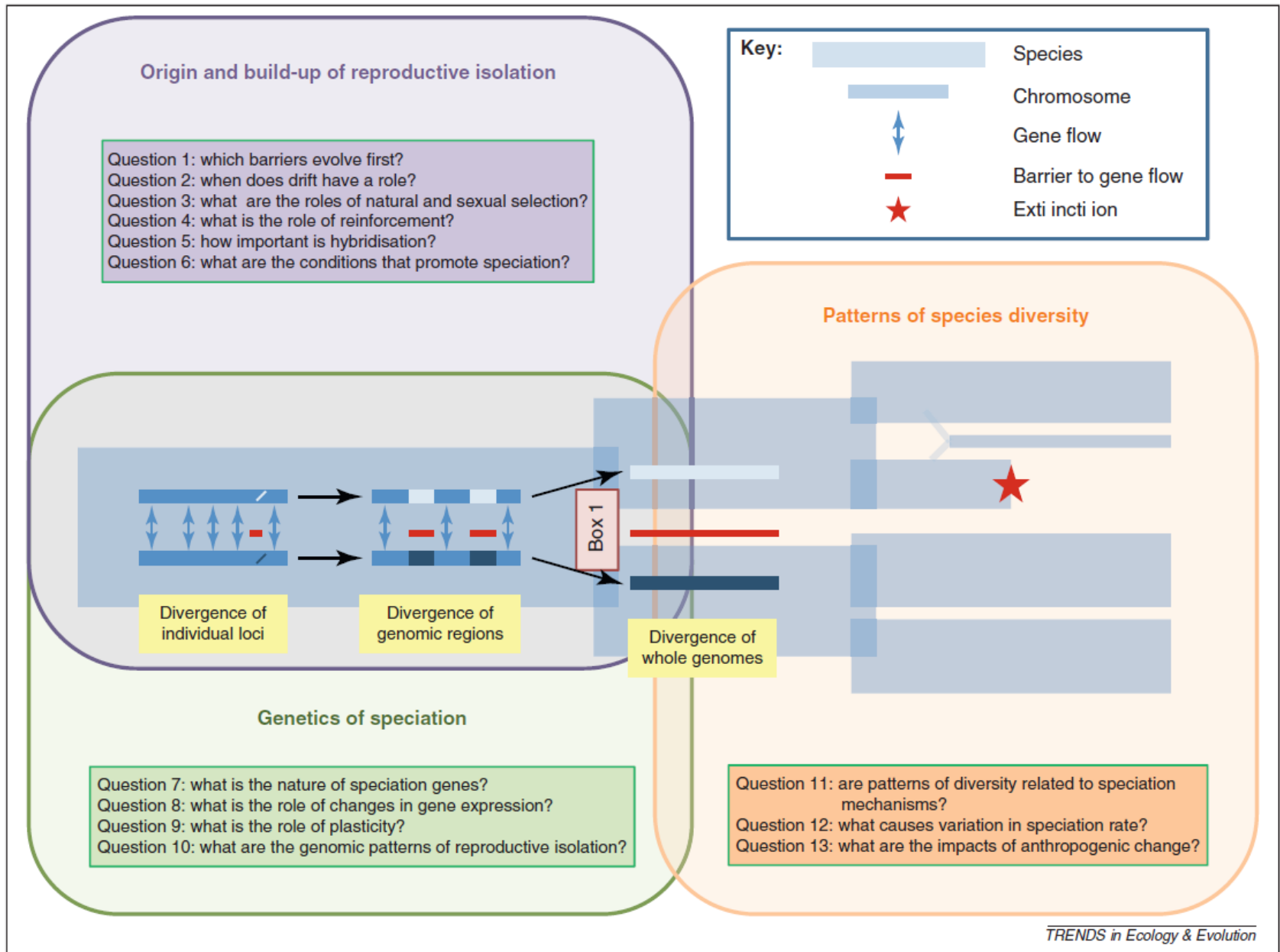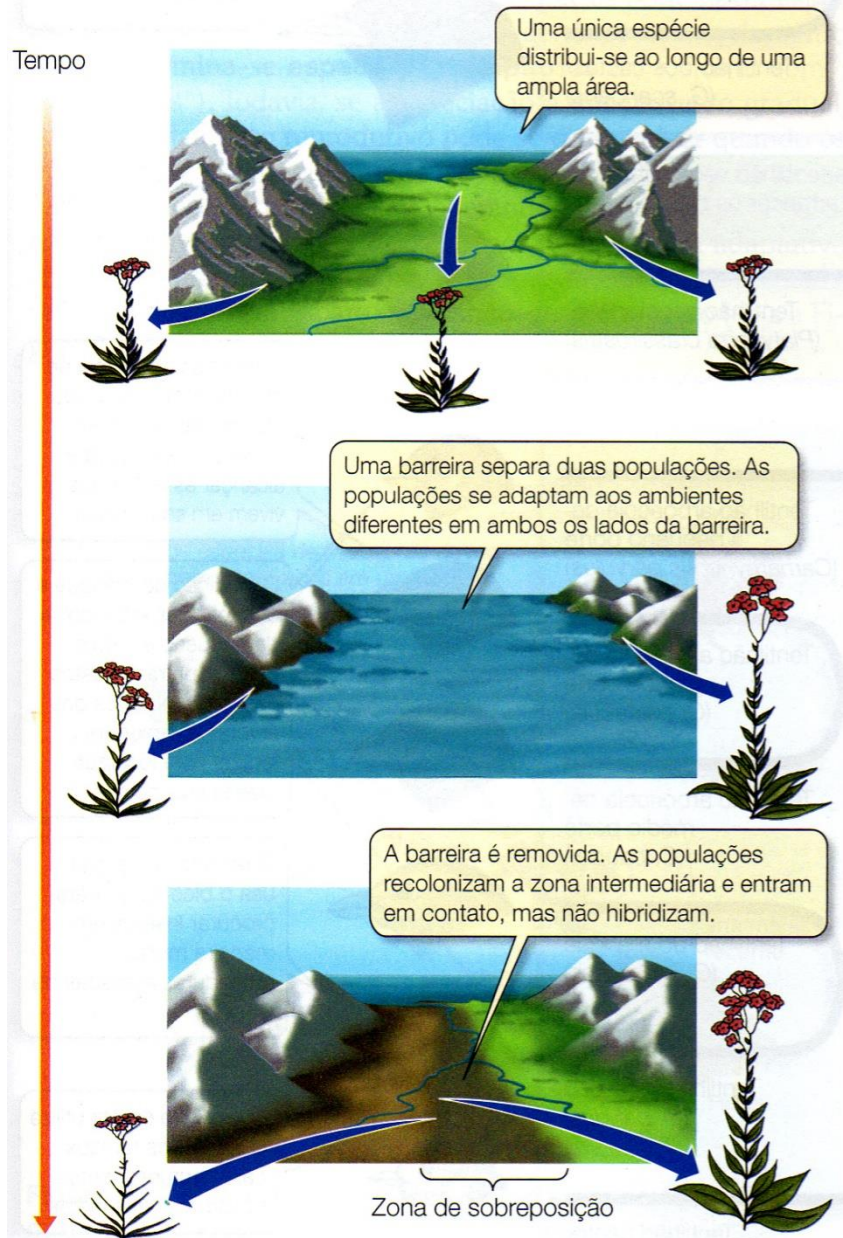
The Marie Curie Speciation Network 2011

Origin and build-up of reproductive isolation

Question 1: which barriers evolve first?
Question 2: when does drift have a role?
Question 3: what are the roles of natural and sexual selection?
Question 4: what is the role of reinforcement?
Question 5: how important is hybridisation?
Question 6: what are the conditions that promote speciation?

Key:

Species
Chromosome
Gene flow
Barrier to gene flow
Exti incti ion

Patterns of species diversity

Box 1

Divergence of
individual loci

Divergence of
genomic regions

Divergence of
whole genomes

Genetics of speciation

Question 7: what is the nature of speciation genes?
Question 8: what is the role of changes in gene expression?
Question 9: what is the role of plasticity?
Question 10: what are the genomic patterns of reproductive isolation?

Question 11: are patterns of diversity related to speciation
              mechanisms?
Question 12: what causes variation in speciation rate?
Question 13: what are the impacts of anthropogenic change?

TRENDS in Ecology & Evolution

Figure 1. Outstanding questions in relation to the processes of speciation and diversification in sexual eukaryotes.

Especiação alopátrida

Sadava et al. 2009

Uma única espécie distribui-se ao longo de uma ampla área.

Uma barreira separa duas populações. As populações se adaptam aos ambientes diferentes em ambos os lados da barreira.

A barreira é removida. As populações recolonizam a zona intermediária e entram em contato, mas não hibridizam.

Zona de sobreposição

Figura 23.3 Especiação alopátrica A especiação alopátrica pode ocorrer quando uma população divide-se em duas populações separadas por uma barreira física, como pelo aumento do nível do mar.

Especiação alopátrida

a

b

c

Time

Barrier

d

e
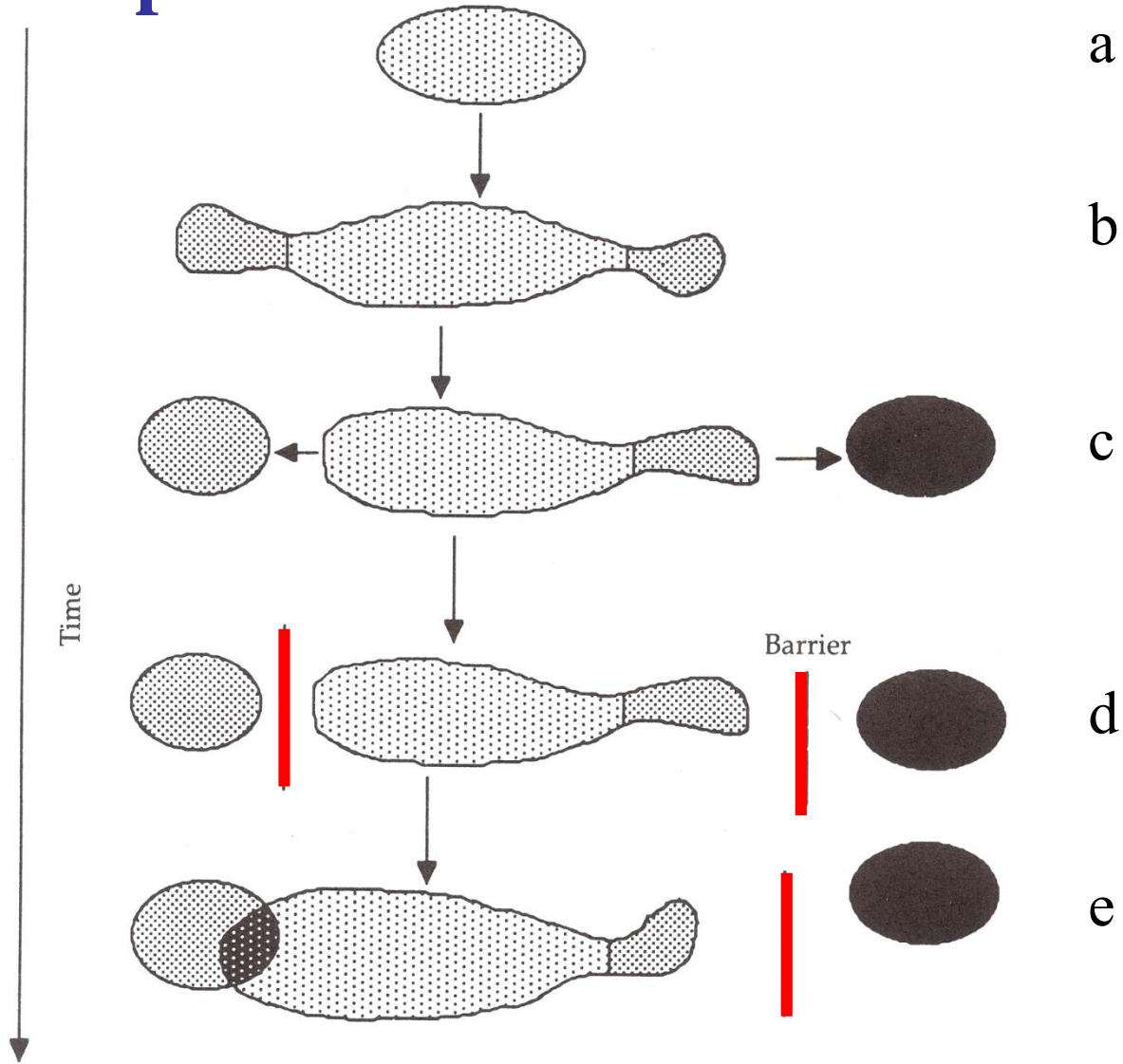
Diagram illustrating how species can evolve through time

Especiação alopátrida

(A) *Platanus occidentalis* (Plátano americano)

(B) *Platanus hispanica* (Plátano europeu)

Figura 23.9 Geograficamente separados, morfologicamente semelhantes Embora separados pelo Oceano Atlântico por pelo menos 20 milhões de anos, os plátanos americano e europeu divergiram muito pouco em aparência.

ESPECIAÇÃO ALOPÁTRIDA:

Princípio do Fundador

**Vicariância = intrusão de barreira:
uma distribuição contínua fica fragmentada
em 2 ou + populações distintas.**

**(Termo "vicariante" não é usado para
novas populações fundadas
por dispersão a longa distância).**

ESPECIAÇÃO
Citogenética e biogeografia

Rivero-Guerra 2008
Bot. J. Linn. Soc. 157: 797-807.

Santolina ageratifolia (Asteraceae) na Espanha
62 pops:
2 níveis de ploidia, lados distintos da montanha:
2n = 18 (espectro ecológico mais amplo!)
2n = 36 (autopoliploidia)

Kissling et al 2008 – Gentianaceae-Exaceae na África
disploidias e poliploidia

ESPECIAÇÃO SIMPÁTRIDA

Aneuploidias, poliploidias.

Grant 1967, Stebbins 1971, Lewis 1979:
Em plantas poliploidização originou spp novas muitas vezes!

Autopoliploidia
Alopoliploidia - + comum

O ancestral **diplóide** tem duas cópias de cada cromossomo.

A maioria dos gametas produzidos pelo híbrido triplóide não é viável porque tem um número incorreto de cromossomos.

Gametas haplóides (uma cópia de cada cromossomo)

Meiose

Cruzamento

A prole F₁ é triplóide (três cópias de cada cromossomo).

Meiose

Meiose

Gametas diplóides (duas cópias de cada cromossomo)

O ancestral **tetraplóide** tem quatro cópias de cada cromossomo.

ESPECIAÇÃO SIMPÁTRIDA
Sadava et al. 2009

Figura 23.7 Tetraplóides logo ficam reprodutivamente isolados dos diplóides Mesmo que a prole triplóide entre parentes tetraplóides e diplóides sobreviva e atinja a maturidade sexual, a maioria dos seus gametas tem aneuploidias. Esses indivíduos triplóides são efetivamente estéreis (por simplicidade, o diagrama mostra apenas três cromossomos, a maioria das espécies tem mais do que isso).

Um híbrido tetraplóide tem uma área quase contínua ao redor de Spokane, Washington.

T. pratensis (salsify)

A distribuição dos híbridos tetraplóides (●) é mais ampla do que aquela das espécies parentais diplóides (△).

Washington

Idaho
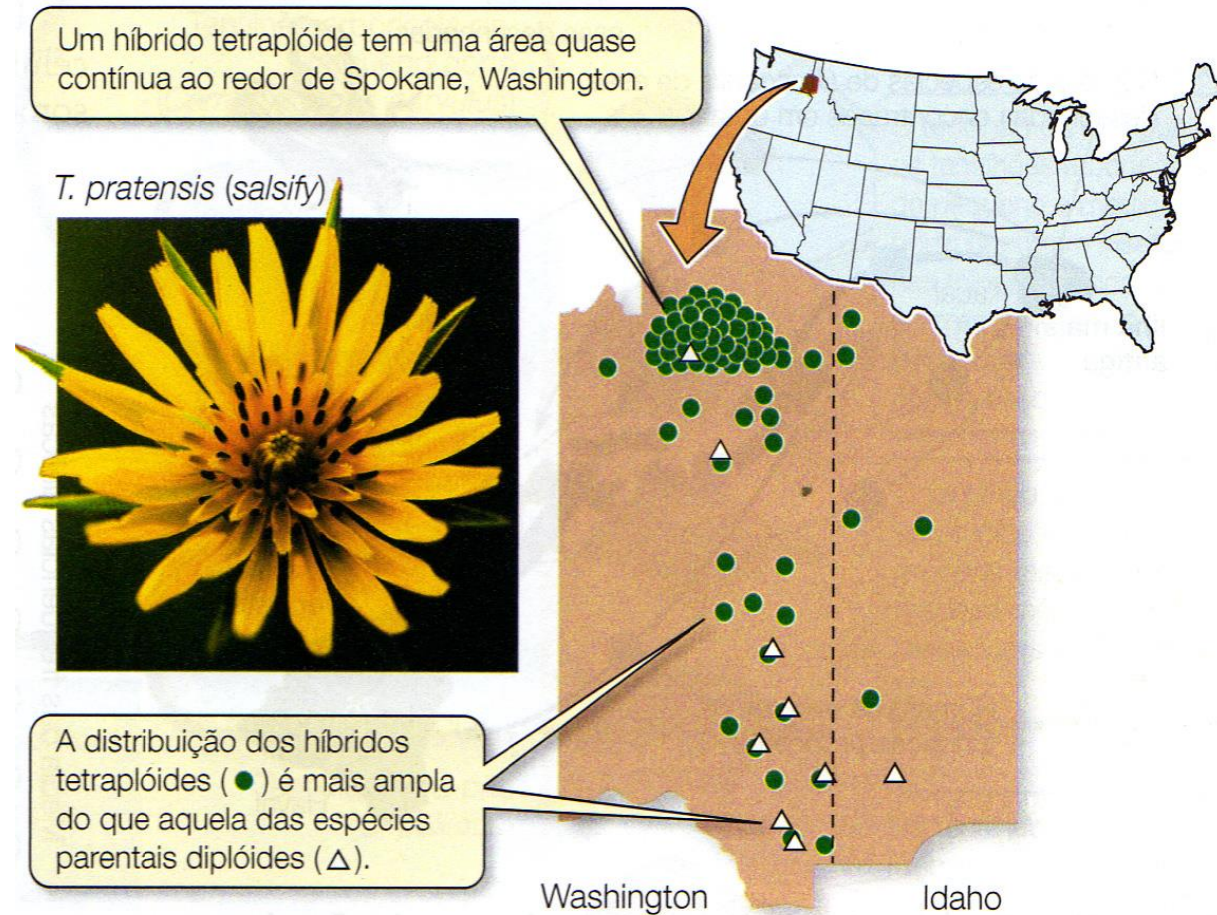
Figura 23.8 Poliplóides podem ter mais sucesso do que os seus ancestrais As espécies do gênero *Tragopogon* são membros da família do girassol. O mapa mostra a distribuição de três espécies parentais diplóides e duas espécies tetraplóides híbridas de *Tragopogon* no leste do estado de Washington e no Idaho.

Sadava et al. 2009
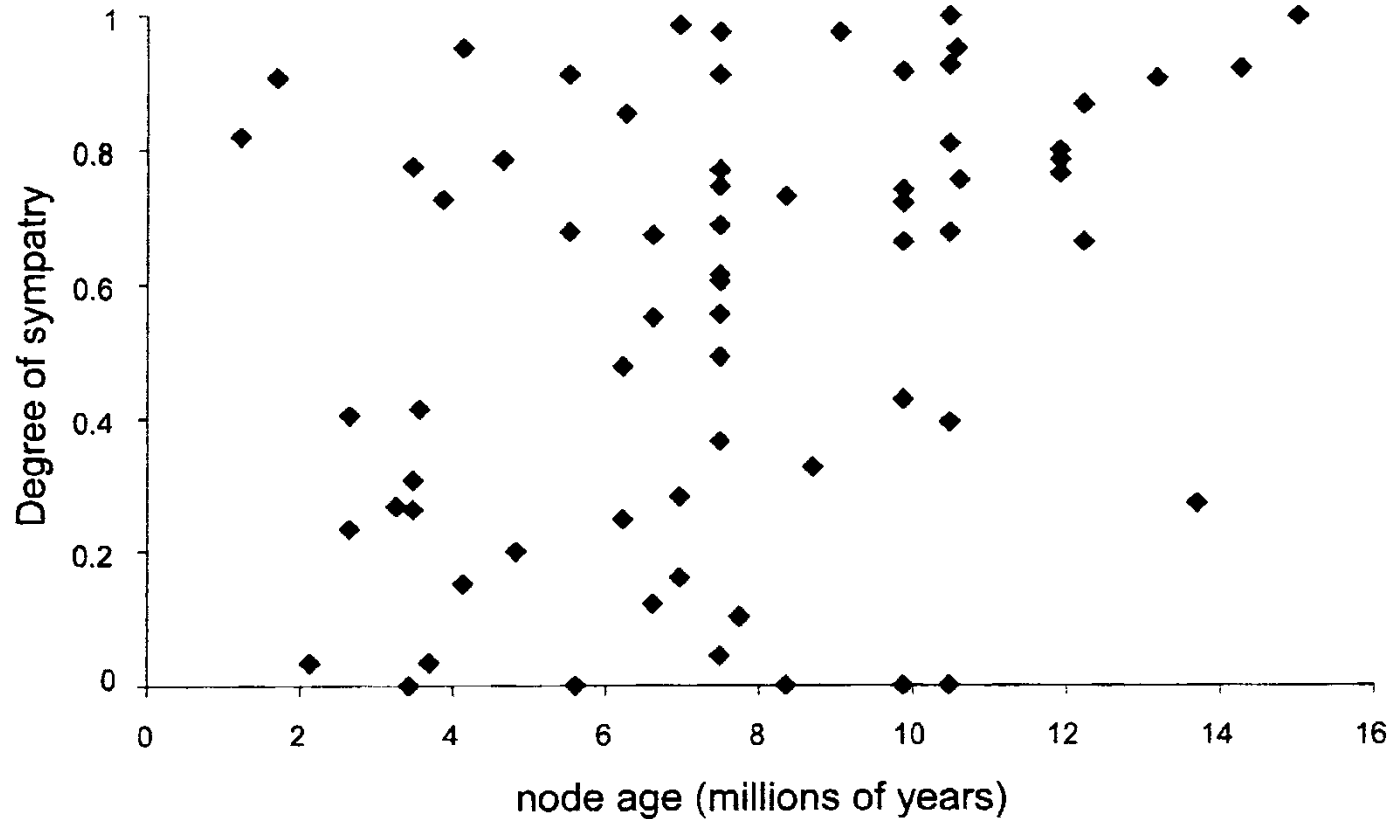
Fig. 6. The degree of sympatry between sister clades of *Protea* in relation to node age.

Barraclough & Reeves 2005 *in* Baker *et al.*

Adaptive radiation in Galapagos finches, showing the diversity of beak shapes and diets. A single ancestor, a grassquit, colonized the archipelago. Subsequent allopatric speciation events, due to repeated episodes of colonization and divergence, produced five genera and 13 species. (After Futuyma 1998, based on Purves et al. 1997; Grant 1986.)

IRRADIAÇÃO ADAPTATIVA: diferenciação ecológica

Brown & Lomolino 1998

Seed eaters
- *Geospiza magnirostris*
- *Geospiza fortis*
- *Geospiza fuliginosa*
- *Geospiza difficilis*
- *Geospiza conirostris*
- *Geospiza scandens*

Bud eater
- *Platyspiza crassirostris*

Insect eaters
- *Camarhynchus parvulus*
- *Camarhynchus psittacula*
- *Camarhynchus pauper*
- *Cactospiza heliobates*
- *Cactospiza pallida*
- *Certhidea olivacea*

Blue-black grassquit
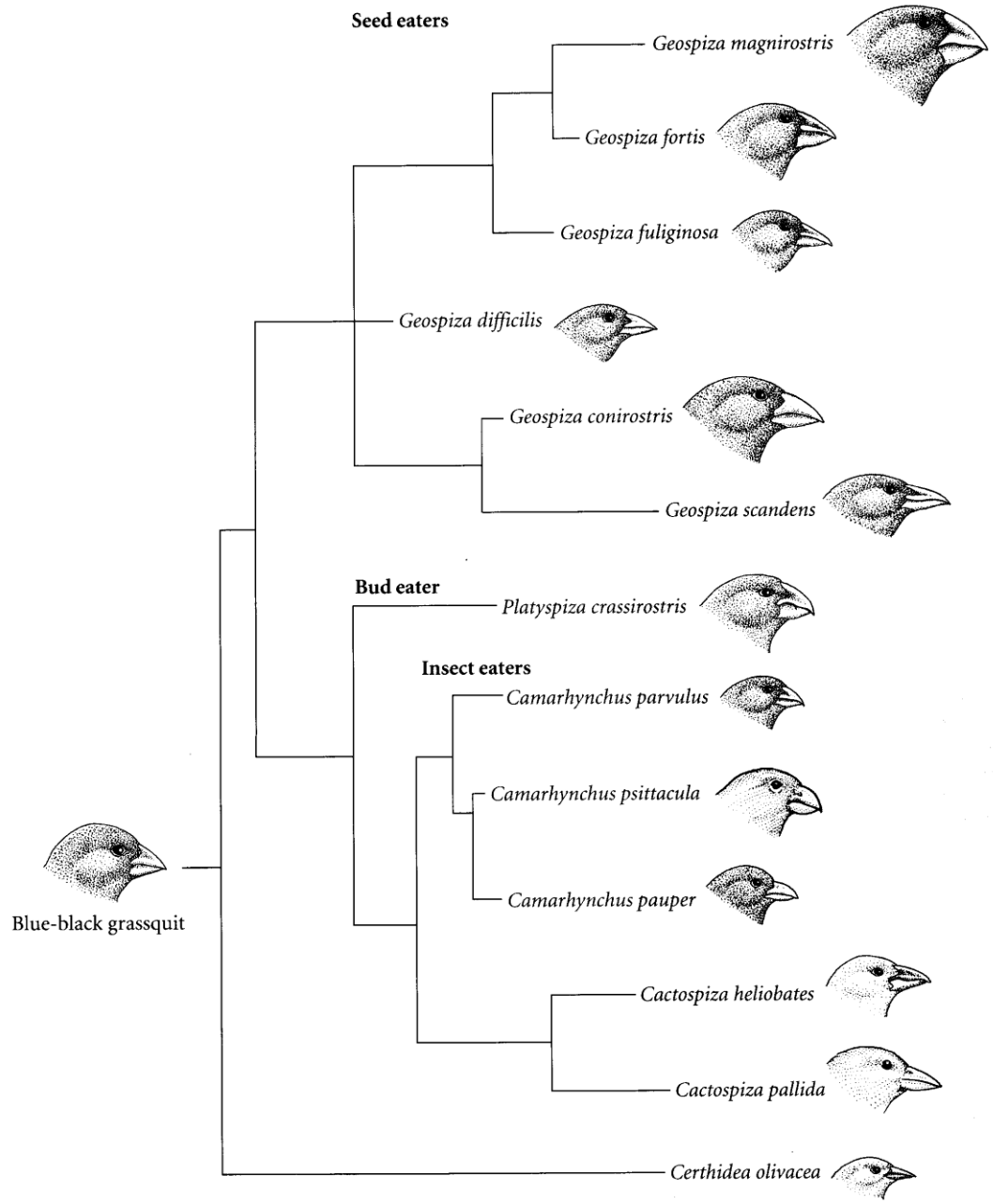
IRRADIAÇÃO ADAPTATIVA: diferenciação ecológica
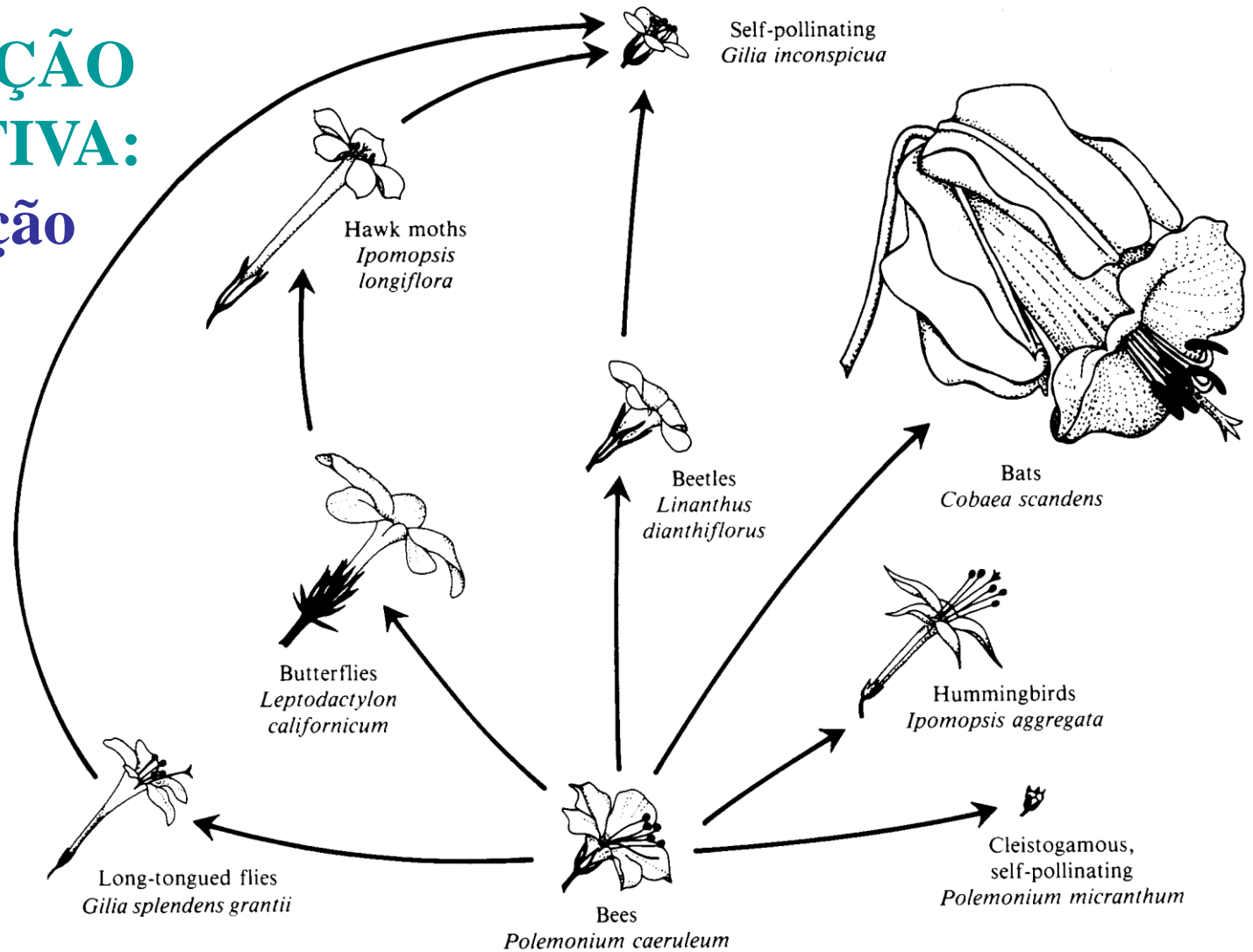
Brown & Gibson 1983

Adaptive radiation in floral characteristics related to pollination in the phlox family, **Polemoniaceae**. It is inferred that a generalized bee-pollinated ancestor similar to *Polemonium caeruleum* gave rise to flowers of different form, color, and attractants, specialized to use different kinds of animals as pollinators or (in some cases) to be self-pollinated. Although members of this family have radiated to exploit different pollinators, plants in some other families have convergently evolved flowers similar to some of these to use the same pollinators. (From The Process of Evolution by P. R. Erlich and R. W. Holm. 1963)

IRRADIAÇÃO ADAPTATIVA

Havaí

Biota nativa com

mil spp de angiospermas

10 mil spp de insetos

mil spp de caracóis

100 spp de aves

Figura 23.15 Evolução rápida entre as espadas-de-prata havaianas Acredita-se que as espadas-de-prata havaianas, três gêneros da família do girassol, descendem todas de um ancestral comum (*Madia sativa*) que colonizou o Havaí a partir da costa do Pacífico da América do Norte. As quatro plantas mostradas aqui são mais proximamente relacionadas do que parecem julgando pela sua morfologia.

Madia sativa (tarweed)

Argyroxiphium sandwicense

Wilkesia hobdyi

Sadava et al. 2009

Dubautia menziesii
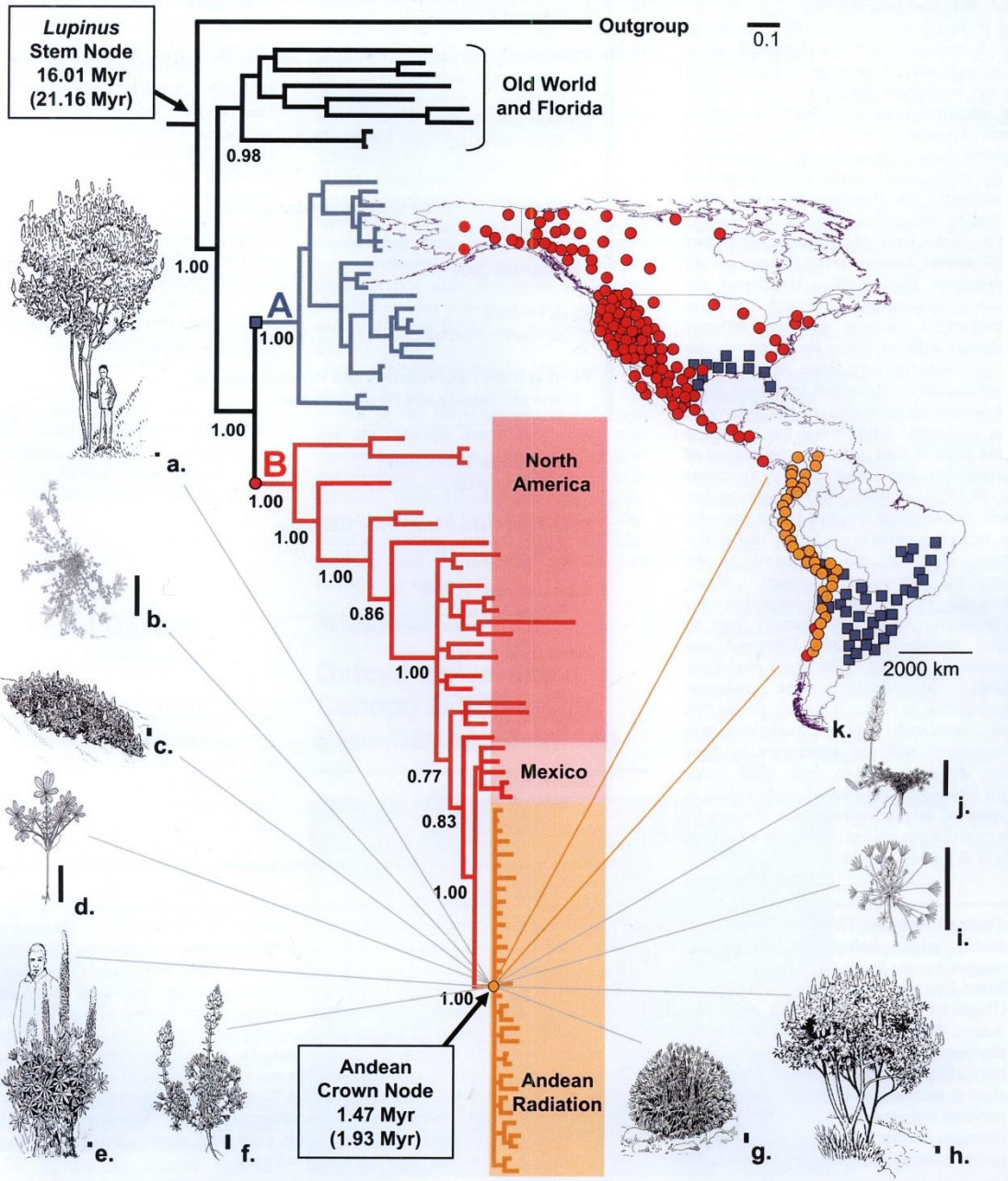
Lupinus
Hughes &
Eastwood 2006
PNAS

Willis & Niklas 2004

Table 1. Factors favouring speciation, extinction or stasis of plant populations in an allopatric speciation model.

factors	favouring speciation	favouring extinction	favouring stasis	explanation
small isolated populations	✓	✓	×	low genetic variance and the potential for rapidly fixed allelic variants or mutations would favour speciation. The imposition of ecological stress or inbreeding depression (because of the rapid accumulation of recessive deleterious genes, i.e. increase in homozygosity) would favour extinction
large or contiguous populations	×	×	✓	
fluctuating population size (owing to founder effects)	✓	✓	×	founder effects could provide novel adaptive allelic combinations that would favour speciation, whereas maladaptive combinations would favour extinction
stable population size	×	×	✓	
self-pollination	✓	×	✓	severely restricts gene flow among populations; favours the emergence of adaptive mutations, but also favours stasis in the absence of adaptive mutations
self-incompatibility in pollination	×	×	✓	necessitates out-breeding, thereby increasing gene flow among neighbouring individuals or populations and decreasing the probability of reproductive isolation (and thus allopatric speciation)
unequal males and females (in dioecious systems)	✓	✓	×	a redundancy of ovulate flowers in a population can either result in extinction or genetic diversity, which in turn favours speciation with the appearance of adaptively functional mutations or chromosomal variants
equal males and females (in dioecious systems)	✓	×	×	favours high genetic diversity
short-lived seed banks	×	✓	×	if environmental conditions become too extreme, they are likely to exceed the tolerance limits of most or all variants left behind by a population
long-lived seed-banks	×	×	✓	populations can be recruited when environmental conditions return to normal
ecological specialists	×	✓	×	if an organism is a specialist and if the environment changes rapidly, it is likely that the niche of the organism will disappear, so speciation and stasis are not favoured
ecological generalists	×	×	✓	adaptation to many habitat types increases the probability of surviving rapid environmental changes or local disturbance

Sexton et al. 2009

Evolution and ecology of species range limits

Table 1 Summary of major theoretical models addressing geographic range limits, with key findings

MODELS OF RANGE LIMITS[a]		
No evolution and without underlying environmental heterogeneity		
Framework	**Key findings**	**References**
Random dispersal (diffusion) with an Allee effect	Negative growth at low density can prevent a population from dispersing beyond its current range	Keitt et al. 2001, Lewis & Kareiva 1993
Spatially explicit competition	Parapatric ranges form owing to competitive exclusion (e.g., colonization patterns maintained by priority effects)	Case et al. 2005, Fowler & Levin 1984, Yodzis 1978
Random dispersal of hybridizing species	Parapatric ranges form owing to reduced hybrid fitness limiting population expansion	Case et al. 2005, Goldberg & Lande 2006
No evolution and with environmental heterogeneity		
Framework	**Key findings**	**References**
Demographic parameters vary along gradients (single- or multispecies models)	Limits to population growth along an environmental gradient result in a range limit. Corresponds to fundamental (single species) or realized niche limitation (multispecies)	Case et al. 2005, Hochberg & Ives 1999, Holt & Barfield 2009, Pulliam 2000, Roughgarden 1979
Environmental gradients in metapopulation models	Variation in colonization and extinction along gradients can result in range limits. Sharp range limits are possible even over shallow gradients owing to patch extinction-colonization dynamics	Carter & Prince 1981, Case et al. 2005, Holt & Keitt 2000, Lennon et al. 1997
Temporal or spatial heterogeneity in dispersal	Range limits result from environmentally determined patterns of dispersal (ocean or air currents)	Gaylord & Gaines 2000
	Spatial or temporal variation in dispersal can stall population expansion and create temporary range limits	Holt et al. 2005b, Shigesada et al. 1986
	Dispersal barriers can "attract" parapatric range limits owing to competition or hybridization over otherwise homogenous space	Goldberg & Lande 2007
With evolution and environmental heterogeneity		
Framework	**Key findings**	**References**
Gene flow (dispersal), selection, and adaptation along an environmental gradient	Gene flow from large, well-adapted populations may prevent adaptation in marginal populations. Depends on the rate of adaptation (genetic variance, selection) and steepness of the gradient. Assumes constant genetic variance	Kirkpatrick & Barton 1997
	Range limits are harder to achieve if genetic variation is not constant, because migration can increase variation in peripheral populations and facilitate adaptation	Alleaume-Benharira et al. 2006, Barton 2001
	Incorporation of competitive interactions among species makes range limits easier to achieve, as presence of a better-adapted competitor along a gradient can reduce peripheral populations and increase asymmetry in gene flow	Case & Taper 2000
	Dispersal barriers limit gene flow and allow for local adaptation and spread. If gene flow is restricting a species range, species borders should not be associated with dispersal barriers	Goldberg & Lande 2007
	The strength and form of density-dependent population regulation can influence the likelihood that a species adapts to peripheral populations by influencing demographic asymmetries in peripheral and central populations	Barton 2001, Filin et al. 2008
Selection and gene flow in a source sink scenario	Gene flow can provide a demographic and genetic "rescue effect" in sink populations, facilitating adaptation. Niche expansion may proceed in a punctuated fashion	Holt 2003, Holt & Gomulkiewicz 1997, Gomulkiewicz et al. 1999

(Continued)

EXTINÇÃO

70% de todos os seres vivos extintos há 65 m.a. (limite do Cretáceo e Terciário)

Raup 1989:
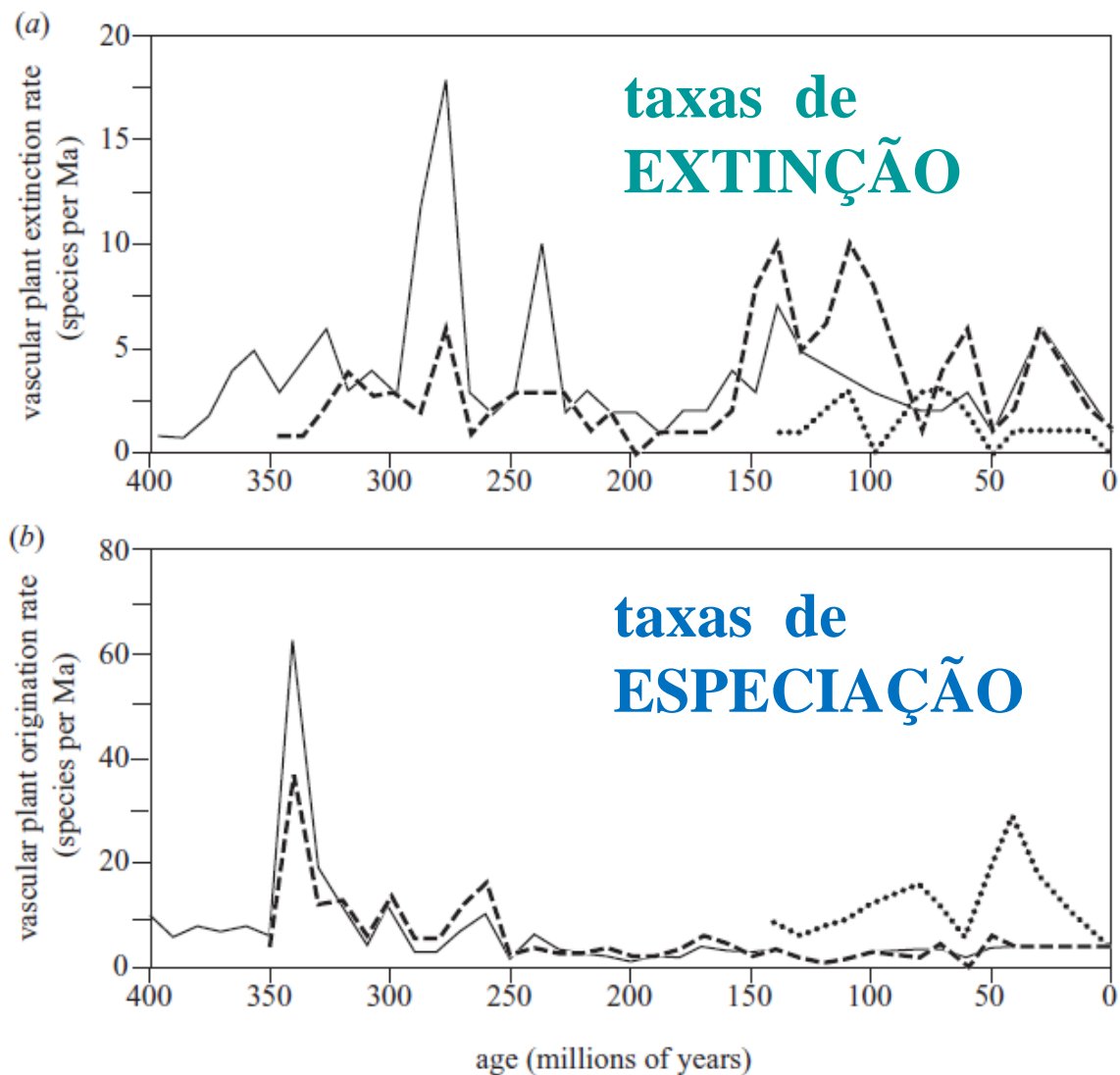**88% a 96% de todas as spp. marinhas foram extintas em curto período no fim do Permiano (235 m.a.)**

Reprinted from Stanley, 1986, with permission.
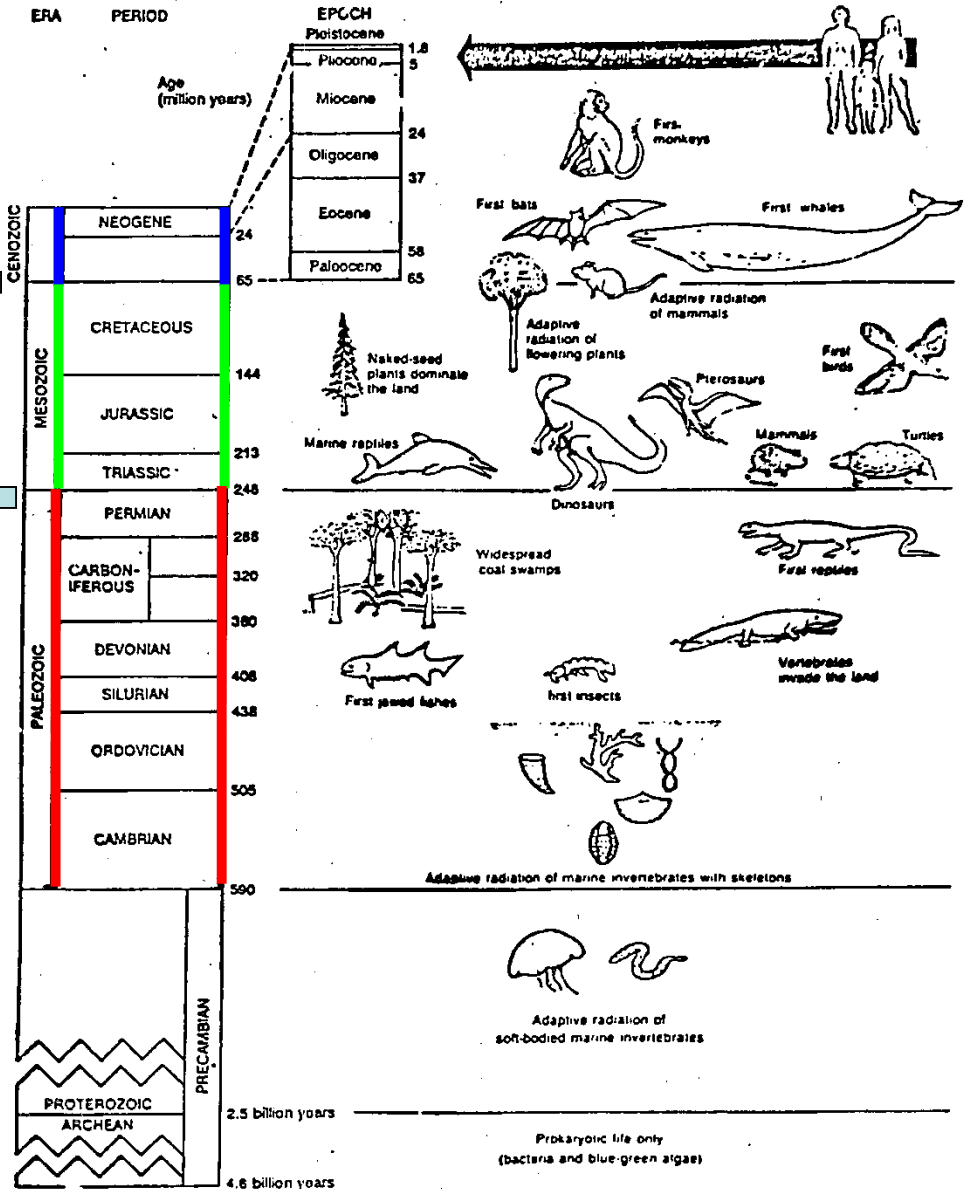
Plantas vasculares

2004

taxas de
EXTINÇÃO

taxas de
ESPECIAÇÃO

Figure 9. (*a*) Vascular plant extinction and (*b*) origination rate, over the past 400 Myr for the three plant reproductive clades (angiosperms (dotted lines); gymnosperms (dashed lines); and pteridophyte (solid lines)).

	1788	Atual		1788	Atual

Gaston 2003
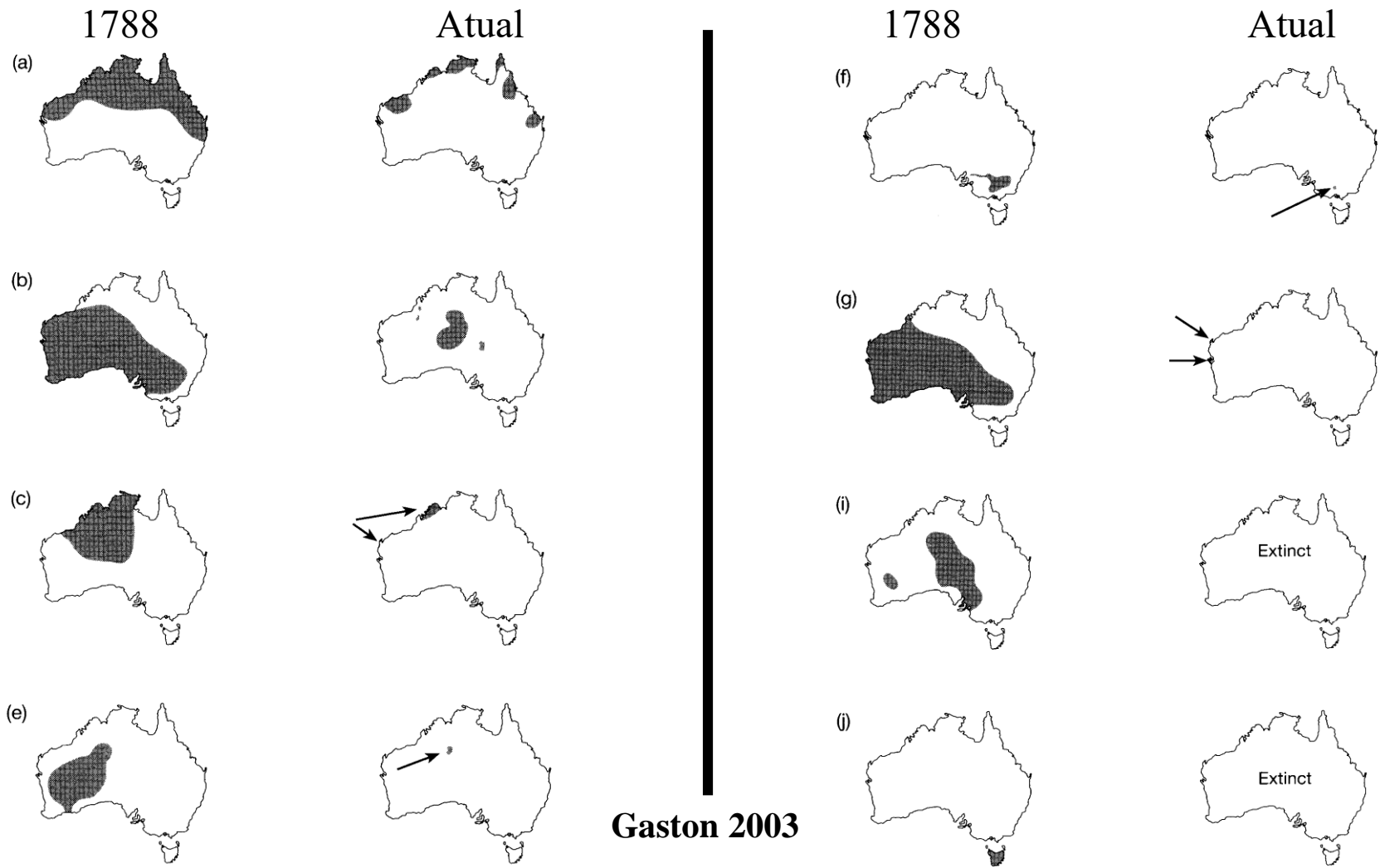
Geographic range contractions of some Australian species, with distribution in 1788 on left and at present on right, for (a) northern quoll *Satanellus hallucatus*, (b) rabbiteared bandicoot *Macrotis leucura*, (c) golden bandicoot */sodon auratus*, (e) western hare wallaby *Lagorchestes hirsutus*, (f) trout cod *Maccullochella macquariensis*, (g) burrowing bettong *Bettongia lesueur*, (i) pig-footed bandicoot *Chaeropus ecaudatus*, and (j) thylacine *Thylacinus cynocephalus*. From the collation of Burgman and Lindenmayer (1998).

Extinções recentes

200 anos homem dizimou centenas de spp.:
caça, destruição de habitats, introdução de novos predadores e pragas, parasitas e doenças.

Castanea dentata (Fagaceae) – árvores abundantes da América do Norte Oriental até 1904, quando fungo patogênico *Endothia parasitica* foi introduzido acidentalmente da Ásia, onde há espécies de *Castanea* resistentes. Em 40 anos todas as castanheiras adultas foram eliminadas da Am N.

Extinção em massa e a possível 3° grande extinção?
P. Ward 1997. *O fim da evolução. Extinções em massa e a preservação da biodiversidade.* Editora Campus, Rio de Janeiro.
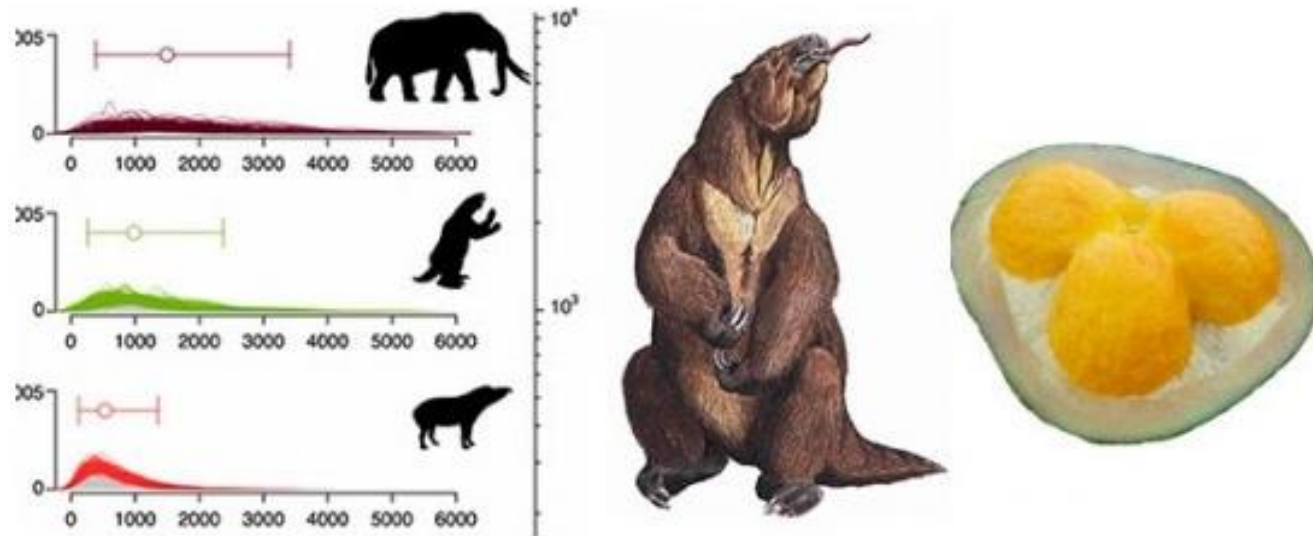
Pleistocene megafaunal extinctions and the functional loss of long-distance seed-dispersal services
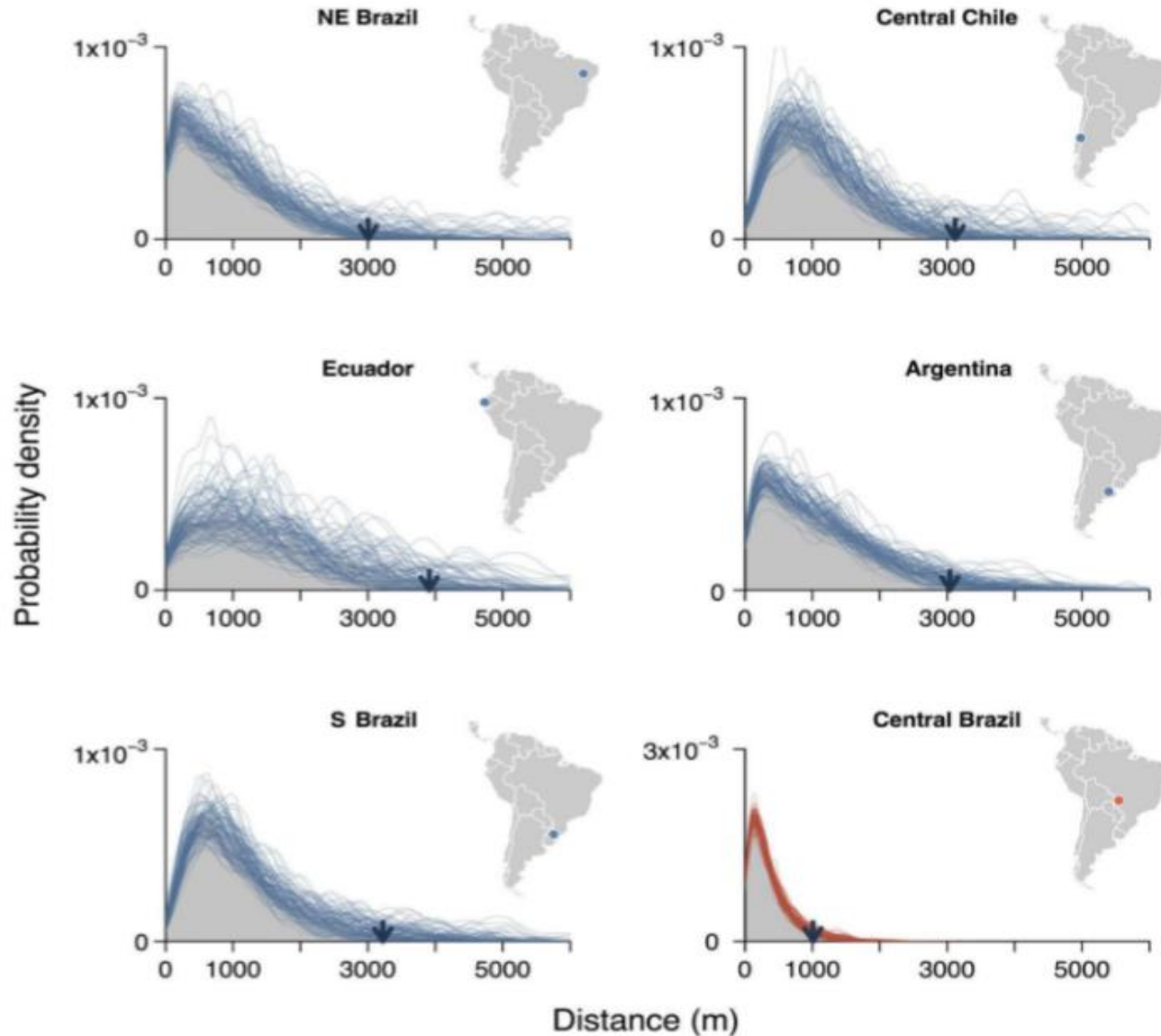
Figure 3. Total seed-dispersal kernels depicting seed dispersal of a large-seeded plant by large mammals in past (blue) and modern (red) mammalian assemblages representing specific locations. Animal movement simulated as a Brownian walk (BW). Each line represents one of 100 simulations. Arrows show the 95th percentile, which defines the magnitude of LDD events. Approximate locations of the six analyzed sites are depicted in the inset maps.

Labels within figure:
- Geographic range — 10 miles
- Region — 2 miles
- Cluster of limestone glades — 0.5 miles
- Glade showing aggregates of individuals — 100 yards
- Aggregate of individuals — 10 yards
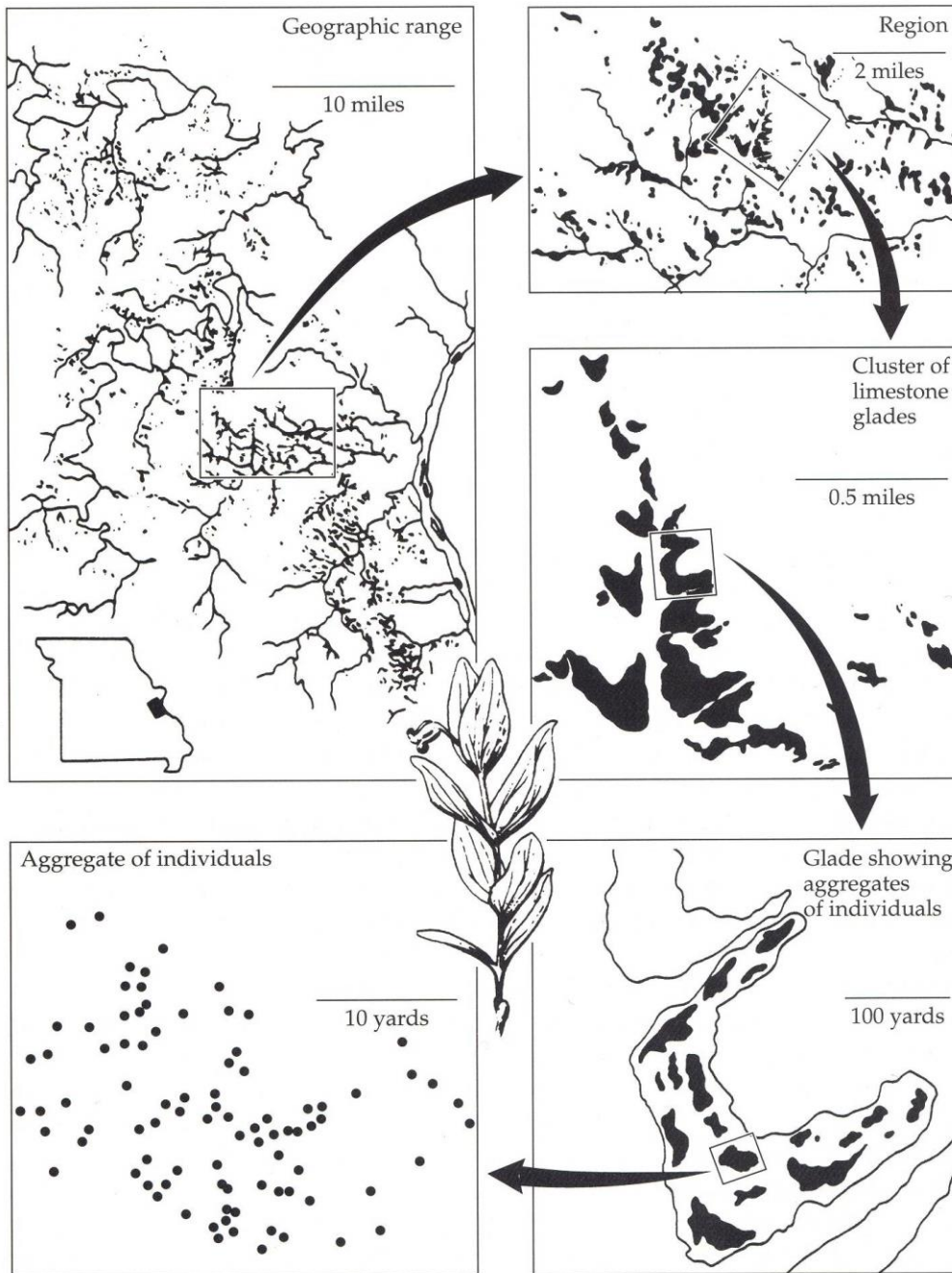
Erickson's classic depiction of the distribution of the shrub *Clematís fremontíí*, within the state of Missouri in the central United States, on different spatial scales. The largest scale shows the geographic range based on known collecting localities. Successively smaller scales show the distribution of populations. The smallest scale shows the dispersion of individual plants within a single local population. Note that at all scales the distribution is patchy, and that areas where plants are found are separated by uninhabited areas. Erickson 1945.
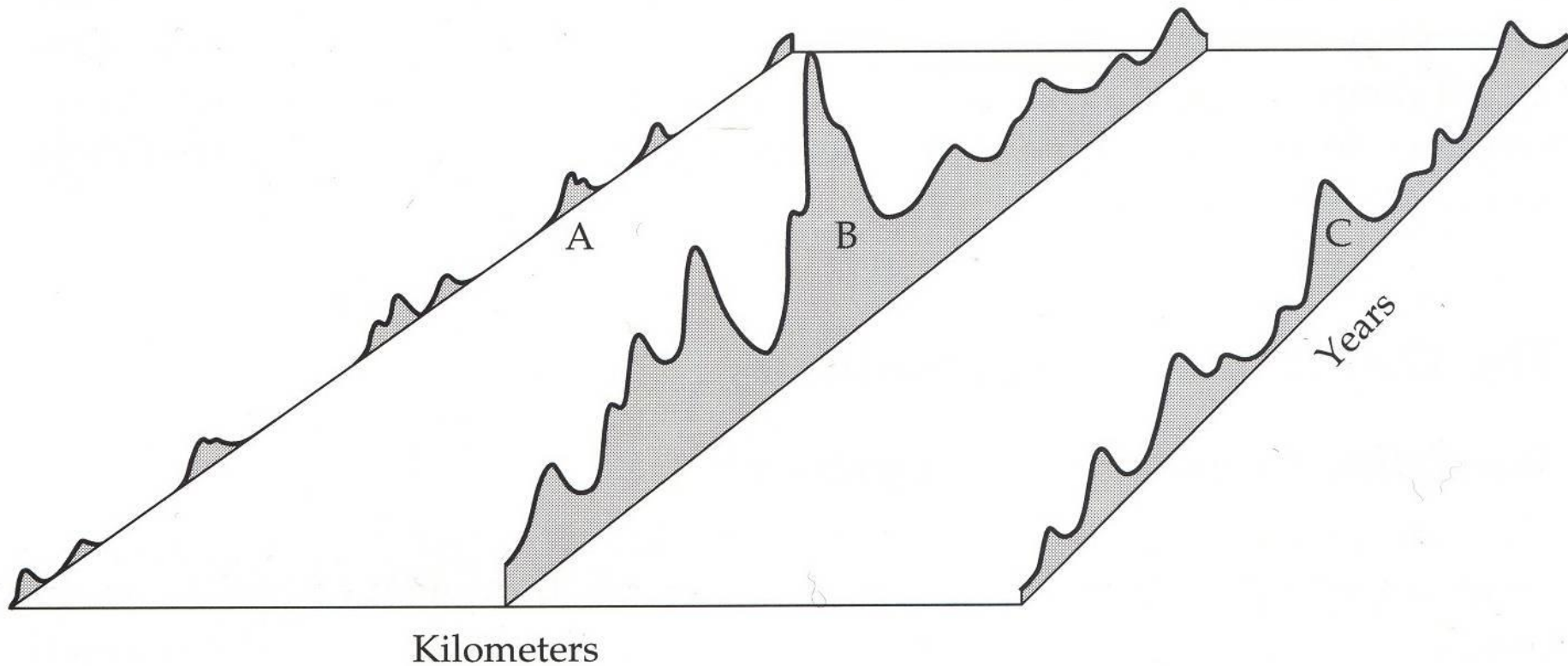
A schematic diagram showing **how the abundance and distribution of a hypothetical organism might vary in time and space.** Shown are fluctuations in abundance over many years at three different localities (A-C) separated by distances of several kilometers. Note that all three populations fluctuate. At locality A, which is presumably at the margin of the local or geographic range of the species, only a few individuals are intermittently present, indicating repeated episodes of local extinction and recolonization.

Andrewartha & Birch 1954.
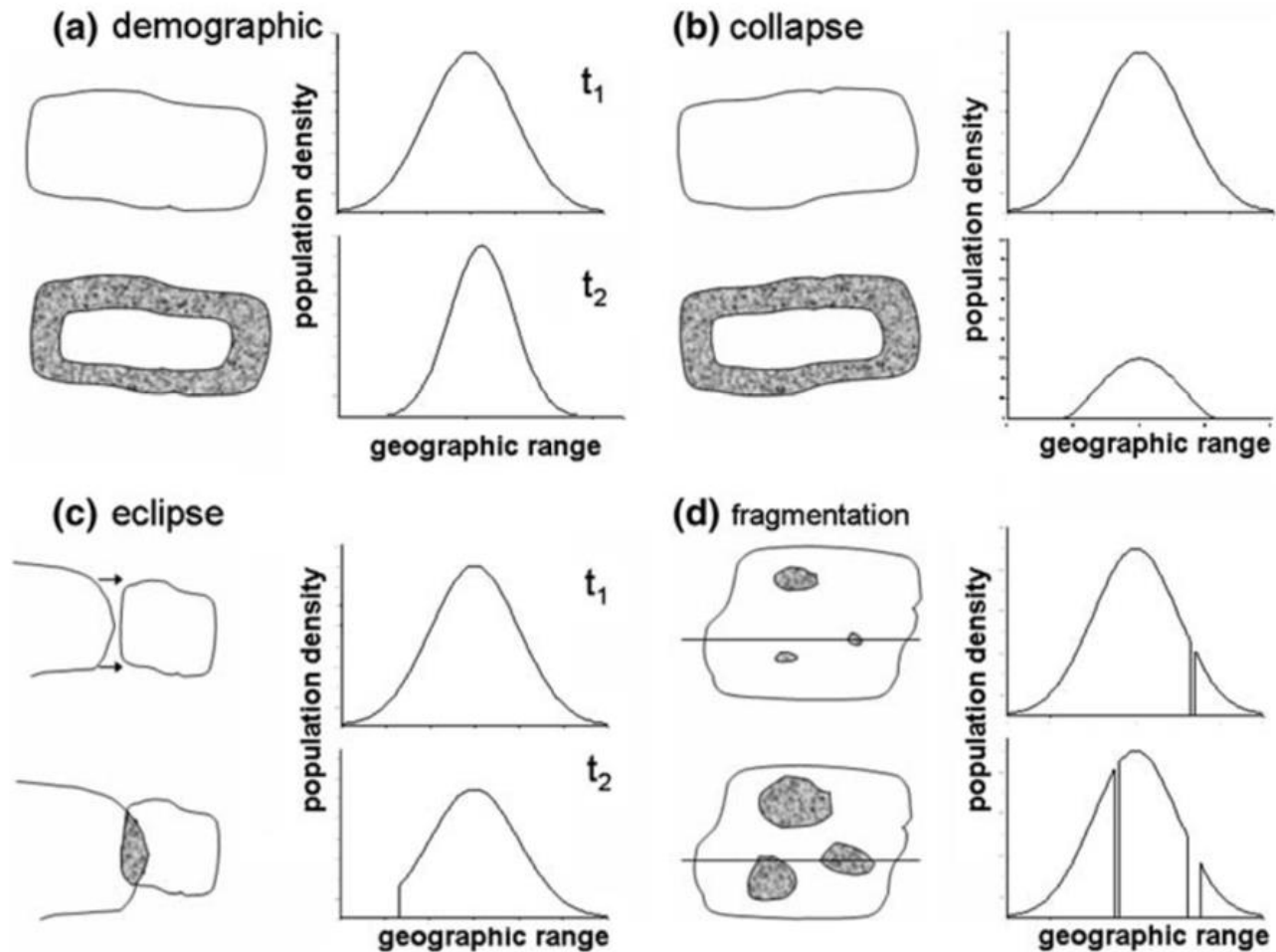
Figure 1. Four possibilities of range decline: (a) demographic decline, (b) range collapse, (c) range eclipse, and (d) fragmentation. In (c), one species invades the area of another one, thereby eventually wiping out the latter (grey shades represent areas already invaded). Each picture on the left shows the area not yet invaded at times t_1 and t_2. The graphs on the right show the effect the invader has on the density profile of the invaded species. The density profile for range fragmentation is the profile at the line transect given in the figures of the

Dispersal
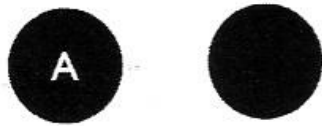
Ancestral population
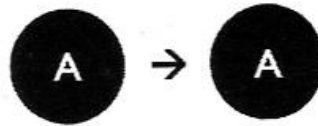
Dispersal over barrier

Subsequent differentiation

Vicariance

Ancestral widespread population

Barrier appears

Subsequent differentiation

Extinction

Ancestral widespread population
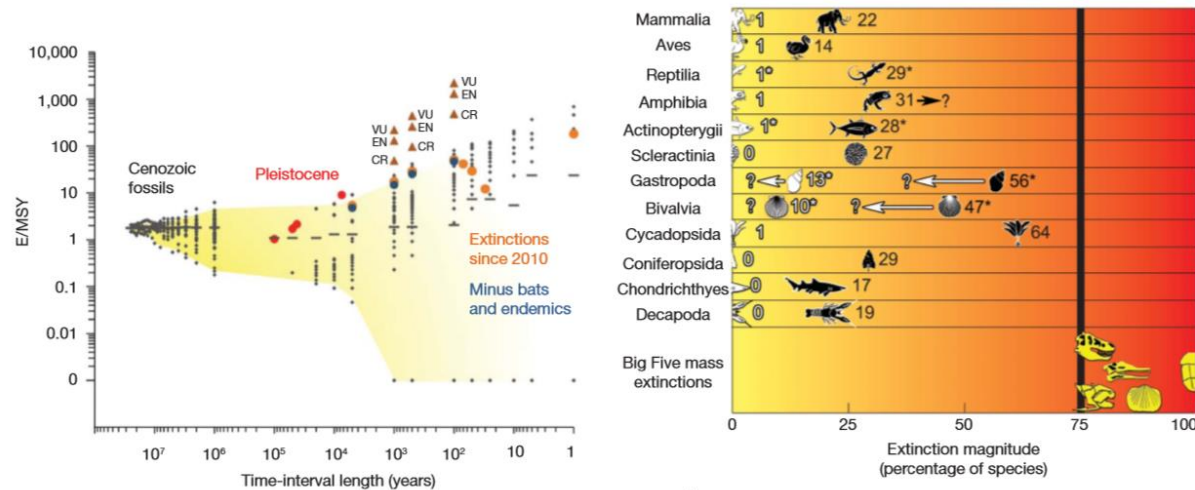
Extinction

Subsequent differentiation

Tipo de Especiação ?

Figure 2.5 Three main biogeographic processes: dispersal, vicariance, and extinction.

Morrone 2009

Barnosky et al. 2011 *Nature*

Has the Earth's sixth mass extinction already arrived?

Anthony D. Barnosky[1,2,3], Nicholas Matzke[1], Susumu Tomiya[1,2,3], Guinevere O. U. Wogan[1,3], Brian Swartz[1,2], Tiago B. Quental[1,2]†, Charles Marshall[1,2], Jenny L. McGuire[1,2,3]†, Emily L. Lindsey[1,2], Kaitlin C. Maguire[1,2], Ben Mersey[1,4] & Elizabeth A. Ferrer[1,2]

Palaeontologists characterize mass extinctions as times when the Earth loses more than three-quarters of its species in a geologically short interval, as has happened only five times in the past 540 million years or so. Biologists now suggest that a sixth mass extinction may be under way, given the known species losses over the past few centuries and millennia. Here we review how differences between fossil and modern data and the addition of recently available palaeontological information influence our understanding of the current extinction crisis. Our results confirm that current extinction rates are higher than would be expected from the fossil record, highlighting the need for effective conservation measures.
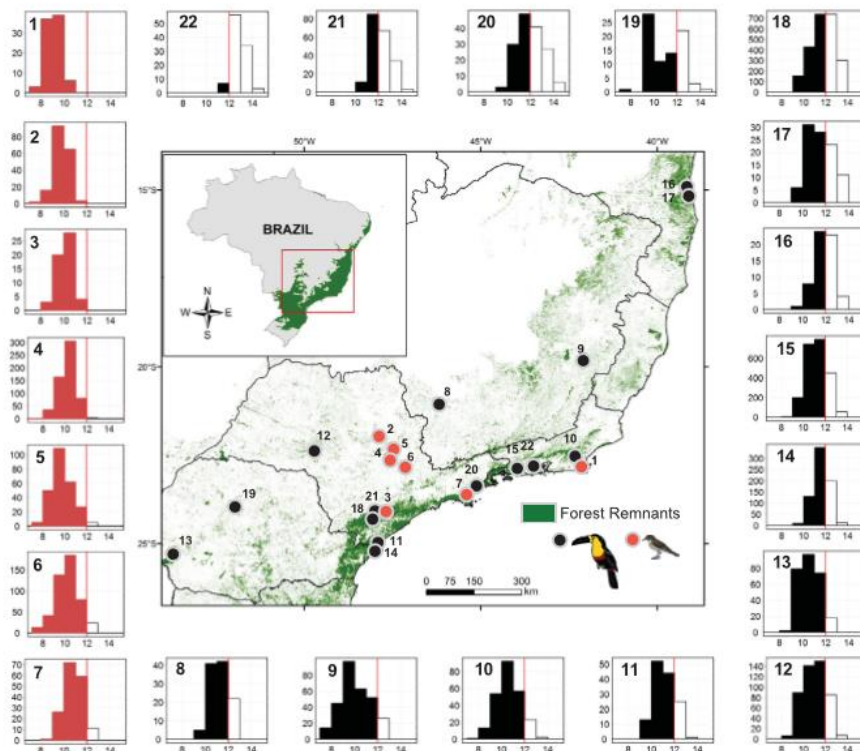
Figure 1 | Relationship between extinction rates and the time interval over which the rates were calculated, for mammals. Each small grey datum point represents the E/MSY (extinction per million species-years) calculated from taxon durations recorded in the Paleobiology Database[30] (million-year-or-more time bins) or from lists of extant, recently extinct, and Pleistocene species compiled from the literature (100,000-year-and-less time bins)[6,32,33,89–97]. More than 4,600 data points are plotted and cluster on top of each other. Yellow shading encompasses the 'normal' (non-anthropogenic) range of variance in extinction rate that would be expected given different measurement intervals; for more than 100,000 years, it is the same as the 95% confidence interval, but the fading to the right indicates that the upper boundary of 'normal' variance becomes uncertain at short time intervals. The short horizontal lines indicate the empirically determined mean E/MSY for each time bin. Large coloured dots represent the calculated extinction rates since 2010. Red, the end-Pleistocene extinction event. Orange, documented historical extinctions averaged (from

Figure 2 | Extinction magnitudes of IUCN-assessed taxa[6] in comparison to the 75% mass-extinction benchmark. Numbers next to each icon indicate percentage of species. White icons indicate species 'extinct' and 'extinct in the wild' over the past 500 years. Black icons add currently 'threatened' species to those already 'extinct' or 'extinct in the wild'; the amphibian percentage may be as high as 43% (ref. 19). Yellow icons indicate the Big Five species losses: Cretaceous + Devonian, Triassic, Ordovician and Permian (from left to right). Asterisks indicate taxa for which very few species (less than 3% for gastropods and bivalves) have been assessed; white arrows show where extinction percentages are probably inflated (because species perceived to be in peril are often assessed first). The number of species known or assessed for each of the groups listed is: Mammalia 5,490/5,490; Aves (birds) 10,027/10,027; Reptilia 8,855/1,677; Amphibia 6,285/6,285, Actinopterygii 24,000/5,826, Scleractinia (corals) 837/837; Gastropoda 85,000/2,319; Bivalvia 30,000/310, Cycadopsida 307/307; Coniferopsida 618/618; Chondrichthyes 1,044/1,044; and Decapoda 1,867/1,867.
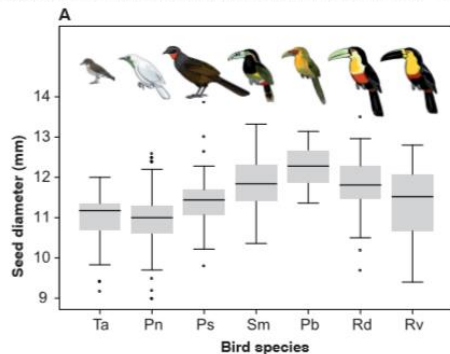
Fig. 1. Geographic variation in seed size in palm populations. Seed size (seed diameter in millimeters, *x* axis) frequency distributions (number of seeds, *y* axis) of 22 palm (*E. edulis*) populations in the remnants of the Brazilian Atlantic forest (green areas). The numbers refer to the population codes given in table S1. The red dots (codes 1 to 7) are defaunated sites, where large-gape frugivores are locally extinct or rare; the black dots are nondefaunated sites (codes 8 to 22). The vertical red line marks the upper size limit for successful dispersal by small birds (gape size 12 mm) in the absence of large-gape frugivores. The solid bars in the histograms indicate seed sizes below this threshold.

Functional Extinction of Birds Drives Rapid Evolutionary Changes in Seed Size

Local extinctions have cascading effects on ecosystem functions, yet little is known about the potential for the rapid evolutionary change of species in human-modified scenarios. We show that the functional extinction of large-gape seed dispersers in the Brazilian Atlantic forest is associated with the consistent reduction of the seed size of a keystone palm species. Among 22 palm populations, areas deprived of large avian frugivores for several decades present smaller seeds than nondefaunated forests, with negative consequences for palm regeneration. Coalescence and phenotypic selection models indicate that seed size reduction most likely occurred within the past 100 years, associated with human-driven fragmentation. The fast-paced defaunation of large vertebrates is most likely causing unprecedented changes in the evolutionary trajectories and community composition of tropical forests.
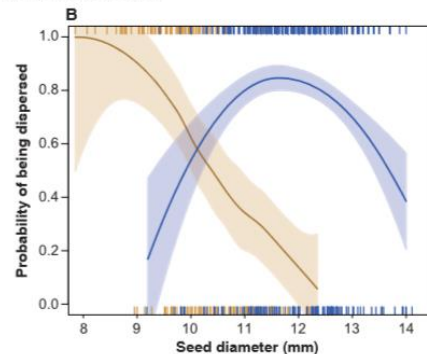
Fig. 2. Patterns of fruit preferences by frugivorous birds and consequences for phenotypic selection on seed size. (A) Seed size variation of the palm (*E. edulis*) fruits consumed by birds (from left to right): white-necked thrush (Ta, *Turdus albicollis*), bare-throated bellbird (Pn, *Procnias nudicollis*), rusty-margined guan (Ps, *Penelope superciliaris*), spot-billed toucanet and saffron toucanet (Sm, *Selenidera maculirostris*; Pb, *Pteroglossus bailloni*), and red-breasted and channel toucan (Rd, *Ramphastos dicolorus*; Rv, *R. vitellinus*). The boxes include the mean (horizontal black line), ± 1 SE (gray box), the 95% confidence interval (vertical lines), and outlier values (circles). **(B)** The probability of the dispersal of palm seeds as a function of seed diameter in defaunated forest sites (orange), where large-gape frugivorous birds are functionally extinct, and in nondefaunated forests (blue) [see (*15*) for the trends in local areas; fig. S3]. The vertical lines in the rugged plot indicate the individual seed sizes of undispersed and dispersed seeds.

Fig. 3. Simulated phenotypic trends in seed size after loss of major frugivores. Expected trajectories over time, estimated from the phenotypic selection model, of the seed size reduction after defaunation in two Atlantic forest types (rainforest and semideciduous forest) (*15*). The vertical dashed lines with larger open dots denote the position along the mean trajectory when the predicted seed diameter is the closest to the present observed mean seed diameter in defaunated forests. The position where the dashed lines intercept the *x* axis represents the minimum time for the seeds to reach the present-day seed diameter mean value according to the model. Solid dots show the mean values (±1 SD) of the simulated seed size for consecutive years after defaunation.
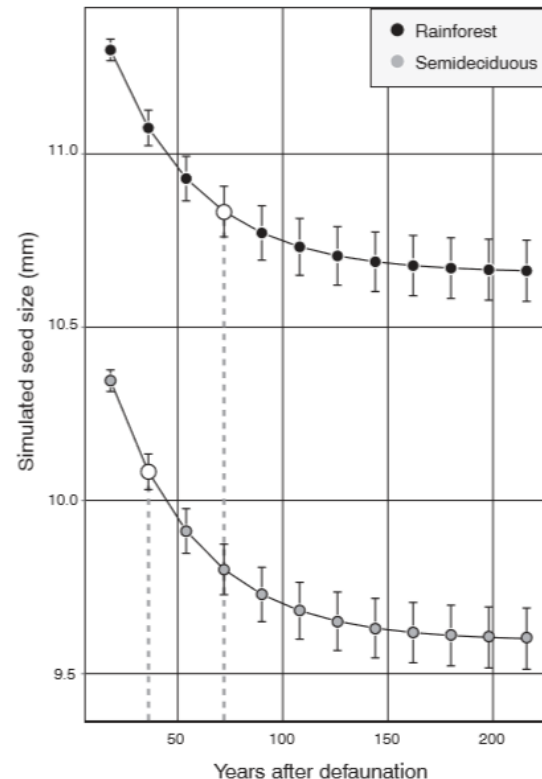
Fossil biogeography: a new model to infer dispersal, extinction and sampling from palaeontological data

Silvestro et al. 2016
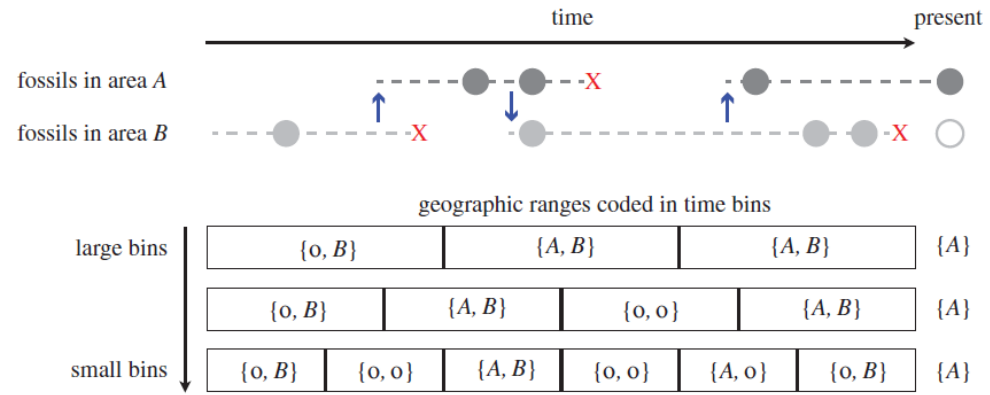
Figure 1. Effect of different time bins on the coding of biogeographic ranges through time. Dashed lines indicate the true geographical history of the lineage, involving three dispersals (arrows) and three extinction events (crosses). Circles indicate the sampled fossil occurrences, the empty circle at the present indicates that the taxon is currently absent from area B. The sampled ancestral states (indicated with O in equations (2.4), (2.5)) are here coded using large, intermediate and small time bins and shown at the bottom part of the plot.
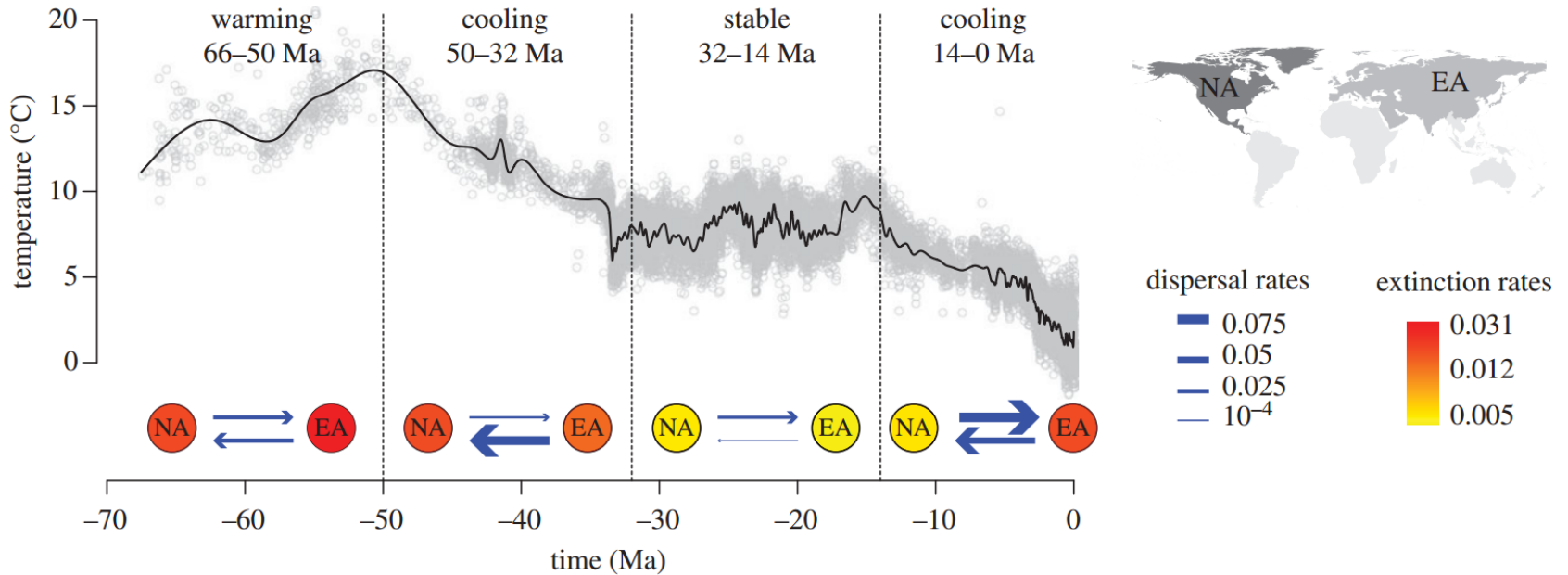
Figure 6. Cenozoic dispersal and extinction rates of vascular plants in North America (NA) and Eurasia (EA). Posterior estimates of the dispersal and extinction rates are calculated within four time frames, after combining 100 replicates to account for dating uncertainties in the fossil record. The temperature curve was obtained from Zachos *et al.* [61].

Willis & Niklas 2004

Table 1. Factors favouring speciation, extinction or stasis of plant populations in an allopatric speciation model.

factors	favouring speciation	favouring extinction	favouring stasis	explanation
small isolated populations	✓	✓	×	low genetic variance and the potential for rapidly fixed allelic variants or mutations would favour speciation. The imposition of ecological stress or inbreeding depression (because of the rapid accumulation of recessive deleterious genes, i.e. increase in homozygosity) would favour extinction
large or contiguous populations	×	×	✓	
fluctuating population size (owing to founder effects)	✓	✓	×	founder effects could provide novel adaptive allelic combinations that would favour speciation, whereas maladaptive combinations would favour extinction
stable population size	×	×	✓	
self-pollination	✓	×	✓	severely restricts gene flow among populations; favours the emergence of adaptive mutations, but also favours stasis in the absence of adaptive mutations
self-incompatibility in pollination	×	×	✓	necessitates out-breeding, thereby increasing gene flow among neighbouring individuals or populations and decreasing the probability of reproductive isolation (and thus allopatric speciation)
unequal males and females (in dioecious systems)	✓	✓	×	a redundancy of ovulate flowers in a population can either result in extinction or genetic diversity, which in turn favours speciation with the appearance of adaptively functional mutations or chromosomal variants
equal males and females (in dioecious systems)	✓	×	×	favours high genetic diversity
short-lived seed banks	×	✓	×	if environmental conditions become too extreme, they are likely to exceed the tolerance limits of most or all variants left behind by a population
long-lived seed-banks	×	×	✓	populations can be recruited when environmental conditions return to normal
ecological specialists	×	✓	×	if an organism is a specialist and if the environment changes rapidly, it is likely that the niche of the organism will disappear, so speciation and stasis are not favoured
ecological generalists	×	×	✓	adaptation to many habitat types increases the probability of surviving rapid environmental changes or local disturbance