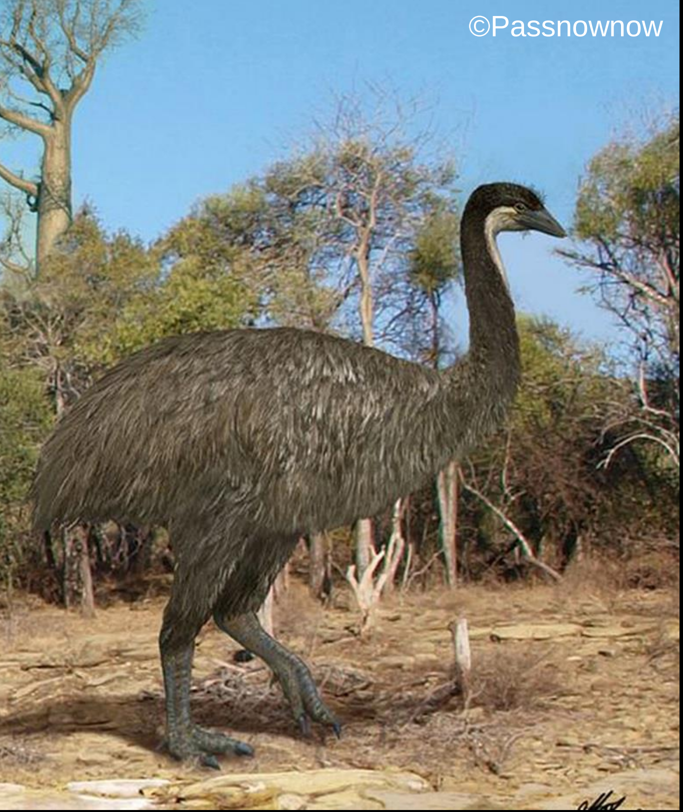
Madagascar’s Orphans of Extinction

Southern Asia

803064AI (R00941) 5-04

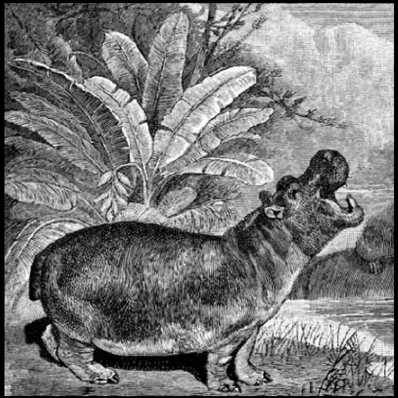

©Nick Garbutt
© Eckhard Lietzow


©Passnownow


©Smokeybjb


©Smokeybjb


©Velizar Simeonovski




©Roman Uchytel

Neotropical Anachronisms: The Fruits the Gomphotheres ate

Janzen & Martin - Science 1982

Crescentia cujete
calabash tree, C America

Gleditsia triacanthos
honey locust, N America

Maclura pomifera
Osage orange, N America

Dispersal Anachronisms in South America

Paulo Guimarães, Mauro Galetti, Pedro Jordano 2008

OPEN ACCESS Freely available online

PLoS one

Seed Dispersal Anachronisms: Rethinking the Fruits Extinct Megafauna Ate

Paulo R. Guimarães Jr.[1,3], **Mauro Galetti**[2], **Pedro Jordano**[3]*

1 Departamento de Física da Matéria Condensada, Instituto de Física Gleb Wataghin, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil, 2 Laboratório de Biologia da Conservação, Universidade Estadual Paulista (UNESP), Rio Claro, São Paulo, Brazil, 3 Integrative Ecology Group, Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas (CSIC), Sevilla, Spain

Abstract

Background: Some neotropical, fleshy-fruited plants have fruits structurally similar to paleotropical fruits dispersed by megafauna (mammals $>10^3$ kg), yet these dispersers were extinct in South America 10–15 Kyr BP. Anachronic dispersal systems are best explained by interactions with extinct animals and show impaired dispersal resulting in altered seed dispersal dynamics.

Methodology/Principal Findings: We introduce an operational definition of megafaunal fruits and perform a comparative analysis of 103 Neotropical fruit species fitting this dispersal mode. We define two megafaunal fruit types based on previous analyses of elephant fruits: fruits 4–10 cm in diameter with up to five large seeds, and fruits >10 cm diameter with numerous small seeds. Megafaunal fruits are well represented in unrelated families such as Sapotaceae, Fabaceae, Solanaceae, Apocynaceae, Malvaceae, Caryocaraceae, and Arecaceae and combine an overbuilt design (large fruit mass and size) with either a single or few (<3 seeds) extremely large seeds or many small seeds (usually >100 seeds). Within-family and within-genus contrasts between megafaunal and non-megafaunal groups of species indicate a marked difference in fruit diameter and fruit mass but less so for individual seed mass, with a significant trend for megafaunal fruits to have larger seeds and seediness.

Conclusions/Significance: Megafaunal fruits allow plants to circumvent the trade-off between seed size and dispersal by relying on frugivores able to disperse enormous seed loads over long-distances. Present-day seed dispersal by scatter-hoarding rodents, introduced livestock, runoff, flooding, gravity, and human-mediated dispersal allowed survival of megafauna-dependent fruit species after extinction of the major seed dispersers. Megafauna extinction had several potential consequences, such as a scale shift reducing the seed dispersal distances, increasingly clumped spatial patterns, reduced geographic ranges and limited genetic variation and increased among-population structuring. These effects could be extended to other plant species dispersed by large vertebrates in present-day, defaunated communities.

Citation: Guimarães PR Jr, Galetti M, Jordano P (2008) Seed Dispersal Anachronisms: Rethinking the Fruits Extinct Megafauna Ate. PLoS ONE 3(3): e1745. doi:10.1371/journal.pone.0001745

Editor: Dennis Marinus Hansen, University of Zurich, Switzerland

Received June 8, 2007; **Accepted** January 15, 2008; **Published** March 5, 2008

Funding: The study was supported by public funding from the Spanish Ministerio de Ciencia y Tecnología (BOS2000-1366-C02-01, REN2003-00273, CGL2006-00373) and RNM-305 (Junta de Andalucía) to PJ, CNPq (Bolsa de Produtividade), FAPESP, FUNDUNESP and IFS to MG and FAPESP to PRG (01/1737-3); our collaboration was also funded by CYTED and a CNPq-CSIC institutional agreement.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: jordano@ebd.csic.es

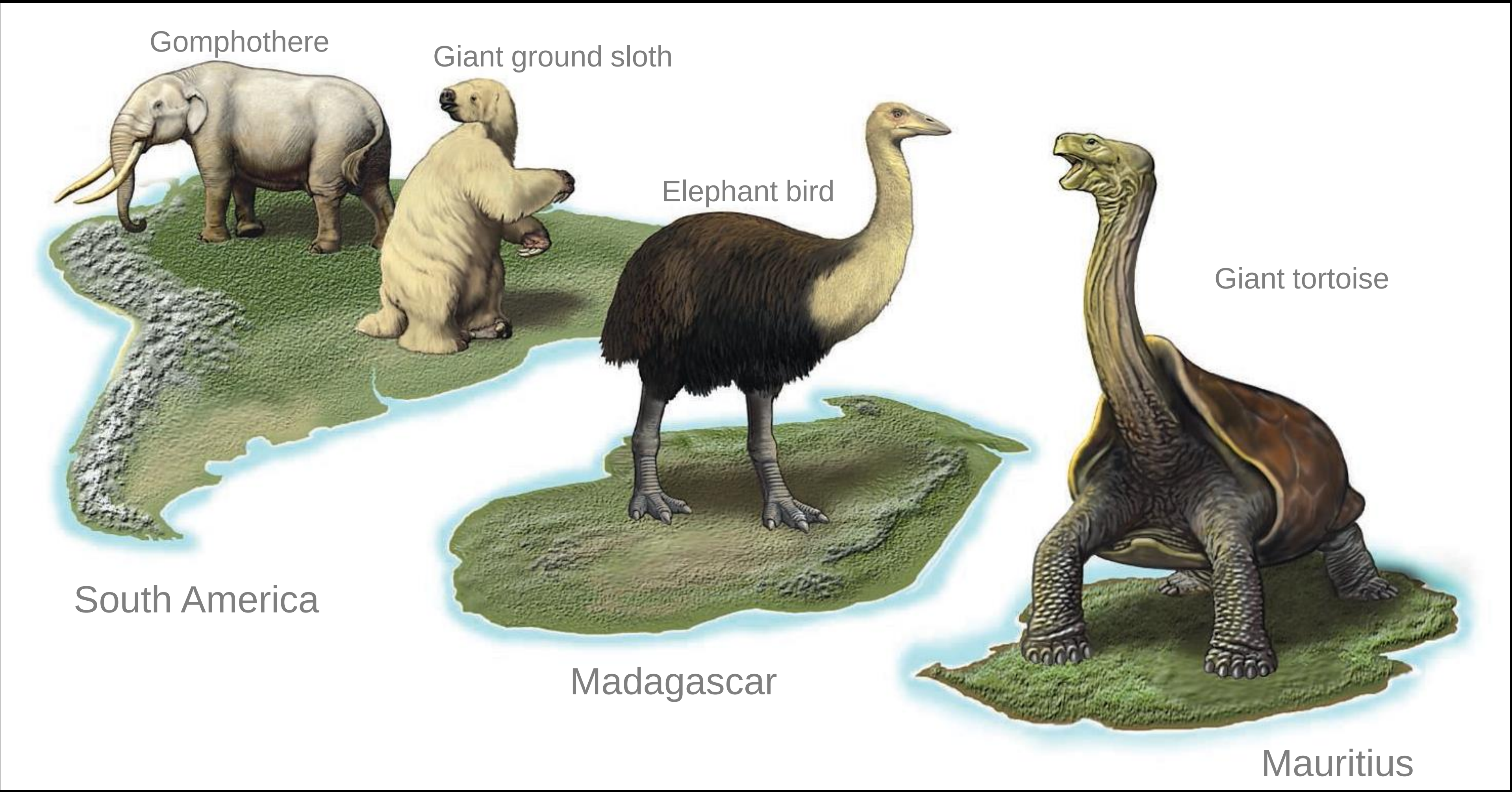
Introduction

The strong evidence that positive density-dependent mortality occurs in seeds, seedlings, juvenile and adult plants in several different species suggests that seed dispersal is a key process in plant communities [1,2]. Fruit traits certainly play a key role in the outcomes of interactions with seed dispersers, affecting the seed dispersal effectiveness (*sensu* [3]), and negative consequences for plant populations can be expected if the dispersal process is absent or impaired (e.g., [4,5]). Yet, a large fraction of extant fleshy fruits show trait combinations that largely reflect their history of shared ancestry [6], not present-day adaptations to seed dispersers. In analogy with "ghosts of the competition past", some combinations of fruit traits that can be found in extant communities suggest "ghosts of past mutualisms" [7,8].

Many ecological studies have identified diverse interactions with the frugivorous fauna in different communities, usually ranging from a few to tens of species recorded feeding on the fruit of a given plant species [9,10]. Even after recognizing that the plant-frugivore interaction can operate on exapted traits [11] of fruits, its outcomes have key functional effects on the demography, regeneration and gene flow patterns of the plants. Consequently, some structural patterns in fruits may be associated with distinct assemblages of seed dispersers [12]. In this context, the paradoxical existence of fruits with apparent adaptations for the dispersal by some groups of animals, in areas where these animals are now extinct, is an interesting topic with deep consequences for evolution, ecology and conservation of plant diversity. In fact, the loss of large mammals is still ongoing, and current defaunation scenarios have been shown to have serious consequences for plant populations [13–16].

The Forgotten Megafauna

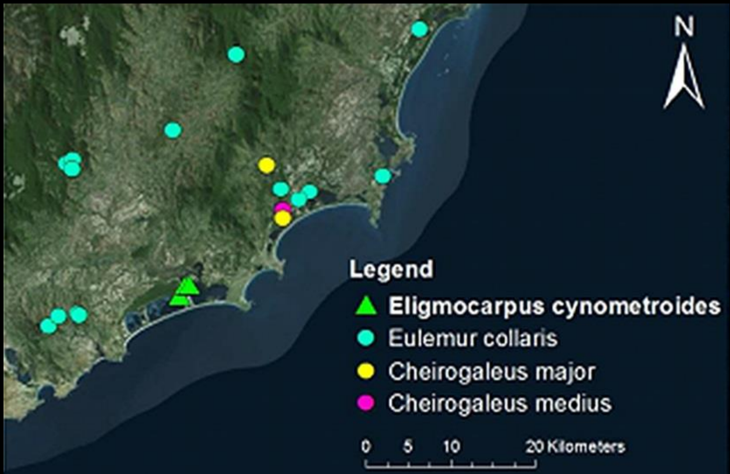
Hansen & Galetti - Science 2009



c. 10,500 years BP c. 2000-400 years BP c. 250 years BP (1844?)

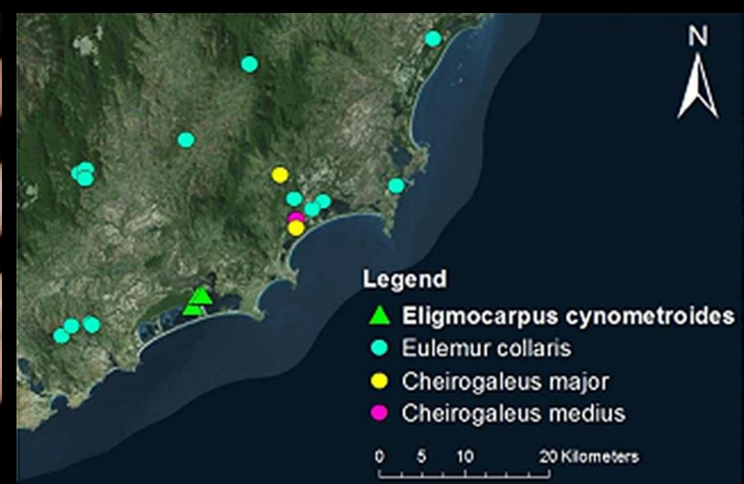
Dispersal Anachronism

Animal-dispersed fruits which display strikingly unfit traits and patterns to meet the physical capabilities and sensory preferences of extant dispersers.



Indicators of dispersal anachronisms

- "Riddle of the rotting fruit"
- Inefficient dispersal by extant animals
- Gape size and seed size don't' match
- Patchy or restricted distribution



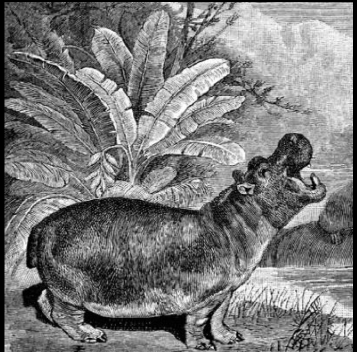
Extant animal dispersers in Madagascar

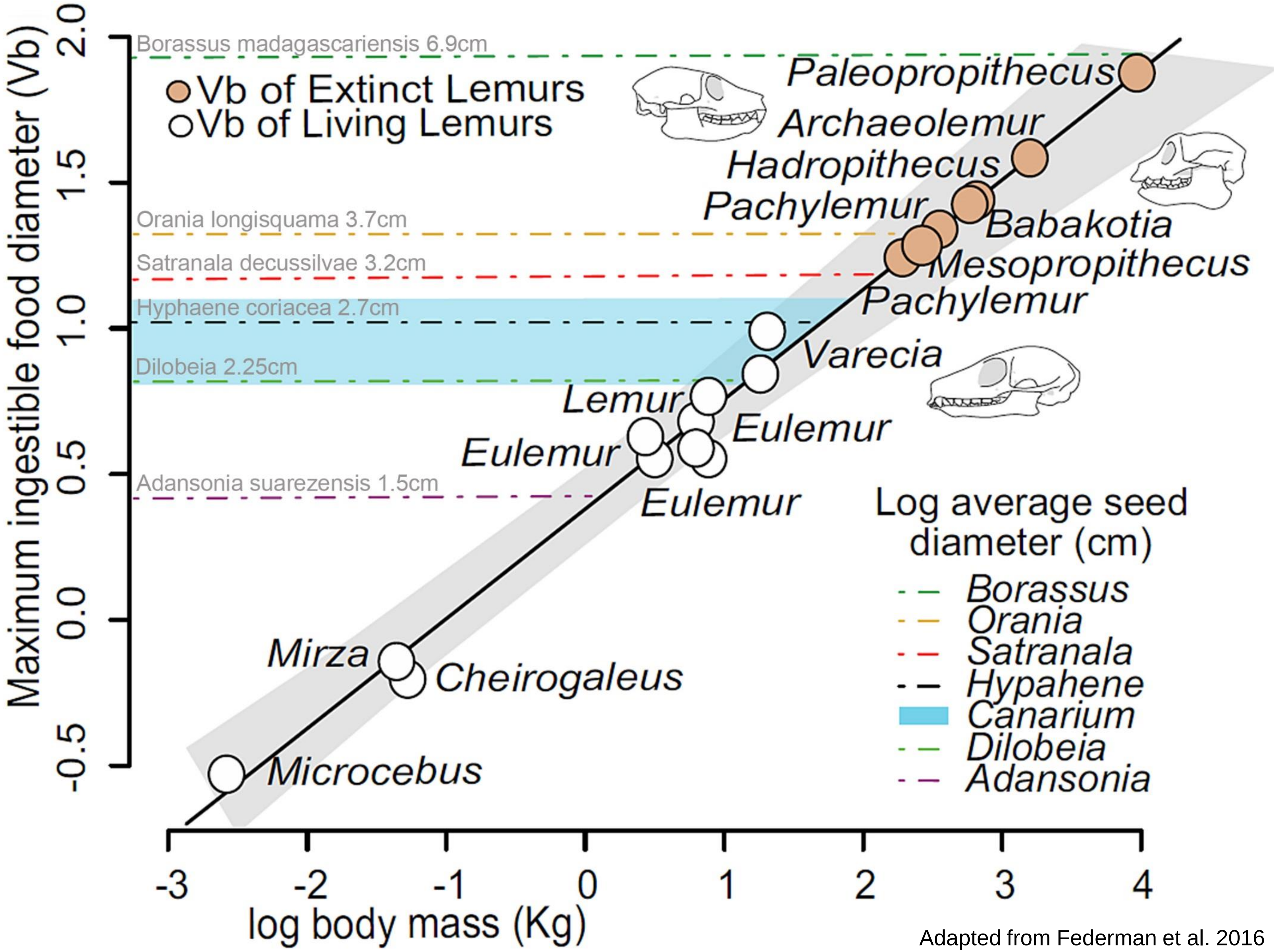
- **Lemurs (21)**
- Bats (3)
- Birds (5)
- Reptiles (1)
- Rodents
- Introduced livestock?

Cattle, horse, sheep, goats and bushpigs

Madagascar's Extinct Megafauna

- Dramatic loss of animal species between c. 2000 and 400 BP
- At least 48 species of large mammals, birds and reptiles lost
- Likely cause: human activities
- Megafauna in Madagascar = every extinct species larger than the largest extant native frugivore (> *Varecia rubra,* 3400g)





Adapted from Federman et al. 2016

Madagascar’s extinct giant lemurs

Megafauna in Madagascar = every extinct species larger than the largest living native frugivore (> *Varecia rubra,* 3400g)

Species	Diet	BW	Max. Ø
Palaeopropithecus ingens (sloth lemur)	Mixed	52.6	4.24
Archaeolemur majori (monkey lemur)	Frugivore	24.5	3.43
Hadropithecus stenognathus (monkey lemur)	Mixed	16.7	3.09
Babakotia radofilai (sloth lemur)	Frugivore	16.2	3.06
Pachylemur jullyi (giant ruffed lemur)	Frugivore	12.8	2.87
Mesopropithecus globiceps (sloth lemur)	Mixed	10.6	2.72
Pachylemur insignis (giant ruffed lemur)	Frugivore	10.0	2.68
Varecia rubra & V. variegata ruffed lemur	Frugivore	3.4	2.46
Eulemur macaco Black lemur	Frugivore	2.3	2.46

Palaeopropithecus ingens

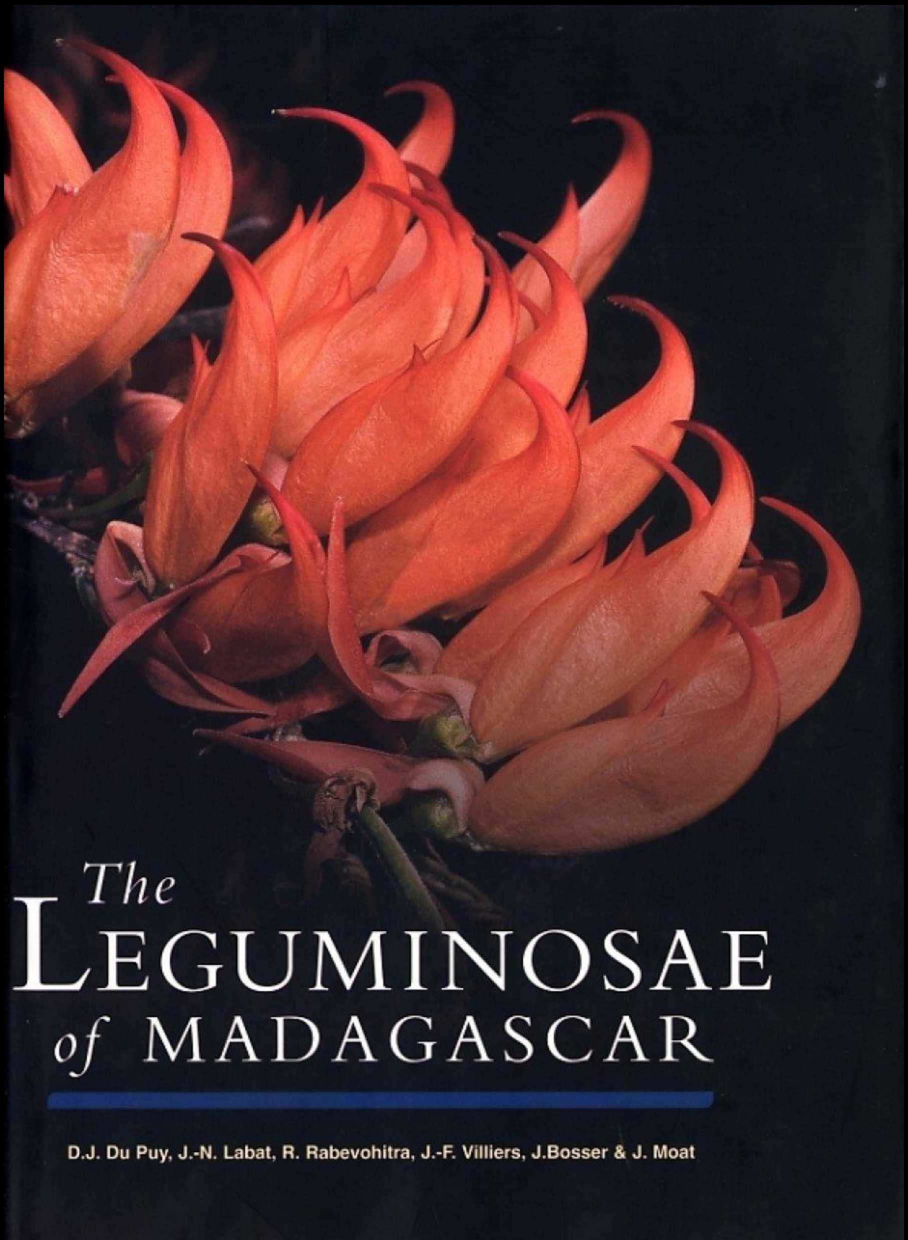
Varecia rubra

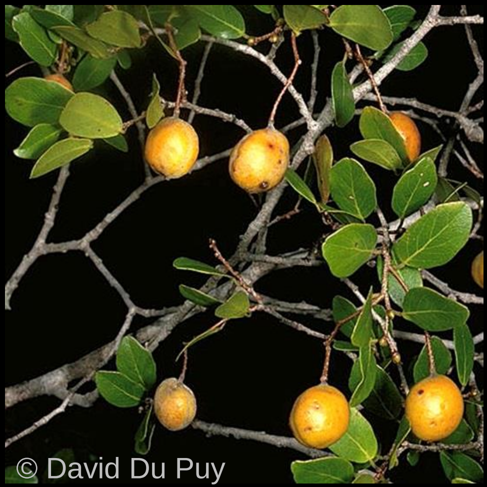
Degrees of anachronism
(modified after Barlow 2000)

A) **EXTREME**: no native dispersers

B) **POTENTIAL**: 5 ≤ native dispersers

Dispersal anachronisms in Madagascan legumes?

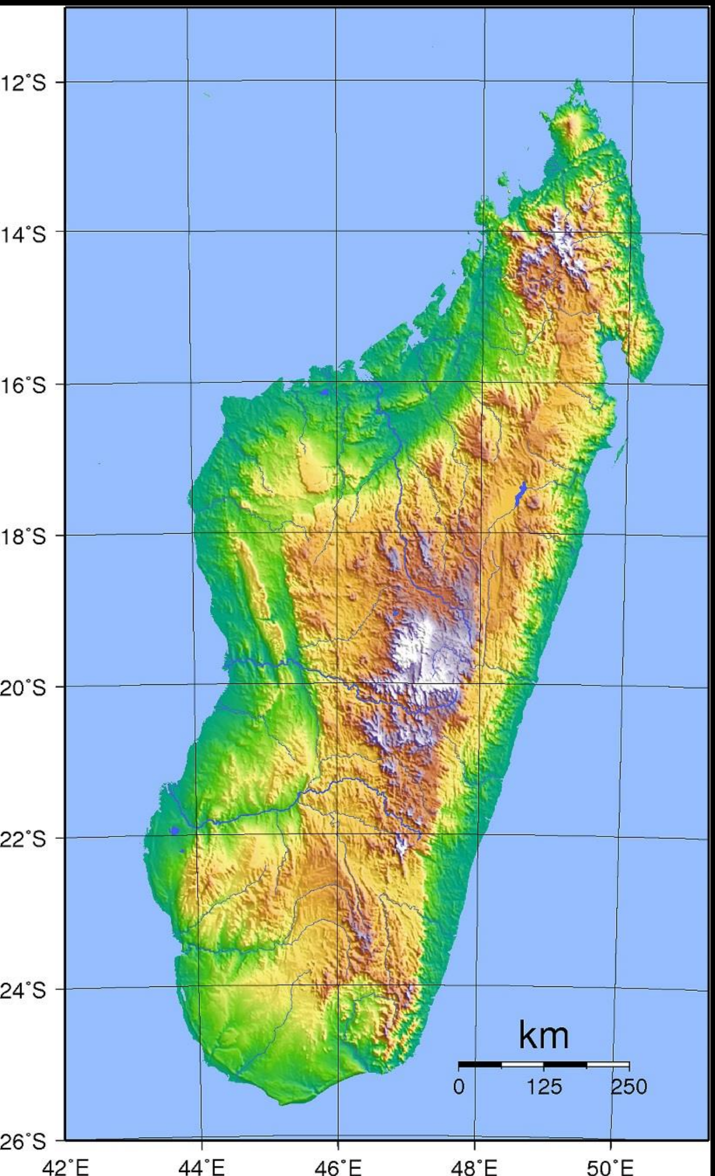




Madagascar's Flora

- 10,650 angiosperm species, 84% endemism (Callmander et al. 2011)
- With 626 species Leguminosae is 3rd most species rich family
  (Orchidaceae ca. 850 spp, Rubiaceae ca. 650 spp)
- 70% endemism in Leguminosae (450±5 species)

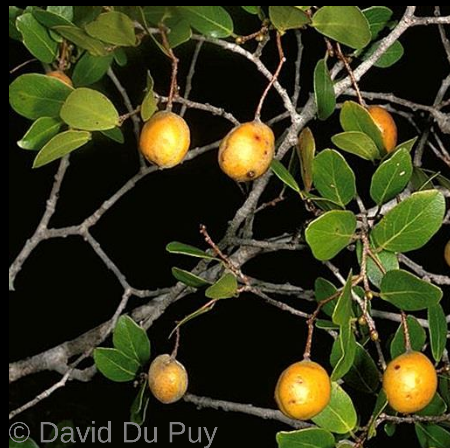
At least 27 Madagascan legume species are endozoochorously dispersed



Photos © David Du Puy

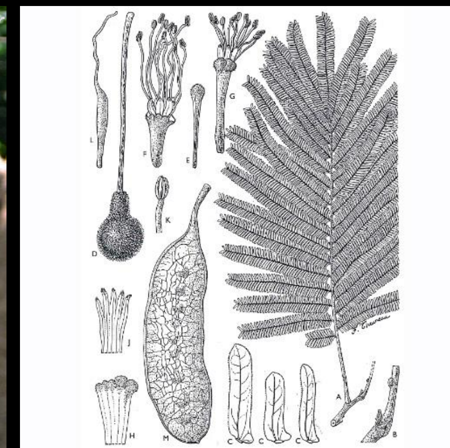
Only 4 species of Leguminosae are known to be dispersed by animals

Eulemur fulvus fulvus
Common brown lemur



Baudouinia fluggeiformis
(Caesalpinioideae)

Eulemur macaco
Black lemur



Parkia madagascariensis
(Mimosoideae)

Eulemur macaco
Black lemur

Cordyla madagascariensis
(Papilionoideae)

Lemur catta
Ring-tailed lemur

Tamarindus indica
tamarind (Caesalpinioid.)

Results

- 27 species have animal dispersed fruits
- Based on seed size, 6 endemic species qualify as anachronistic

Species	IUCN	Anachronism	Pot. Disp.
1) *Erythrina hazomboay*	VU	Extreme	0
2) *Erythrina madagascariensis*	LC	Potential	2 birds
3) *Erythrina perrieri*	CR	Potential	2 birds
4) *Adenanthera mantaroa*	NE	Potential	2 birds
5) *Strongylodon madagascariensis*	LC	Potential	4 lemurs
6) *Erythrophleum couminga*	NE	Potential	5 lemurs

Results

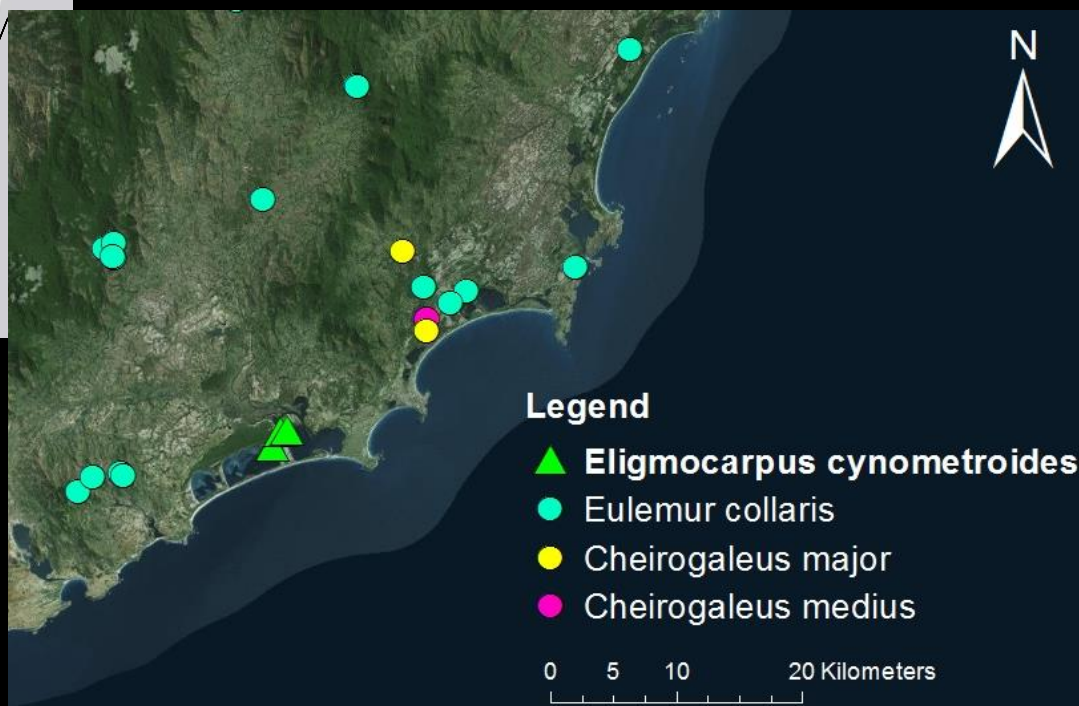
- 27 species have animal dispersed fruits
- Based on seed size, 6 endemic species qualify as anachronistic

Species	IUCN	Anachronism	Pot. Disp.	Distribution
1) *Erythrina hazomboay*	VU	Extreme	0	**0**
2) *Erythrina madagascariensis*	LC	Potential	2 birds	2
3) *Erythrina perrieri*	CR	Potential	2 birds	2
4) *Adenanthera mantaroa*	NE	Potential	2 birds	2
5) *Strongylodon madagascariensis*	LC	Potential	4 lemurs	2
6) *Erythrophleum couminga*	NE	Potential	5 lemurs	0

Species	IUCN	Anachronism	Pot. Disp.	Distribution
Eligmocarpus cynometroides	CR	L-Extreme	18 lemurs	**0**

Eligmocarpus cynometroides

- 21 individuals left (Devey et al. 2013)
- Critically Endangered



Why are we doing this?

Consequences of megafauna extinction

Decrease in total number of seeds dispersed

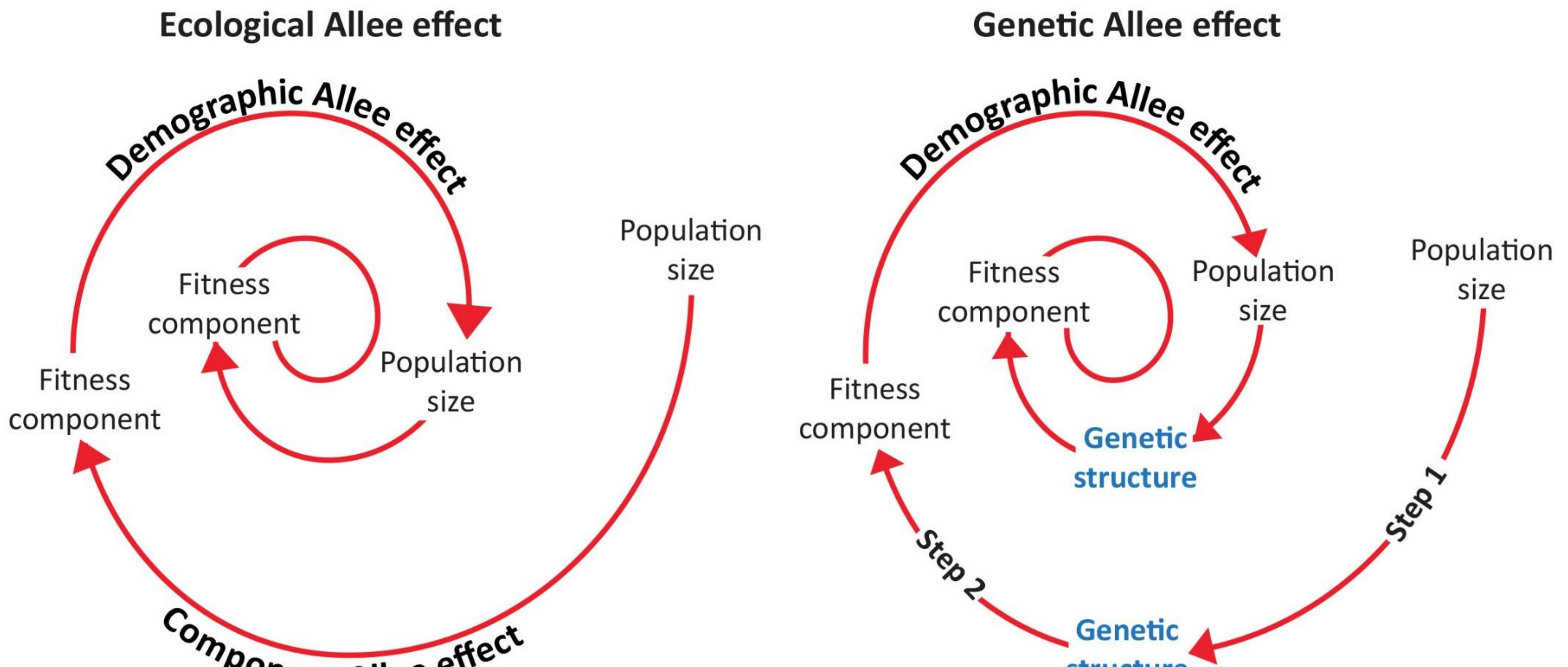
Reduced seed dispersal distances & areas

Reduced geographic ranges

Restricted gene flow via seeds leading to:

- Limited genetic variation within populations
- High genetic differentiation between populations

The genetic Allee effect



from Luque et al. 2016





Non-dispersal eventually means extinction!

PROCEEDINGS B

rspb.royalsocietypublishing.org

Research

Cite this article: Caughlin TT, Ferguson JM, Lichstein JW, Zuidema PA, Bunyavejchewin S, Levey DJ. 2015 Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Proc. R. Soc. B* **282**: 20142095.
http://dx.doi.org/10.1098/rspb.2014.2095

Received: 22 August 2014
Accepted: 14 October 2014

Subject Areas:
ecology, environmental science, plant science

Keywords:
seed dispersal, overhunting, tree population, tropical forest dynamics, extinction, spatial model

Author for correspondence:
T. Trevor Caughlin
e-mail: trevorcaughlin@ufl.edu

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2014.2095 or via http://rspb.royalsocietypublishing.org.

THE ROYAL SOCIETY
PUBLISHING

Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages

T. Trevor Caughlin[1,2], Jake M. Ferguson[1], Jeremy W. Lichstein[1], Pieter A. Zuidema[3], Sarayudh Bunyavejchewin[4] and Douglas J. Levey[1,5]

[1]Department of Biology, University of Florida, PO Box 118525, Gainesville, FL 32611, USA
[2]Conservation Ecology Program, King Mongkut's University of Technology Thonburi, 49 Soi Tientalay 25, Bangkhuntien-Chaitalay Road, Thakham, Bangkhuntien, Bangkok 10150, Thailand
[3]Forest Ecology and Forest Management Group, Wageningen University and Research Centre, PO Box 47, 6700 AA Wageningen, The Netherlands
[4]Royal Thai Forest Department, Chatuchak, Bangkok 10900, Thailand
[5]Division of Environmental Biology, National Science Foundation, Arlington, VA 22230, USA

Overhunting in tropical forests reduces populations of vertebrate seed dispersers. If reduced seed dispersal has a negative impact on tree population viability, overhunting could lead to altered forest structure and dynamics, including decreased biodiversity. However, empirical data showing decreased animal-dispersed tree abundance in overhunted forests contradict demographic models which predict minimal sensitivity of tree population growth rate to early life stages. One resolution to this discrepancy is that seed dispersal determines spatial aggregation, which could have demographic consequences for all life stages. We tested the impact of dispersal loss on population viability of a tropical tree species, *Miliusa horsfieldii*, currently dispersed by an intact community of large mammals in a Thai forest. We evaluated the effect of spatial aggregation for all tree life stages, from seeds to adult trees, and constructed simulation models to compare population viability with and without animal-mediated seed dispersal. In simulated populations, disperser loss increased spatial aggregation by fourfold, leading to increased negative density dependence across the life cycle and a 10-fold increase in the probability of extinction. Given that the majority of tree species in tropical forests are animal-dispersed, overhunting will potentially result in forests that are fundamentally different from those existing now.

1. Introduction

Animal populations in tropical forests are threatened by overhunting, even in areas that are otherwise protected [1–3]. Large frugivores, including most primates and ungulates, are often the first animals to disappear [1,4]. If animal-mediated seed dispersal is important for maintaining viable populations of trees, overhunting may lead to tropical forest degradation, including loss of biodiversity and decreased biomass [5–7]. Comparisons between hunted and non-hunted sites generally reveal lower rates of seed dispersal and lower seedling abundance of animal-dispersed tree species in hunted sites [8–11]. The most comprehensive study to date tracked changes in a tree community as hunting increased over a 15-year period and found increased spatial aggregation and decreased sapling recruitment for animal-dispersed tree species, leading to an overall decline in sapling biodiversity [12]. While these empirical studies provide convincing evidence of short-term negative impacts of overhunting on tree populations, there is a discrepancy between these empirical results and the general finding of demographic studies

Caughlin et al. 2014:

Disperser loss leads to a 10-fold increase in the probability of extinction

What next?

- Comparative study of dispersal anachronisms in Madagascar

Satranala decussilvae
Arecaceae

Adansonia spp.
Malvaceae

Canarium spp.
Burseraceae

Euclinia suavissima
Rubiaceae

Symphonia spp.
Clusiaceae

Strychnos spp.
Loganiaceae

Landolphia obliquinervia
Apocynaceae

Ampelosycios humblotii
Passifloraceae

Colubrina spp.
Rhamnaceae

Ropalocarpus lucidus
Sphaerocepalaceae

Brexiella spp.
Celastraceae

Salacia spp.
Celastraceae

What next?

- Comparative study of dispersal anachronisms in Madagascar
- Paleontological evidence
  (e.g. subfossil seeds from coprolites, drill cores, etc.)

Acknowledgements

The Joseph Jones and Daisy and Graham Rattenbury Charitable Trust

At Kew:

Kathy Willis

Stuart Cable

Gwilym Lewis

Aurélie Grall

David Du Puy

In Madagascar (KMCC):

Hélène Ralimanana

Franck Rakotonasolo

Guy Onjalalaina

Romer Rabarijaona

Tatamo Andrianantenaina

Externally:

Sven Buerki (Natural History Museum, London, UK)

Steve Goodman (Field Museum Chicago/Madagascar)

Kim Valenta (McGill University Montreal, Canada)

Hiroki Sato (Kyoto University, Japan)


Thank you!