Fourth International Symposium/Workshop on

# **Frugivores and Seed Dispersal**

# Theory and its application in a changing world

# **Program and Abstracts**



9 - 16 July 2005 Brisbane, Australia

## Fourth International Symposium/Workshop on Frugivores and Seed Dispersal

Theory and its application in a changing world



# Frugivores & Seed Dispersal Australia 2005

# **PROGRAM AND ABSTRACTS**

9-16 July 2005

Griffith University Brisbane, Australia

Sponsored by



National Science Foundation







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### ACKNOWLEDGEMENTS

#### **Organising Committee**

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Supported by:

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#### **Sponsoring Institutions**

Griffith University CSIRO Sustainable Ecosystems Rainforest CRC Araucaria Ecotours National Science Foundation (USA)

Student Prizes were kindly donated by:

David Snow	David kindly donated the use of his name for the oral
	presentation award. The committee chose the name <i>David Snow</i>
	Award in recognition of the immensely important contribution
	David has made to the field of Frugivores and Seed Dispersal.
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CSIRO Publishing	Life of Marsupials by Hugh Tyndale-Biscoe.

We would also like to acknowledge William T. Cooper, who gave us permission to use his artwork for the conference.

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Thanks to all others who helped but were not mentioned here.

### INTRODUCTION

In the year 2000, the Organising Committee of the Third Symposium on Frugivores and Seed Dispersal stated, "Now is the time to gather researchers to highlight unanswered questions and to chart the future course of the field". That time has come again.

The study of seed dispersal and the animals that drive and interact with it has been developing, and maturing, at an impressive rate. While many of the concepts and methods that have been fundamental throughout its history have maintained their currency, fresh approaches have provided new perspectives on the process and its ramifications leading to the development of a suite of exciting new questions. Similarly, developments across the full range of methods employed in the field have seen the rise of new tools for testing theory, including issues that have until now remained the preserve of theoreticians.

The ways in which our understanding can be applied is also expanding. We face a time when application of our ecological understanding to the conservation of our biota and to the sustainable management of our ecosystems is urgent. The conservation of remnant ecosystems, the management of fragmented landscapes, the restoration of degraded landscapes, controlling the spread of invasive weeds, the recovery of threatened species and the ecological sustainability of our human landscapes are all endeavours that require the knowledge of key ecological processes. Seed dispersal, and the attendant life-histories, behaviours and strategies of its participants, is one of these processes.

Hence, when choosing the theme of this conference we felt it was important to emphasise the two key elements of the field's development in the last decade:

- 1. the strong development of underpinning theory resting on a solid foundation of empirical studies; and
- 2. the need to apply our understanding to the solution of some of the world's ecological problems.

With researchers representing 27 countries, we hope this meeting will be productive and inspiring. In particular, we hope it will take stock of where we are and where we are going, once again identifying the important unanswered questions, problems and avenues to which we can apply our understanding.

Day	Start	Finish	Event
Saturday 9 July	17:30		Registration opens; informal gathering at the bar plus displays
Sunday 10 July	10:00	18:30	Conference Day Tour
	18:30	21:30	Welcome Reception and Registration
Monday 11 July	07:30	08:30	Registration
	08:30	09:00	Welcome Address
	09:00	10:40	Plenary Symposium 1: Determinants of Plant Recruitment Patterns
	10:40	11:25	Morning Tea
	11:25	13:30	Plenary Symposium 1: Determinants of Plant Recruitment Patterns (continued)
	13:30	15:00	Lunch/Posters
	15:00	15:45	Session A: Seed Dispersal and Plant Traits
	15:45	16:30	Afternoon Tea
	16:30	17:30	Session A: Seed Dispersal and Plant Traits (continued)
	17:30	18:30	Posters; drinks and nibbles
Tuesday 12 July	08:30	08:35	Announcements
	08:35	10:15	Plenary Symposium 2: Evolution of Fruit Traits
	10:15	11:00	Morning Tea
	11:00	13:30	Plenary Symposium 3: Measuring Seed and Seedling Shadows
	13:30	14:55	Lunch/Posters
	14:55	15:30	Session B: Symposium on Revegetation
	15:30	16:15	Afternoon Tea
	16:15	17:30	Session B: Symposium on Revegetation (continued)
Wednesday 13 July	08:30	08:35	Announcements
	08:35	10:15	Plenary Symposium 4: Frugivore Impacts
	10:15	11:00	Morning Tea
	11:00	13:05	Plenary Symposium 5: Conservation of Dispersal Systems
	13:05	14:25	Lunch/Posters
	14:25	15:30	Session C: Symposium on Fragmented Landscapes
	15:30	16:15	Afternoon Tea
	16:15	17:30	Session C: Symposium on Fragmented Landscapes (continued)
	19:00		Conference Dinner

### PROGRAM OVERVIEW

Day	Start	Finish	Event
Thursday 14 July	08:30	10:15	Session D (concurrent with Session F): Dispersal and Plant Community Composition
	08:30	10:00	Session F (concurrent with Session D): Frugivore Community Composition
	10:15	11:00	Morning Tea
	11:00	12:30	Session E (concurrent with Session G): Frugivore Studies
	11:00	12:30	Session G (concurrent with Session E): Fruit Characters and Fruit-Frugivore Interactions
	12:30	13:45	Lunch
	13:45	14:30	Session H: The Effects of Frugivore Gut Retention on Seeds
	14:30	15:10	Afternoon Tea
	15:10	17:00	Session I: Symposium on Invasive Plants
	17:00		Announcements and Prize Presentations (prior to informal gathering at club)
Friday 15 July	08:30	09:00	Announcements
	09:00	12:40	Workshop 1: Invasive Plants
	09:00	12:40	Workshop 2: What are the Major Frugivory and Seed Dispersal Issues that can Best, or Perhaps Only, be Addressed by Large- scale, International Collaborative Research?
	10:00	11:00	Morning Tea (available for delegates)
	12:40	14:00	Lunch
	14:00	15:00	Posters
	15:00	17:30	Workshop 3: How do we Foster International Collaborative Research?
	15:30	16:00	Afternoon Tea (available for delegates)



### GENERAL INFORMATION

#### Parking

Car parking at Griffith University costs \$5.00 per day, and is available at East Carpark bays B, C and D (see http://www.griffith.edu.au/locations/maps/na\_map.pdf). Parking areas will be sign-posted. Vouchers can be purchased at vending machines at the entrance to the University and at the entrance to the Carpark. Vending machines take coins only (excluding 50 cent pieces). Please ensure you have the correct change before arriving, as delegates will be fined for failing to pay parking fees.

#### **Registration Desk**

Registration will open on Saturday evening (17:30 - 19:00) in the mezzanine of the Hub (N11 on Griffith Map), which is just near the accommodation (N39). We will be opening the bar at the Campus Club (N71) for informal drinks and gatherings. The bar will open from 17:30 and close at 20:00 (don't forget dinner for those being catered for by the Griffith colleges closes at 19:00; see below). The Campus Club Kitchen will not be open for meals that night.

From Sunday onwards, the Registration Desk will be located at the reading pits (beneath N16, northern side), where poster sessions and trade tables will also be held. We will have a Welcome Reception on Sunday commencing at 18:30. The Registration Desk will be attended at the following times unless otherwise announced or sign-posted:

Saturday 9 July		Mezzanine of the Hub (N11)
Sunday 10 July		Reading pit (north side of N16)
Monday 11 July	07:30 – 18:30	Reading pit (north side of N16)
Tuesday 12 July	07:30 – 18:00	Reading pit (north side of N16)
Wednesday 13 July	07:30 – 18:00	Reading pit (north side of N16)
Thursday 14 July	07:30 – 18:00	Reading pit (north side of N16)
Friday 15 July	07:30 – 18:00	Reading pit (north side of N16)

Please use the registration desk as your main port of call for information and assistance. The conference organising team and volunteers will also wear especially coloured name tags so that they can be easily identified if you need assistance away from the desk.

#### Student Oral and Poster Paper Competitions

We are pleased to announce the **David Snow Award** for the best oral presentation by a student. All students are eligible for the award and should indicate their eligibility at registration.

**First prize** will be a copy of *Fruits of the Australian Tropical Rainforest* by Wendy and William T. Cooper (valued at \$235.00 and donated by Nokomis Editions; see http://nokomis.com.au/html/fruits.html), plus \$100.00 cash from Earthwatch Institute Australia. **Second prize** will be \$100.00 from Earthwatch Institute Australia.

We are also pleased to be running a poster competition for the most engaging, inspiring and well-organised poster displaying solid science.

**First prize** will be a copy of *Life of Marsupials* by Hugh Tyndale-Biscoe (valued at \$89.95 and donated by CSIRO publishing; see http://www.publish.csiro.au/pid/4781.htm), plus \$100.00 cash from Earthwatch Institute Australia. **Second prize** will be \$100.00 from Earthwatch Institute Australia.

#### Instructions to Authors

#### **Oral Presentations**

PowerPoint presentations will be shown on lecture theatre data projectors. These will be run from PCs. It will be most efficient if presentations are run from PowerPoint for PCs. Adobe Acrobat Reader will be available. Overhead projectors and whiteboards will also be available.

We can also accommodate Macintosh programs such as Keynote, howeve you must contact the Organising Committee ahead of time as we are unable to provide a Macintosh laptop (you will need to bring your own).

You will need to have your presentation loaded on to the theatre computer in the appropriate room during the break prior to your session. For those speaking in the first sessions in the mornings, please load your presentations at the end of the previous day. A volunteer will be available to assist you with loading of presentations. If you can't find anyone when you wish to load, contact the Registration Desk.

#### Presentation Length

Plenary Papers (those people speaking on Monday, Tuesday or Wednesday mornings):

- 20 minutes' maximum spoken presentation; with
- 5 minutes' question time.

*Contributed Papers* (those speaking on Monday, Tuesday or Wednesday afternoons or on Thursday):

- 12 minutes' maximum spoken presentation; with
- 3 minutes' question time.

#### Poster Presentations

Posters will be hung on free-standing display boards. Please bring Velcro tabs to hang your poster. Each poster has been allocated the space of 1188cm high by 840 wide, which is equivalent to portrait A0-sized paper. All poster presenters should take their posters to the Registration Desk on arrival, where they will be allotted a numbered location to display them.

#### Meals, Breaks and Social Events

Morning and afternoon teas and lunches will be at slightly different times and of slightly different duration each day so please check the program. Breaks will be held in the undercroft near the reading pit.

Evening meals for those using Griffith University accommodation will be provided in the Colleges dining room, which is in the Hub building (N11) between 17:45 and 19:00.

For those arranging their own meals, the Campus Club (N71) kitchen will be open weeknights until 19:30. Information on off-campus restaurants and public transport options will be available at the Registration Desk.

The conference day tour (Sunday 10 July) will depart from the car park outside the Ecocentre (N68) at 10:00.

A Welcome Reception will be held at the Campus Club following the conference day tour (18:30 - 21:30). You should go to the reading pits to register first.

The Conference Dinner will be held on Wednesday evening at 19:00 at the Campus Club (N71).

### SCIENTIFIC PROGRAM

#### Saturday 9 July 2005

17:30......Registration opens; informal gathering at the bar plus displays

#### Sunday 10 July 2005

10:00 – 18:30..... Conference Day Tour Visit to a nearby subtropical rainforest to view local plants and animals and discuss ideas in a natural setting; Return via a fruitbat colony to watch a flyout.

18:30 – 21:30..... Welcome Reception and Registration

#### Monday 11 July 2005

07:30 – 08:30..... Registration (Reading Pit) 08:30 – 09:00..... Welcome Address (Northern Theatre 1)

#### PLENARY SYMPOSIUM 1: DETERMINANTS OF PLANT RECRUITMENT PATTERNS (Northern Theatre 1; Chair: Joe Wright)

09:00 - 09:25	<b>Tomás A. Carlo, Juan M. Morales, Juliann E. Aukema</b> Competition, facilitation, and context-dependence in seed-dispersal.
09:25 – 09:50	Héctor Godínez-Alvarez and Pedro Jordano
	Seed dispersal by frugivores: An empirical approach to analyse their
	demographic consequences.

- 09:50 10:15..... Helene C. Muller-Landau and Frederick R. Adler How dispersal affects interactions with natural enemies and their contribution to diversity maintenance.
- 10:15 10:40..... Charles Kwit, D. Levey, C. Clark, and J. Poulsen Out of one shadow and into another: causes and consequences of spatially contagious seed dispersal by frugivores.
- 10:40 11:25..... Morning Tea

### PLENARY SYMPOSIUM 1 (CONTINUED)

(Northern Theatre 1; Chair: Pierre-Michel Forget)

11:25 – 11:50..... Eugene W. Schupp What is a suitable site, or, where does a seed really want to land?

11:50 – 12:15	<b>Tad C. Theimer and Catherine A. Gehring</b> Terrestrial vertebrates, tree seedlings and mycorrhizal spores: When and how will terrestrial vertebrates affect survival, dispersal and richness?
12:15 – 12:40	Rachel E. Gallery, James W. Dalling, Lindsay K. Higgins, A. Elizabeth Arnold Role of seed-infecting fungi in the recruitment limitation of neotropical pioneer species.
12:40 – 13:05	Sabrina E. Russo, S.J. Davies and S. Tan The influence of dispersal mode and seed size on soil specialization of tree species in a Bornean rain forest.
13:05 – 13:30	Ran Nathan New perspective on long-distance seed dispersal.
13:30 - 14:45	Lunch
	SESSION A: SEED DISPERSAL AND PLANT TRAITS (Northern Theatre 1; Chair: Tomas Carlo)
14:45 – 15:00	<b>Robert Kooyman and Maurizio Rossetto</b> The impact of dispersal on genetic structure and species distribution: experimental studies from northern New South Wales.
15:00 – 15:15	Friederike A. Voigt, R. Arafeh, E. M. Griebeler and K. Böhning-Gaese Does seed dispersal matter? Comparative population genetics of two congeneric tropical trees.
15:15 – 15:30	<b>Carmen Castor</b> The forgotten ones: seeds that have no dispersal syndrome. Secondary seed dispersal in a high mountian community.
15:30 – 15:45	<b>Debra M. Wotton, Dave Kelly and J. J. Ladley</b> How important are 'keystone' dispersers? Pigeons and large seeds in New Zealand.
15:45 - 16:30	Afternoon Tea
	<b>SESSION A (CONTINUED)</b> (Northern Theatre 1; Chair: Tad Theimer)
16:30 – 16:45	<b>Don Butler</b> What can fruit morphology tell us about species abundance at regional scales?

16:45 – 17:00	K. Greg Murray, Mauricio Garcia-C., Joseph W. Veldman, William S. Mungall, Garth B. Rotman, and Adrienne L. Hull Pioneer seeds in Neotropical cloud forest soils: Patterns of mortality, chemical defenses, and consequences for persistence in an unpredictable environment.
17:00 – 17:15	Huiping Zhou, Jin Chen, Fan Chen Does ant-mediated seed dispersal alter spatial pattern and spatial genetic structure of <i>Globba lancangensis</i> (Zingiberaceae)?
17:15 – 17:30	<b>Silvia Lomáscolo, Pablo Speranza and Rebecca Kimball</b> The correlated evolution of fruit size and color in Ficus (Moraceae) supports the dispersal syndrome hypothesis.

17:30 - 18:30..... Posters; drinks and nibbles

### Tuesday 12 July 2005

#### 08:30 - 08:35..... Announcements

	PLENARY SYMPOSIUM 2: EVOLUTION OF FRUIT TRAITS (Northern Theatre 1; Chair: Richard Corlett)
08:35 – 09:00	Pierre-Michel Forget, Andrew J. Dennis, Patrick A. Jansen, Joanna A. Lambert and David A. Westcott Seed allometry and frugivore size: Conflict between seed dispersal patterns in tropical rainforests.
09:00 – 09:25	Ido Izhaki, Hagar Melamed-Tadmor, Natarajan Singaravelan, Ella Tsahar, Noam Cohen, Alon Lotan, Malka Halpern, Moshe Inbar, Gidi Ne'eman The role of secondary metabolites in shaping and mediating pollination and seed dispersal.
09:25 – 09:50	Mauro Galetti, Camila Donatti, Marco A. Pizo, P. Guimarães Jr. and Pedro Jordano Living in a world of ghosts: The seed dispersal by the megafauna in the Pantanal of Brasil
09:50 - 10:15	Joshua Tewksbury and Douglas Levey Frugivory and fruit phenotypes: integration within and across plant- animal interactions
10:15 - 11:00	Morning Tea
	<b>PLENARY SYMPOSIUM 3: MEASURING SEED AND</b> <b>SEEDLING SHADOWS</b> (Northern Theatre 1; Chair: Bette Loiselle)
11:00 – 11:25	Andrew J. Dennis and David A. Westcott Seed dispersal at community and landscape scales: incorporating functional classifications of dispersers and fruit into the study of an ecological process.
11:25 – 11:50	<b>David A. Westcott and Andrew J. Dennis</b> Where do all the seeds go? Estimating the dispersal curves generated by a community of frugivores.
11:50 – 12:15	<b>Pedro Jordano</b> Frugivores, seeds and genes: analysing the key elements of a seed shadow.
12:15 – 12:40	Britta Denise Hardesty, Stephen Hubbell and Eldredge Bermingham Genetic evidence that long distance seedling recruitment is commonplace in a vertebrate-dispersed Neotropical tree.

12:40 – 13:05	<b>Kimberly M. Holbrook</b> Seed dispersal in Amazonia Ecuador: toucan-generated seed shadows and genetic based models of a neotropical nutmeg.
13:05 – 13:30	Michael A. Steele, Amy McEuen, John Carlson, Peter Smallwood, Thomas Contrerars, and William Terzaghi Deciphering the effects of scatter- hoarding mammals on dispersal and establishment of the oaks: Inconsistencies between seed and seedling shadows.
13:30 - 14:55	Lunch/Posters
	<b>SESSION B: SYMPOSIUM ON REVEGETATION</b> (Northern Theatre 1; Organisers: John Kanowski and Carla Catterall)
14:55 – 15:00	Carla Catterall Welcome and introduction.
15:00 - 15:15	John Kanowski, Carla P. Catterall, Grant Wardell-Johnson and
	Frugivores and plant recruitment in different types of reforestation in cleared rainforest landscapes of tropical and subtropical Australia.
15:15 – 15:30	Wendy Neilan, Carla P. Catterall, John Kanowski and Stephen
	McKenna Frugivorous birds and rainforest regeneration in camphor laurel- dominated subtropical regrowth.
15:30 - 15:45	Louise Shilton
	The role of fruit-bats (Megachiroptera, Pteropodidae) in rebuilding and reconnecting the tropical forests of the Krakatau archipelago, Indonesia.
15:45 – 16:30	Afternoon Tea
16:30 – 16:45	<b>Zhishu Xiao and Zhibin Zhang</b> The role of scatter-hoarding rodents in forest restoration: A case study in rodent-dispersed oil tea <i>Camellia oleifera</i> in a fragmented forest.
16:45 – 17:00	Sandra Bos Mikich and Rafael Fernando da Silva Possette Do artificial bird perches improve seed rain as natural ones do? A field test in the Brazilian Araucaria forest.
17:00 – 17:15	Ken L. Tinley Perch-base thickets and berry birds: Keystones of arid Australia.

General discussion.

### Wednesday 13 July 2005

08:55 - 09:00	Announcements		
	<b>PLENARY SYMPOSIUM 4: FRUGIVORE IMPACTS</b> (Northern Theatre 1; Chair: Helene Muller-Landau)		
09:00 - 09:25	<b>Pablo R. Stevenson</b> Estimates of the number of seeds dispersed by a population of primates in a lowland forest in western Amazonia.		
09:25 - 09:50	Bette A. Loiselle, John G. Blake and Pedro Blendinger Seed dispersal by manakins (Aves: Pipridae) in a species rich tropical wet forest.		
09:50 – 10:15	Anna Traveset, J. Rodríguez, and B. Pías What does happen to a seed when it travels through a digestive tract?		
10:15 – 11:00	Morning Tea		
	<b>PLENARY SYMPOSIUM 5: CONSERVATION OF</b> <b>DISPERSAL SYSTEMS</b> (Northern Theatre 1; Chair: Sabrina Russo)		
11:00 – 11:25	<b>Richard T. Corlett</b> Pollination and seed dispersal: Which should conservationists worry about most?		
11:25 – 11:50	<b>Katrin Böhning-Gaese</b> Do seed dispersers matter? A biogeographical approach.		
11:50 – 12:15	Wesley R. Silva and Paulo R. Guimarães Jr Complex networks of plant-frugivore interactions: Predicting the effects of extinctions in the Atlantic forest of south-eastern Brazil.		
12:15 – 12:40	Ronda Green Application of frugivory theory to conservation: an Australian perspective.		
12:40 - 13:05	<b>S. Joseph Wright</b> The impact of hunters on seed dispersal in a tropical forest.		
13:05 – 14:25	Lunch		

SESSION C: SYMPOSIUM ON FRAGMENTED LANDSCAPES

(Northern Theatre 1; Organiser: Cath Moran)

- 14:25 14:30..... Cath Moran Welcome and introduction.
- 14:30 14:45..... Alexine Keuroghlian, Donald P. Eaton, Arnaud Desbiez
   Potential extinction of key frugivores in habitat fragments: The importance of fruit availability and diversity trends in different neotropical ecosystems.
- 14:45 15:00......**Norbert J. Cordeiro** Forest fragmentation affects mixed species foraging flocks: An hypothesis on implications for seed dispersal.
- 15:00 15:15..... Cath Moran, Carla P. Catterall and Ronda J. Green Differences between frugivores in diet selection have implications for seed dispersal in a fragmented subtropical rainforest landscape of eastern Australia.
- 15:30 16:15..... Afternoon Tea
- 16:15 16:30..... Jennifer M. Cramer, Rita Mesquita and G. Bruce Williamson Differential effects of forest fragmentation on seed disperal of two rainforest trees.
- 16:30 16:45.....**Nina Farwig, Bärbel Bleher and Katrin Böhning-Gaese** Consequences of forest fragmentation on seed dispersal and population genetic structure of Prunus africana in Kenya.
- 16:45 17:00...... **Jacqueline Weir** Patterns of seed dispersal by birds in the degraded upland landscape of Hong Kong, China.
- 17:00 17:15..... Angel Y. Y. Au Patterns of seed deposition in the degraded upland landscape of Hong Kong, China.
- 17:15 17:30..... Cath Moran General discussion.
- 19:00..... Conference Dinner

#### Thursday 14 July 2005

#### SESSION D (CONCURRENT WITH SESSION F): DISPERSAL AND PLANT COMMUNITY COMPOSITION (Northern Theatre 1; Chair: David Westcott)

08:30 - 08:45..... Jessie Wells, Andrew Lowe, Andrew J. Dennis, David A. Westcott and Matt Bradford Seed dispersal and natural regeneration of secondary rainforests in the Wet Tropics. 08:45 - 09:00......Natalia Norden, Jérôme Chave, Pierre Belbenoit, Adeline **Caubère, Patrick Châtelet and Pierre-Michel Forget** Spatial patterns of seed rain in a pristine rainforest in French Guiana: How far are frugivores responsible of seed shadow? 09:00 – 09:15..... Matthew J. Ward and David C. Paton Local movement patterns of the mistletoebird. Dicaeum Hirundinaceum: Implications for mistletoe seed shadow. 09:15 – 09:30..... Glen Hoye Kamakazi flying foxes and their potential role in shaping the biota of remote islands. 09:30 – 09:45..... Orr Spiegel and Ran Nathan Dispersal effectiveness as a function of spatial scale in a fleshy fruited desert plant dispersed by two avian frugivores. 09:45 - 10:00..... Kara L. Lefevre and F. Helen Rodd Does human disturbance of tropical rainforest influence fruit removal by birds? 10:00 - 10:15..... Alon Lotan and Ido Izhaki The impact of environmental conditions on fruit nutritional value of a desert plant (Ochradenus baccatus). SESSION F (CONCURRENT WITH SESSION D): FRUGIVORE COMMUNITY COMPOSITION (Macrossan N16 03; Chair: Eugene Schupp) 08:30 – 08:45..... **Palitha** Jayasekara, Udayani Rose Weerasinghe, Siril Wijesundara and Seiki Takatsuki Variation in space and time of fruit use by birds and mammals in Sinharaja tropical rain forest in Sri Lanka. 08:45 – 09:00..... Wangworn Sankamethawee and George A. Gale

Frugivory and seed dispersal of evergreen forest vegetation, eastern Thailand.

09:00 - 09:15	Johanna Choo and Edmund Stiles	
	A field-based comparison of avian frugivory in Sarawak and the Peruvian Amazon: Is there really less fruit available for frugivorous hirds in the Asian transfer approach to the Nectronics?	
	birds in the Asian-tropics compared to the Neotropics?	
09:15 - 09:30	Ruhyat Partasasmita and Keisuke Ueda	
	The role of frugivorous birds as seed dispersal agents in a tropical	
	shrubland of Java, Indonesia.	
09:30 - 09:45	Dave Kelly, Alastair W. Robertson, Jenny J. Ladley, and Sandra	
	H. Anderson	
	Is dispersal easier than pollination? New Zealand as a test case.	
09:45 – 10:00	Camila Iotte Donatti and Mauro Galetti	
	Consequences of defaunation on seed dispersal, seed predation and	
	seedlings recruitment of the brejaúva palm (Astrocaryum	
	aculeatissimum) in the Atlantic Forest.	
10:15 – 11:00	Morning Tea	
	SESSION E (CONCURRENT WITH SESSION G):	
	FRUGIVORE STUDIES	
	(Northern Theatre I; Chair: Andrew Dennis)	
11:00 – 11:15	Alfredo Valido and Jens M. Olesen	
	Importance of lizard as seed dispersers.	
11:15 – 11:30	Daniel Bennett	
	Diet of a giant frugivorous monitor lizard (Varanus olivaceus) in the	
	Philippines and implications for the dispersal of pandanus seeds.	
11.30 - 11.45	Jane Marshall, Adrienne Markey and Janice M. Lord	
1100 1110	Further studies on the possible influence of lizard frugivory on the	
	evolution of fruit colour within the New Zealand flora.	
11.45 - 12.00	Thomas R. Engel	
11.10 12.00	Long-term latrine use by Viverrids and Herpestids: Dispersal theory	
	and its application on vanishing forests.	
12.00 - 12.15	Iuliet Vanitharani and V. Chelladurai	
12.00 12.13	Latidens salimalii (Salim Ali's fruit bat): A reliable seed disperser of	
	southern Western Ghats; India.	
12.15 12.20	Maria T. Murphy, Mark I. Carkeklig and Ciles F. St. I. Handy	
12.13 - 12.30	Seed-caching by the woylie ( <i>Rettongia penicillata</i> ) improves	
	recruitment and regeneration of sandalwood (Santalum spicatim) in	
	Western Australia.	

#### SESSION G (CONCURRENT WITH SESSION E): FRUIT CHARACTERS AND FRUIT-FRUGIVORE INTERACTIONS

(Macrossan N16 03; Chair: Ronda Green)

11:00 – 11:15	<b>Shernice Soobramoney and Colleen T. Downs</b> Lipid-rich versus sugar-rich fruits: effects on digestive efficiency and food choice of the redwinged starling <i>Onychognathus morio</i> .
11:15 – 11:30	Ella Tsahar, Carlos Martínez del Rio, Ido Izhaki and Zeev Arad Can birds be ammonotelic? Nitrogen balance and excretion in fruit and nectar eating birds.
11:30 – 11:45	. H. Martin Schaefer and Veronika Schaefer Fruit colours as signals to seed dispersers.
11:45 – 12:00	. <b>Keisuke Ueda and Hirosi Arima</b> Inconspicuous dry fruits dispersed by resident birds in Japan.
12:00 – 12:15	. Kevin C. Burns Ecological drift predicts fruit-frugivore interactions in a temperate rainforest.
12:15 – 12:30	. <b>Tatyana A. Lobova and Scott A. Mori</b> 'Bat-fruit Syndrome': Myths and reality in the neotropics.
12:30 - 13:40	. Lunch
	SESSION H: THE EFFECTS OF FRUGIVORE GUT RETENTION ON SEEDS (Northern Theatre 1: Chair: Katrin Bohning-Gaese)
12:45 14:00	SESSION H: THE EFFECTS OF FRUGIVORE GUT RETENTION ON SEEDS (Northern Theatre 1; Chair: Katrin Bohning-Gaese)
13:45 – 14:00	SESSION H: THE EFFECTS OF FRUGIVORE GUT RETENTION ON SEEDS (Northern Theatre 1; Chair: Katrin Bohning-Gaese) Alastair W Robertson, Amy P. Trass, Jenny J. Ladley and Dave Kelly Assessing the benefits of frugivory for seed germination: Barking up the wrong tree?
13:45 – 14:00 14:00 – 14:15	<ul> <li>SESSION H: THE EFFECTS OF FRUGIVORE GUT RETENTION ON SEEDS (Northern Theatre 1; Chair: Katrin Bohning-Gaese)</li> <li>Alastair W Robertson, Amy P. Trass, Jenny J. Ladley and Dave Kelly Assessing the benefits of frugivory for seed germination: Barking up the wrong tree?</li> <li>Nicole D. Gross-Camp Monitoring chimpanzee seed dispersal: Temporal aspects of seed persistence and germination.</li> </ul>
13:45 – 14:00 14:00 – 14:15 14:15 – 14:30	<ul> <li>SESSION H: THE EFFECTS OF FRUGIVORE GUT RETENTION ON SEEDS (Northern Theatre 1; Chair: Katrin Bohning-Gaese)</li> <li>Alastair W Robertson, Amy P. Trass, Jenny J. Ladley and Dave Kelly Assessing the benefits of frugivory for seed germination: Barking up the wrong tree?</li> <li>Nicole D. Gross-Camp Monitoring chimpanzee seed dispersal: Temporal aspects of seed persistence and germination.</li> <li>Soumya Prasad, Jagdish Krishnaswamy and Ravi Chellam Dispersal of seeds that ruminants regurgitate: <i>Phyllanthus emblica</i> Linn. (Euphorbiaceae) at Rajaji National Park, India.</li> </ul>

#### SESSION I: SYMPOSIUM ON INVASIVE PLANTS

(Northern Theatre 1; Organiser: Yvonne M. Buckley)

15:10 – 15:15..... **Yvonne M. Buckley** Welcome and introduction. 15:15 – 15:30..... Richard T. Corlett Interactions between exotic plants and native frugivores in Hong Kong, China. 15:30 – 15:45..... Carl Gosper and Gabrielle Vivian-Smith Weeds and figbirds – dietary importance and dispersal in Brisbane. 15:45 – 16:00.....Sandra Anderson, S. Heiss-Dunlop and J. Flohr A moving feast: bird dispersal of weeds into conservation areas. 16:00 – 16:15..... David A. Westcott and Andrew J. Dennis Can we predict dispersal characteristics of invaders before they invade? 16:15 – 16:30...... Melissa Setter, Matt Bradford, Bill Dorney, Ben Lynes, Jim Mitchell, Stephen Setter and David A. Westcott Animal dispersal of pond apple, a weed of tropical Australian wetlands. 16:30 - 16:45..... Gabrielle Vivian-Smith, Carl R. Gosper, Anita Wilson and Kate Hoad The fruit- and seed-damaging fly, Ophiomyia lantanae: Seed predator, recruitment promoter or dispersal disrupter of the invasive plant, Lantana camara? 16:45 – 17:00..... **Yvonne M. Buckley** Modelling the spread of invasive plants by frugivores. 17:00..... Announcements and Prize Presentations (prior to informal gathering at club)

#### Friday 15 July 2005

08.30 -	09.00	Announcements
00.50	07.00	

- 09:00 12:40...... WORKSHOP 1 Invasive Plants (Northern Theatre 1; Organiser: Yvonne M. Buckley)
- 09:00 12:40...... WORKSHOP 2 What are the Major Frugivory and Seed Dispersal Issues that can Best, or Perhaps Only, be Addressed by Large-scale, International Collaborative Research? (Macrossan N16 03; Organiser: Eugene Schupp)
- 10:00 11:00..... Morning Tea (available for delegates)
- $12{:}40-14{:}00{\ldots}{\ldots}Lunch$
- 14:00 15:00..... Posters
- 15:00 17:30...... WORKSHOP 3 How do we Foster International Collaborative Research? (Macrossan N16 03; Organiser: Eugene Schupp)
- 15:30 16:00..... Afternoon Tea (available for delegates)

**Note to Delegates:** Other workshops and round tables will arise during the course of the conference. We will keep a notice board with the times and locations of new workshops at the Registration Desk and in Northern Theatre 1.

### ABSTRACTS IN ORDER OF PRESENTATION

#### Tomás A. Carlo<sup>1</sup>, Juan M. Morales<sup>2</sup> and Juliann E. Aukema<sup>3</sup>

#### COMPETITION, FACILITATION, AND CONTEXT-DEPENDENCE IN SEED-DISPERSAL

<sup>1</sup>Ecology and Evolutionary Biology Department, University of Colorado, USA <sup>2</sup>Ecology and Evolutionary Biology Department, University of Connecticut, USA <sup>3</sup>International Institute of Tropical Forestry, USDA Forest Service, USA (arlo@colorado.edu)

Understanding the web of ecological interactions that shapes the distribution of species is a primary goal of ecology, and seed-dispersal processes are believed to be fundamental to building and sustaining species diversity and spatial patterns in plant communities. Because frugivores disperse the seeds of many plant species, understanding plant communities requires an understanding of how frugivore dispersal patterns are affected by plant distribution, and vice versa.

Seed dispersal patterns may be affected by indirect interactions such as competition or facilitation at the scale of neighbourhoods when plant species share dispersal agents. We used simulation models, field experiments, and field studies to investigate how frugivores generated indirect plant-plant interactions. We found theoretical and empirical evidence that, for avian-dispersed plants, the rates of fruit-removal and shapes of seed shadows depend critically on ecological context. Factors like plant-frugivore ratios, plant aggregation patterns, and plant neighbourhood composition can dictate how many, how far, and where seeds are dispersed. Positive interactions involving indirect plant-plant facilitation can couple with directional seed-dispersal patterns and leave clear prints on plant species distributions while promoting the spatial linkage of species.

We suggest that understanding community patterns and dynamics of animal-dispersed plant populations must take into account the intricacies of frugivore-mediated interactions.

#### Héctor Godínez-Alvarez<sup>1</sup> and Pedro Jordano<sup>2</sup>

# SEED DISPERSAL BY FRUGIVORES: AN EMPIRICAL APPROACH TO ANALYZE THEIR DEMOGRAPHIC CONSEQUENCES

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 <sup>2</sup>Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Pabellón del Perú, Avda. María Luisa s/n, E-41013 Sevilla, Spain.

(hgodinez@campus.iztacala.unam.mx)

Seed dispersal is a key stage in the life cycle of plants because it contributes to the recruitment of new individuals to populations. Different studies have suggested that seed dispersal has important demographic consequences and its study is essential to completely understand the population dynamics of plants. However, no study at present has analyzed all stages of the seed dispersal process and determined its consequences by means of an explicitly demographic approach. Since successful seed dispersal is the outcome of a mutualistic interaction between animals and plants, it is expected that it has net positive effects on the populations of each participant species. Effects of seed dispersal should ideally be reflected as increases or, at least, as the maintenance of the population growth rate of animals and plants. Thus, this requires an understanding of frugivore effects beyond fruit removal. In this work, we discuss some ideas about how to integrate studies of seed dispersal by frugivores with plant demographic studies, as a possible way of understanding the effects of seed dispersal on the population growth rate of plants.

#### Helene C. Muller-Landau<sup>1</sup> and Frederick R. Adler<sup>2</sup>

## HOW DISPERSAL AFFECTS INTERACTIONS WITH NATURAL ENEMIES AND THEIR CONTRIBUTION TO DIVERSITY MAINTENANCE

<sup>1</sup>University of Minnesota and <sup>2</sup>University of Utah, USA (hmuller@umn.edu)

Seed dispersal helps offspring escape specialized natural enemies concentrated around their parents. Thus, seed dispersal influences the effects of natural enemies on recruitment rates and the density-dependence of these effects at different spatial scales. Although this link has long been recognized, the roles of dispersal patterns in determining the strength of density-dependence and the associated contribution to diversity-maintenance remain little explored.

We use models parameterized with empirical data to investigate how the patterns of seed dispersal and natural enemy dispersal influence the rate and density-dependence of depredation by natural enemies at different scales, and thereby affect population regulation and community diversity. We find that the effects of seed dispersal distances depend on natural enemy dispersal distances. When natural enemies disperse short distances, longer seed dispersal distances result in stronger density-dependence, stricter population regulation, and higher diversity even though overall predation rates by natural enemies are lower than under short seed dispersal distances.

In contrast, when natural enemies disperse long distances, diversity is highest for short seed dispersal distances. We also find that the quantities traditionally measured in empirical studies of Janzen-Connell effects are not well-correlated with the strength of the associated contribution to diversity maintenance. We demonstrate that this contribution can instead be quantified from empirical seed dispersal, enemy dispersal and enemy attack functions. Finally, we use these methods to explore how changes in seed dispersal due to hunting and fragmentation are likely to affect the diversity-maintaining impact of interactions with natural enemies

#### Charles Kwit., D. Levey, C. Clark, and J. Poulsen

#### OUT OF ONE SHADOW AND INTO ANOTHER: CAUSES AND CONSEQUENCES OF SPATIALLY CONTAGIOUS SEED DISPERSAL BY FRUGIVORES

Savannah River Ecology Laboratory, Savannah River Site, Bldg. 737-A, Aiken SC 29808, USA (kwit@srel.edu)

Two population-level processes link seed dispersal to the maintenance of species richness:

- 1. seed rain by vertebrate frugivores generates a leptokurtic distribution of seeds relative to their source; and
- 2. seed mortality is density-dependent.

The spatial distribution and species richness of trees has been viewed as a result of how these processes interact. Quantifying the first is difficult, whereas quantifying and experimentally testing the second is relatively easy. Hence, most attention has focused on the second.

We argue that many patterns of seed rain and their relationship to density-dependent mortality are generally unexplored and may have important community-level consequences. We focus on contagious seed dispersal – in particular, dispersal beneath heterospecific fruiting trees – and explain how it may alter opportunities for maintenance of species richness when seed predators and pathogens are generalists. First, we outline situations in which contagious seed dispersal is most likely by emphasizing that overlapping fruiting phenologies and dietary mixing of fruits by frugivores are key. Next, we construct a heuristic model to predict the population- and community-level consequences of contagious dispersal. We suggest that the outcome of contagious dispersal may differ along the temperate to tropical latitudinal gradient. Finally, we emphasize the importance of tackling neglected assumptions of the Janzen-Connell hypothesis in the context of contagious dispersal, and outline potential approaches towards that end.

#### **Eugene W. Schupp**

# WHAT IS A SUITABLE SITE, OR, WHERE DOES A SEED REALLY WANT TO LAND?

Department of Forest, Range and Wildlife Sciences, Utah State University, Logan UT 84322-5230, USA (schupp@cc.usu.edu)

In this talk I will very briefly give an overview of the original concept of the 'safe site' and the misuse the term has received for decades. I will then discuss in more detail two more recent concepts, (1) Facilitation, and (2) Life History Conflicts, in the context of understanding how we determine the best sites for seeds to be dispersed to.

Facilitation in this context refers to cases where existing plants benefit new plant establishment by, for example, ameliorating physical stress. The existing plant can, however, simultaneously interfere with the establishment of new plants through competition – the result we see as the net effect in the interaction is the effect that is strongest. With simultaneous positive and negative effects, theory suggests that with increasing stress the net effect can switch from a net negative effect to a net positive effect as the benefits of facilitation increase relative to the detriments of competition. Thus, an existing plant may have a net positive effect in some years and some places but a net negative effect in other years and other places.

Life History Conflicts refers to situations where environmental conditions suitable for some life history stages (e.g. seed survival) may be unsuitable for other stages (e.g. seedling growth and survival). In this context, the net suitability of a site for new plant establishment is the sum of the benefits and detriments associated with that site across life history stages. As with facilitation, the suitability of a given 'type' of site (e.g. beneath a shrub) can vary from year-to-year and from place-to-place with changes in precipitation, temperature, seed predator abundances, pathogens, etc. Thus, both of these concepts tell us that determining the suitability of a site from the perspective of seed dispersal may be more complex than we have tended to assume in that the suitability is likely to be highly context dependent.

#### Tad C. Theimer and Catherine A. Gehring

#### TERRESTRIAL VERTEBRATES, TREE SEEDLINGS AND MYCORRHIZAL SPORES: WHEN AND HOW WILL TERRESTRIAL VERTEBRATES AFFECT SURVIVAL, DISPERSAL AND RICHNESS?

Department of Biological Sciences, Box 5640, Northern Arizona University, Flagstaff AZ 86011, USA (Tad.Theimer@nau.edu)

Terrestrial vertebrates impact plant communities by acting as seed dispersers, seed predators, seedling herbivores and as vectors of mycorrhizal spores. The effects of vertebrates are most often determined through studies of interacting subsets of the community, while community-level tests of vertebrate impacts are rarer.

We excluded terrestrial vertebrates from fourteen small plots of Australian tropical rainforest and monitored the response of the tree seedling and mycorrhizal spore communities. Five years of excluding terrestrial vertebrates resulted in significantly higher seedling recruitment, survival, richness and diversity. These patterns for seedlings contrasted with those of mycorrhizal spores, where vertebrate exclusion reduced spore abundance and diversity. We developed a simple conceptual model that indicated that when vertebrates act primarily as agents of seed/spore dispersal, as they do for mycorrhizal spores in our system, they increase local species richness by increasing the rate of local colonization. When vertebrates act primarily as agents of random mortality, as they do for seeds and seedlings in our system, they increase the rate of local extinction and act to depress local species richness. In the latter case, vertebrates increase recruitment limitation and could potentially maintain diversity on larger spatial scales, although this was not the case in our system. Finally, we contrast the role of terrestrial vertebrates in seed/seedling / mycorrhizal spore dynamics in moderately diverse, arbuscular mycorrhizal tropical forests, like those at our Australian site, with ongoing work in temperate North America in a forest dominated by a single ectomycorrhizal pine species.

#### Rachel E. Gallery<sup>1</sup>, James W. Dalling<sup>1</sup>, Lindsay K. Higgins<sup>2</sup> and A. Elizabeth Arnold<sup>2,3</sup>

# ROLE OF SEED-INFECTING FUNGI IN THE RECRUITMENT LIMITATION OF NEOTROPICAL PIONEER SPECIES

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Community-wide dispersal limitation has been proposed as an important mechanism influencing patterns of tree regeneration, and potentially mediating species coexistence in tropical forests. For light-demanding tree species, recruitment can occur when seeds are dispersed in space to pre-existing gap sites, or may arise through 'dispersal in time' requiring seeds to persist in the soil seed bank. Among pioneer species of Barro Colorado Island, Panama, seed persistence varies from a few months to several decades. Here we describe the role of fungi in limiting the survival of species with short-term seed persistence through a case study of four sympatric Cecropia species: C. insignis, C. peltata, C. obtusifoli and C. longipes (Urticaceae). Fresh seeds of these species were surface-sterilized and then buried in common sites below C. insignis trees for five months, before being germinated in a growing house. Overall, seed survivorship varied significantly among burial sites and among species, with higher survivorship for C. longipes. After the germination period, intact seeds were incubated on 2% MEA and fungi appearing in culture were sequenced at the nuclear ribosomal internal transcribed spacer region (nrITS). Seeds were infected by a highly diverse assemblage of ascomycota and basidiomycota with known affinities to endophytes, saprophytes, and pathogens. We discuss the potential for host affinity among seed infecting fungi to influence the survival and distribution of *Cecropia* species.

#### Sabrina E. Russo<sup>1</sup>, S. J. Davies<sup>1</sup> and S. Tan<sup>2</sup>

# THE INFLUENCE OF DISPERSAL MODE AND SEED SIZE ON SOIL SPECIALIZATION OF TREE SPECIES IN A BORNEAN RAIN FOREST

 <sup>1</sup>Center for Tropical Forest Science – Arnold Arboretum Asia Program, Harvard University, 22 Divinity Avenue, Cambridge MA 02138, USA
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Distributions of plant species often correlate with environmental variation, suggesting that ecological sorting of species based on specialization on different habitats influences plant community structure. From an evolutionary perspective, specialization to the local environment may depend on seed dispersal mode and seed size by influencing gene flow between populations. Ecologically, seed-size-mediated trade-offs among seedling establishment ability, fecundity, and arrival may vary among dispersal modes and environments, causing differences in species composition and abundance among habitats.

In a 52 hectare forest dynamics plot in Bornean rainforest, four soil types varying in fertility and moisture have been identified. Species composition within the plot varies significantly among these soils because of strong edaphic biases in species distributions. We quantified variation in dispersal mode and seed size among soils and tested the hypothesis that both the probability of specialization and the soil type on which a species specializes depends on dispersal mode and seed size. We predicted that vertebrate-dispersed and larger-seeded species would less likely be specialists because vertebrates often generate long-tailed dispersal curves, greater seed resources may increase seedling establishment in different environments, and dispersing large seeds into unfavorable habitats may be costly. In contrast, species with more limited dispersal (e.g. members of Dipterocarpaceae, which dominate this forest) would more likely be soil specialists. Given that a species is a specialist, smallerseeded species should specialize on richer soils, whereas larger-seeded specialists should be equally represented among soil types. These analyses are discussed in light of phylogenetic niche conservatism and beta diversity in this forest.
#### **Ran Nathan**

#### NEW PERSPECTIVES ON LONG-DISTANCE SEED DISPERSAL

Movement Ecology Laboratory, Department of Evolution, Systematics and Ecology, Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Edmond J. Safra Campus at Givat Ram, 91904 Jerusalem, Israel (mathan@cc.huji.ac.il)

Interest in dispersal has risen rapidly over the last fifteen years with, in particular, a recent disproportionate increase in interest in long-distance dispersal (LDD).

LDD plays a leading role in determining population spread and colonization success, and can drastically alter the genetic and demographic structure of populations, metapopulations and communities. LDD is thus a key component to processes such as biological invasions, transgene escape, connectivity in fragmented landscapes and range shifts following climate changes. The disproportionate importance of the typically rare and highly stochastic LDD events provides a strong motivation to cope with the inherent challenges associated with defining, understanding, quantifying and predicting LDD. The aim of this review is to highlight recent advances in studying LDD of seeds by various dispersal agents, and to discuss potential avenues for further research. Significant progress has been made chiefly along the following directions: mechanistic modelling of LDD, especially by wind; implementation of genetic methods for quantifying LDD and assessing its impact on population genetics; identification of multiple agents of dispersal and disentanglement of the specific role of particular vectors; and incorporation of realistic dispersal kernels, scale-dependency and landscape heterogeneity in models evaluating the consequences of LDD.

Direct empirical measurement of LDD by all types of dispersal vectors, mechanistic modelling of animal-mediated dispersal and quantification of establishment and survival probabilities following LDD events remain major unresolved challenges in LDD research.

#### **Robert Kooyman and Maurizio Rossetto**

#### THE IMPACT OF DISPERSAL ON GENETIC STRUCTURE AND SPECIES DISTRIBUTION: EXPERIMENTAL STUDIES FROM NORTHERN NEW SOUTH WALES

National Herbarium of New South Wales, Botanic Gardens Trust, Mrs Macquaries Road, Sydney NSW 2000, Australia (robert.kooyman@rbgsyd.nsw.gov.au)

The naturally fragmented distribution of Australian rainforests and the complex evolutionary history of the continents' plant biodiversity provide a unique opportunity to explore some of the factors impacting on gene flow and species distribution.

Extensive molecular-based population dynamic studies across a range of tree species have shown that related taxa occupying similar habitat can exhibit significant differences in genetic structure and distribution. Variation in genetic diversity can be measured at the population, regional and whole species levels and are consistent with patterns ascribable to different fruit/seed sizes and dispersal mechanisms. To confirm such causal effects, complementary *insitu* experimentation and observation, and fine-scale spatial autocorrelation analyses of molecular data were conducted. These confirmed that differences in fruit/seed movement explained the variation in genetic structure among a range of rainforest trees. To further investigate the importance of dispersal on species distribution, correlations between a range of life-history traits and species distributions were assessed across 258 taxa. The results of these analyses demonstrate the influence of fruit/seed characters as components of a larger trait dimension including dispersal on plant species' distributions and population structure(s).

# Friederike A. Voigt<sup>1</sup>, R. Arafeh<sup>2</sup>, E. M. Griebeler<sup>1</sup> and K. Böhning-Gaese<sup>1</sup>

# DOES SEED DISPERSAL MATTER? COMPARATIVE POPULATION GENETICS OF TWO CONGENERIC TROPICAL TREES

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The genetic structure of plant populations is influenced strongly by pollination and seed dispersal, the two vectors for gene flow. Previous studies on a Malagasy and a South African *Commiphora* species revealed that both tree species have similar pollination ecology, but the Malagasy *C. guillauminii* has a much lower seed dispersal rate than the South African *C. harveyi*.

We hypothesized that the lower seed dispersal rate may cause decreased gene flow, resulting in a stronger genetic structuring among the Malagasy than the South African populations. We used AFLP markers to investigate the population genetics of 136 Malagasy and 158 South African *Commiphora* trees. Unexpectedly, the overall genetic differentiation was lower in the Malagasy ( $F_{ST} = 0.05$ ) than in the South African species ( $F_{ST} = 0.16$ ). Nevertheless, the hierarchical F-statistics revealed that most of the inter-population variance in the Malagasy species was between populations within sample sites (72.7–85.5%) whereas in the South African species only a low amount of the genetic differentiation between populations within sample sites (8.4–14.5%) was revealed. This pattern could be caused by low gene flow in Madagascar and high gene flow in South Africa at the scale of populations within sample sites. Spatial autocorrelation analyses suggest that gene flow was restricted mostly to three kilometres in the Malagasy species and to thirty kilometres in the South African species corresponding to the field data on seed dispersal. Thus, seed dispersal seems to be a key factor for the genetic population structure of trees on the local scale.

#### **Carmen Castor**

#### THE FORGOTTEN ONES: SEEDS THAT HAVE NO DISPERSAL SYNDROME. SECONDARY SEED DISPERSAL IN A HIGH MOUNTAIN COMMUNITY

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Alpine plants are exposed to high levels of stress and perturbation. Under these circumstances at the level of vegetation regeneration processes, two seed dispersal strategies are predicted: low dispersal allowing species to exploit a known and less stressful environment close to the mother plant; and long distance dispersal which would permit the exploitation of newly generated sites.

On a South American site, 42% of species disperse by wind (*W*) while 42% lack morphological adaptations for dispersal (NDS). Only 4% are fleshy fruits. When comparing alpine dispersal spectra, differences are attributable to site related effects and growth form. Asteraceae seeds moving over the soil show that NDS do not move relative to *W*. Within a selection of other NDS seeds, morphological characters can explain absence of movement down-slope through incorporation into the soil. Upon extrapolating results to a sub sample of the Andean community (51 species) 75% would be expected to avoid down-slope movement through incorporation of seeds into the soil. Germination phenology can also explain absence of down-slope movement. Persistence in perturbed alpine ecosystems of plants with NDS can be explained by the capacity of seeds to avoid being washed down-hill.

Given the low dispersablity of many seeds in this Andean ecosystem, the question remains of how they came to be there at all. The way we see dispersal of seeds may actually be more complex to the point of using the 'chance dispersal' notion to explain unaccountable colonisation of sites far away from sources. Time scale of observation is also crucial.

#### Debra M. Wotton, Dave Nelly and J. J. Ladley

# HOW IMPORTANT ARE 'KEYSTONE' DISPERSERS? PIGEONS AND LARGE SEEDS IN NEW ZEALAND

School of Biological Sciences, University of Canterbury, New Zealand (dmw61@student.canterbury.ac.nz)

Following the arrival of humans in New Zealand, a number of large frugivorous birds were driven to extinction. At least five large-seeded species now depend almost entirely on the threatened New Zealand pigeon (kereru, *Hemiphaga novaeseelandiae*) for seed dispersal. Or do they?

We show that there are potential replacement dispersers for large-seeded fruits. Fruit size varies considerably within a plant species. Fruit diameter decreases with increasing latitude in contrast to bird size, which increases. Smaller birds than kereru may be able to disperse smaller fruits within a large-seeded species. Plant fitness may or may not be affected if only small seeds are dispersed. In addition, the consequences of any loss of disperser service for plant populations and communities are uncertain. Some species may be buffered from extinction by traits including vegetative reproduction, persistent seed banks, or storage structures. The effects of dispersal disruptions may also not become evident for a long time, especially in long-lived trees.

#### **Don Butler**

# WHAT CAN FRUIT MORPHOLOGY TELL US ABOUT SPECIES ABUNDANCE AT REGIONAL SCALES?

Department of Botany, The University of Queensland, and Queensland Herbarium, Australia (don.butler@epa.qld.gov.au)

Fruit morphology intuitively offers insights into the mobility of plant species. For example, peoples' perceptions of a given species behaviour in landscapes tends to be coloured by whether its fruit is attractive to animals, or if its seeds have wings or plumes that can be blown by the wind. We expect that plants with animal-attracting diaspores will be moved about landscapes better than wind-dispersed species, and that plant species with either fleshy fruit or adaptations for wind dispersal will be more vagile than species with little or no obvious adaptations for seed dispersal. However, associations of seed dispersal syndromes with other aspects of plant morphology, such as plant stature and seed size, mean that seed dispersal syndromes are part of a broader suite of characters, involving complex trade-offs across the phenotype.

This paper briefly outlines associations of broad seed dispersal syndromes, based on fruit morphology, with other plant species attributes in the rainforest flora of southern Queensland. The regional abundance of plant species (measured as frequency in habitat patches) is then considered in relation to species attributes. This enables evaluation of the reliability of intuitive expectations that in patchy habitats such as the rainforests of southern Queensland, species with adaptations for dispersal, such as fleshy fruit, should tend to occur in more habitat patches than species with intuitively less dispersive fruit or seeds. Although there is some evidence supporting this intuitive expectation, association of fruit morphology with regional abundance is complex and depends among other things on the type of habitat examined.

K. Greg Murray<sup>1</sup>, Mauricio Garcia-C. <sup>1</sup>, Joseph W. Veldman<sup>1</sup>, William S. Mungall<sup>2</sup>, Garth B. Rotman<sup>2</sup> and Adrienne L. Hull<sup>1</sup>

#### PIONEER SEEDS IN NEOTROPICAL CLOUD FOREST SOILS: PATTERNS OF MORTALITY, CHEMICAL DEFENSES, AND CONSEQUENCES FOR PERSISTENCE IN AN UNPREDICTABLE ENVIRONMENT.

<sup>1</sup>Department of Biology, Hope College, Holland MI 49423, USA <sup>2</sup>Department of Chemistry, Hope College, Holland MI 49423, USA (gmurray@hope.edu)

As part of a long-term study at Monteverde, Costa Rica, we have measured seed mortality in six cloud forest pioneer plant species since 1993. Using replicated exclusion experiments in the field, we separately estimated rates of mortality associated with macroscopic predators, pathogenic microbes, and reaching the intrinsic limits of viability.

Mortality rates attributable to different agents vary widely among the six plant species; seeds of some species are primarily removed by predators, others are killed mostly *in situ* by microbes, and one species rarely survives more than a year even when protected from both predators and pathogens. Using rates associated with different sources of mortality, we derived composite survivorship functions that correlate strongly with patterns of seed accumulation in the soil. We then used bioassays to assess the toxicity of methanol extracts from each species' seeds to arthropods and microbes. Species with greatest toxicity in bioassays were those that persist longest in the soil, suggesting that differences in longevity are due largely to differences in chemical defense. Using bioassay-directed fractionations of extracts from the most toxic species, *Bocconia frutescens*, we have identified the chemicals toxic to arthropods as dihydrosanguinarine, dihydrochelirubine and dihydrochelerthrine. These alkaloids are found in *Bocconia* seeds at much higher concentrations (~50 mg/g seed material) than in leaves, and are likely responsible for the exceptional longevity of *Bocconia* seeds in the soil. We are currently using a similar approach to identify the compounds in *Bocconia* and other species that are toxic to fungi.

# Huiping Zhou1<sup>1,2</sup>, Jin Chen<sup>1</sup> and Fan Chen<sup>1</sup>

#### DOES ANT-MEDIATED SEED DISPERSAL ALTER SPATIAL PATTERN AND SPATIAL GENETIC STRUCTURE OF GLOBBA LANCANGENSIS (ZINGIBERACEAE)?

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Ant-mediated seed dispersal often occurs over short distances. The extent to which antdispersal can change the seedling spatial pattern and population spatial genetic structure (SGS) is still under discussion.

In this study, *Globba lancangensis*, a bee-pollinated, myrmecochorous perennial herb, was selected to address this question. The study included: 1) intensive field observation of the disperser ant species and the distance seeds were transported; 2) a comparative study of a spatial array of plots that ants could access with plots from which ants were artificially excluded for one year; and 3) SGS of the two kinds of plots was described using inter-simple sequence repeats (ISSRs). There were fourteen ant species involved in seed dispersal and their visitation frequency between the two years of observation was not significantly different. Ant mediated dispersal significantly reduced the aggregation of seedlings. High spatial genetic structuring was only found in distance classes four metres and eight to twelve metres, which was consistent with a gene flow pattern characterized by a limited seed flow mediated via ants. However, the SGS of the plots with ant visitation did not differ significantly from those without ants.

### Silvia Lomáscolo<sup>1</sup>, Pablo Speranza<sup>2</sup> and Rebecca Kimball<sup>1</sup>

# THE CORRELATED EVOLUTION OF FRUIT SIZE AND COLOR IN *FICUS* (MORACEAE) SUPPORTS THE DISPERSAL SYNDROME HYPOTHESIS

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The influence of seed dispersers in the evolution of fruiting plants has often been questioned in studies of fruit evolution. Most such studies, however, have failed to take into account the phylogenetic history of the plants under study, which may confound fruit variation due to common ancestry with adaptive variation. Studies have also used inefficient means of controlling phylogenetic history, such as focusing on conservative taxonomic levels; and have ignored traits that are important for fruit recognition by frugivores, such as fruit colour.

We test the hypothesis that fruit traits evolve in response to the selective pressure of seed dispersers. Under this hypothesis, we predict the existence of two dispersal syndromes, which we define as sets of fruit traits that appear together more often than expected by chance.

- 1. *Mammal Syndrome fruits* should be dull-coloured and large, because mammals are commonly nocturnal and rely more heavily on olfaction than on visual cues for finding fruits, and because they have teeth, allowing them to eat fruits piecemeal.
- 2. *Bird Syndrome fruits* should be brightly coloured and small, because birds are mostly diurnal and have acute colour vision, and because they lack teeth and commonly swallow fruits whole.

Likelihood ratio (likelihood ratio = 3.053; p-value = 0.044; 1006 simulations) and Correlated Changes (0.002 < p-value < 0.07, depending on parameter combinations) tests performed on a molecular phylogeny of 64 species of *Ficus* (Moraceae) support the existence of dispersal syndromes, and suggest that seed dispersers may be important in shaping fruit evolution.

# Pierre-Michel Forget<sup>1</sup>, Andrew J. Dennis<sup>2</sup>, Patrick A. Jansen<sup>3</sup>, Joanna A. Lambert<sup>4</sup> and David A. Westcott<sup>2</sup>

# SEED ALLOMETRY AND FRUGIVORE SIZE: CONFLICT BETWEEN SEED DISPERSAL PATTERNS IN TROPICAL RAINFORESTS

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Following the break up of Gondwana, ancient tropical plants and their seed-dispersing fauna began to evolve independently on different continental plates. While continental drift and other events have allowed some subsequent migration of taxa between continents, the relative isolation of the continents have supposedly allowed animals and plants the opportunity to co-evolve, and to do so on potentially differing trajectories on the different continents. The fruits of many plants are known to be adapted to transportation by present-day frugivores. However, discordances between plant traits and their current dispersers may occur after the extinction of ancestral dispersers and colonisation by new dispersers.

In this paper, we review and compare the allometry of seeds consumed or dispersed by different groups of seed dispersing animals. We do this for the rainforests of America, Africa, and Australia – three independent but formerly connected continents. A multi-partner model of relationships between primary and secondary seed dispersers is presented and discussed. We especially emphasize the effect of seed features such as size, roundness and mass on gut and handling constraints, thus determining whether seeds may be dispersed by transit through the gut, regurgitated and/or carried by small through to large frugivores. We also examine the patterns of allometry in species associated with secondary dispersal.

Ido Izhaki, Hagar Melamed-Tadmor, Natarajan Singaravelan, Ella Tsahar, Noam Cohen, Alon Lotan, Malka Halpern, Moshe Inbar and Gidi Ne'eman

# THE ROLE OF SECONDARY METABOLITES IN SHAPING AND MEDIATING POLLINATION AND SEED DISPERSAL.

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The original definition of chemical compounds as 'secondary' emerged from the notion that they are not absolutely essential to the survival and reproduction of the plant. A wealth of studies have focused on elucidating their role in deterring herbivory. However, secondary compounds are often present in floral and fruit tissues and thus may function in both mutualist and antagonist interactions. This talk will deal with the evolutionary ecology of two multispecies systems of plant-animal interactions: flower-nectarivore-nectar robbers and fruitfrugivore-seed predators.

Plants, in their natural environment, are often under simultaneous selective pressures exerted by several species, including mutualists such as pollinators and seed dispersers, and antagonists such as leaf herbivores, nectar robbers, seed predators and pathogens. Understanding these multispecies interactions is important because so many plants rely on nectarivores and frugivores to pollinate their flowers and disperse their seeds, and so many animals rely on nectar and fruits to meet nutritional requirements. A conceptual framework that has been developed in recent years suggests that in the evolutionary perspective, interactions between flowering plants and their nectar consumers (legitimate pollinators as well as nectar robbers) and between fruiting plants and fruit consumers (legitimate dispersers as well as pulp and seed predators) are mediated by nectar/fruit secondary metabolites. The aim of the talk is to summarize our recent empirical studies in Israel that examined the concept that constitutive and induced secondary metabolites in nectar and fruit play an adaptive role in one of the most critical evolutionary dilemmas of plants: How to make their nectar and/or fruit attractive to legitimate pollinators and/or seed dispersers while being unattractive to nectar robbers, seed predators, pests and pathogens.

#### Mauro Galetti, Camila Donatti, Marco A. Pizo, P. Guimarães Jr. and Pedro Jordano

# LIVING IN A WORLD OF GHOSTS: SEED DISPERSAL BY THE MEGAFAUNA IN THE PANTANAL OF BRASIL.

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One of the seed dispersal anachronisms, the so-called 'megafauna syndrome', has been the subject of considerable debate, much of it stemming from a lack of specific predictions and precise definitions. It is clear that many large-fruited species are poorly fitted to extant seed dispersers. South America was the land of large mammals until the end of the Pleistocene, less than ten thousand years ago. Giant sloths, horses, large armadillos and many other odd creatures certainly played a key role in determining the vegetation structure and in the evolution of fruit attributes.

In this talk, we present some key attributes of the fruits of the 'megafauna syndrome' and some preliminary results from a field study in the Pantanal of Brazil. The Pantanal is the largest wetland in the world (about a quarter of the area of Spain) and holds an anachronistic fruit community. We also present some new findings about how the megafauna fruits have survived without their dispersers and what the consequences of losing such mega-dispersers have been.

# Joshua Tewksbury<sup>1</sup> and Douglas Levey<sup>2</sup>

# FRUGIVORY AND FRUIT PHENOTYPES: INTEGRATION WITHIN AND ACROSS PLANT-ANIMAL INTERACTIONS.

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Virtually all plants interact with animals throughout their life-cycle, and most interact with a wide array of animals playing different functional roles – herbivores, pollinators, seed dispersers, granivores. The study of plant-animal interactions has largely followed these functional delineations, with the vast majority of studies examining only a single interaction. Typically, students of any one interaction are advocates for the importance of the particular interaction that they study. We argue that the ecological and evolutionary relevance of plant-animal interactions is far more complex for the vast majority of species, and that even within disciplines, researchers rarely attempt to integrate the various selective pressures bearing on the phenotype.

Generally lost in the focus on single types of interactions is the realization that one type of interaction may mediate or overwhelm the fitness impacts of other interactions. Drawing from our own research and the growing body of studies explicitly examining the interdependent nature of plant-animal interactions, we explore the consequences of these conditional effects on the evolution of fruit phenotypes, and the ecological consequences of fruit-frugivore relationships. We suggest that the lack of integration across phenotypic characters (fruit morphology, nutrition, chemistry) and the lack of attention to the mediating influences of other plant-animal interactions may be slowing progress in the study of fruit-frugivore relationships. We propose a framework for integrating the study of fruit-phenotypes and frugivory across phenotypic characters and different plant-animal interactions. Our approach focuses attention on whole-plant demography, and the tradeoffs imposed by complex selection on fruit characters.

# Andrew J. Dennis<sup>1,2</sup> and David A. Westcott<sup>1,2</sup>

### SEED DISPERSAL AT COMMUNITY AND LANDSCAPE SCALES: INCORPORATING FUNCTIONAL CLASSIFICATIONS OF DISPERSERS AND FRUIT INTO THE STUDY OF AN ECOLOGICAL PROCESS.

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The process of seed dispersal in tropical rainforests drives and maintains plant community structure and diversity. Understanding the process at community scales has been hampered by its complexity, which is derived from thousands of plant-animal interactions. To describe this process at community scales we have developed an approach that uses functional classifications of 1) seed dispersers that provide similar services, and 2) fruits that provide similar resources. Our classifications can be applied at a variety of scales and locations.

Seed dispersers were classified using measures of the quantity of fruit handled, the nature and quality of that handling, and the diversity of plants to which a service is provided. These three key themes provided a framework to measure 24 traits for 65 vertebrate seed dispersers. Our classification processes reduced 65 frugivores and granivores to 15 functional groups. For fruits, we created a qualitative classification on the basis of fruit characters important in disperser choice and handling and animal diets. We then tested this classification using multivariate analyses by making predictions about how each class of fruits is used by different seed dispersers and disperser functional groups. This process results in a set of 9 fruit classes representing ~1500 of Australia's tropical rainforest plants. The two classifications used in conjunction with our overall framework allow a community-wide estimation of dispersal services for understanding and modelling the outcomes of the dispersal process. They are also a useful tool for recognising the loss or decline in dispersal services when the distribution and abundance of animal populations change due to human impacts.

# David A. Westcott<sup>1,2</sup> and Andrew J. Dennis<sup>1,2</sup>

# WHERE DO ALL THE SEEDS GO? ESTIMATING THE DISPERSAL CURVES CREATED BY A COMMUNITY OF FRUGIVORES.

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Seed dispersal plays a crucial role in structuring plant populations and communities. Consequently, describing dispersal curves is important in understanding the scale and outcomes of their dynamics. Seed dispersal in tropical rainforests is predominantly an animal-vectored process. This has greatly complicated seed shadow estimation and meant that most published dispersal curves were produced by a small proportion of disperser species visiting the focal plant species.

In this paper, we describe the dispersal curves produced by the community of dispersers for plants in Australia's tropical rainforests. We do this for the fleshy-fruited plant community as a whole, as well as for specific fruit functional groups. To estimate dispersal curves both dispersers and fruits were assigned to functional groups (DFGs and FFGs respectively; see Dennis and Westcott, plenary paper abstract). Complete dispersal curves were estimated by identifying the dispersers visiting plants of each FFG and the DFGs they represent. We determined each FFG's passage rates through the guts of each DFG and combined this information with data on the movement patterns of each DFG to estimate the dispersal curve produced. The dispersal curves produced by each DFG were then combined to produce the complete seed shadow for FFGs and the community of fleshy-fruited plants as a whole. Our results indicate dispersal greater than one hundred metres will be a regular occurrence for many FFGs and within the community as a whole, while a small percentage of seeds will receive dispersal beyond one thousand metres. Maximum possible dispersal distances vary with the DFG but can be on the order of tens of kilometres.

#### **Pedro Jordano**

# FRUGIVORES, SEEDS AND GENES: ANALYSING THE KEY ELEMENTS OF A SEED SHADOW.

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A seed shadow is the primary outcome of plant-frugivore interactions, yet we know very little about how different frugivore species contribute to it. The interaction between frugivore foraging and the structure of complex landscapes generates peaks and downs in the seed shadow, which indicates hot spots and empty spots in plant recruitment.

Recent advances in field techniques (use of radioactive markers, radio tracking, etc.), molecular genetics tools (e.g. hypervariable simple-sequence DNA repeats- SSRs or microsatellites), and GIS-based techniques allow a thorough analysis of seed shadows. The deconstruction of a seed shadow involves two steps, 1) working from the source tree and proceeding away from it by determining dispersal distances, and inferring which frugivore species contribute the dispersal events (the 'seed shadow' analysis in strict sense); and b) working from the microhabitat patches where seeds arrive, and inferring which frugivore species contribute the seed rain and from where.

Fruiting trees are key elements in plant-frugivore interactions because they are the source of dispersed seeds, but they also shape the foraging movements of frugivores, are sinks for dispersed seeds and hot spots for pathogens and post-dispersal seed predators. From the microhabitat perspective, different frugivores contribute in different ways to the seed rain arriving at given patches, in terms of dispersal distance, proportion of long distance dispersal events, and the diversity of contributing mother trees. This may generate extensive variation in the makeup of the seed shadow. I examine these key elements of the Prunus mahaleb (Rosaceae) seed shadow, by combining field observations of frugivore foraging, genetic analyses of dispersed seeds to identify maternal trees and statistical models allowing robust estimates for the pattern and frequency of long-distance dispersal events. Even in highly diverse plant-frugivore interactions, specific frugivores may contribute a major fraction of the long-distance dispersal events, or may contribute disproportionately to the seed rain in hot spots for successful recruitment. Long-distance dispersal events, both within and between populations, are probably more frequent than previously thought, but it is not clear how they contribute to patterns of colonisation and gene flow. Its pervasive implications for the maintenance of fragmented populations and for the demographic and genetic makeup of plant populations in complex landscapes remain therefore poorly understood.

# Britta Denise Hardesty<sup>1,2</sup>, Stephen Hubbell<sup>1,2</sup> and Eldredge Bermingham<sup>2</sup>

#### GENETIC EVIDENCE THAT LONG DISTANCE SEEDLING RECRUITMENT IS COMMONPLACE IN A VERTEBRATE-DISPERSED NEOTROPICAL TREE.

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We used microsatellite genetic markers to match seedlings to their maternal and paternal parents in a natural population of the dioecious Neotropical tree, *Simarouba amara* (Simaroubaceae), in a forest in Panama. Our main objectives were to, 1) measure dispersal by calculating distances of successful seedling recruitment in this species, whose seeds are dispersed by vertebrate frugivores, and 2) to compare gene movement via seed and pollen.

In our study, recruitment includes seed dispersal, germination and subsequent seeding establishment. We were particularly interested in documenting the frequency of long-distance recruitment events, defined operationally as recruitment occurring >100m from the maternal parent. Seeds arriving  $\geq$ 50m (i.e. away from the canopy of the parent plant) have likely been moved there due to active dispersal by birds or primates and/or secondary dispersal by terrestrial dispersal agents. In our study, less than 10% of seedlings were produced by the nearest reproductive female and long distance dispersal was frequent. Seventy-four percent of matched seedlings were dispersed >100m. The mean dispersal distance for between established seedlings and their maternal parent was 348m (range 9.3-1005m). We also found that pair-wise seedling distances for half and full sibs generally exceeded 100m (median = 187.4m, mean =  $215.8m \pm 137.0$  SD, range = 0.81-801.6m) and sib distances were significantly different (P<0.0001, T-test) from nearest seedling distances for all 306 seedlings analyzed (median nearest seedling distance = 6.2m, mean = 11.3m, +15.8 SD, range = 0.34-132.8m). Gene movement via pollen was comparable to that of seed; averaging 373.2m (range 1.4-1005.8m). Our findings demonstrate that long distance seed dispersal events frequently result in seedling establishment and suggest that vertebrate frugivores play an important role as seed dispersers in this Neotropical tree.

#### **Kimberly M. Holbrook**

# SEED DISPERSAL IN AMAZONIA ECUADOR: TOUCAN-GENERATED SEED SHADOWS AND GENETIC BASED MODELS OF A NEOTROPICAL NUTMEG.

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Animal-mediated seed dispersal plays a significant role in plant recruitment and thus helps determine species composition of tropical forests. Although several hypotheses have been debated regarding the contribution of seed dispersal to tropical forest diversity, recent work suggests recruitment and dispersal limitation are major components in determining plant community dynamics.

To address dispersal limitation and the influence of seed dispersal on forest diversity, I estimate seed shadows generated by two species of toucans (*Pteroglossus pluricinctus* and *Ramphastos tucanus*) and the seed and seedling shadows of a Neotropical nutmeg, *Virola flexuosa*. This research was conducted in Amazonia Ecuador and is part of a larger study to test predictions of distance-restricted, quantitatively-restricted, and spatially-contagious seed dispersal. To estimate seed shadows from the frugivore perspective, I used radio-telemetry data combined with gut retention times to generate a probability model of the spatial distribution of seeds based only on toucan dispersal. Toucan-generated seed shadows indicate that 82% of *V. flexuosa* seeds are dispersed farther than one hundred meters from the parent tree. In addition, I use microsatellite markers to identify relatedness of seeds and seedlings to maternal trees of *V. flexuosa*. This will allow me to link a seed or seedling with the parent plant, thus providing exact dispersal distances. By using a combination of ecological and genetic methods, this paper contributes to our understanding of how vertebrate seed dispersal may influence the spatial distribution patterns of a Neotropical tree.

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#### DECIPHERING THE EFFECTS OF SCATTER-HOARDING MAMMALS ON DISPERSAL AND ESTABLISHMENT OF THE OAKS: INCONSISTENCIES BETWEEN SEED AND SEEDLING SHADOWS.

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To better understand the impact of dispersers on plant regeneration, forest structure and forest genetics, it is necessary to unravel patterns of both seed dispersal and seedling establishment. To do this, we measured both seed and seedling shadows of several oak species in eastern deciduous forests of North America that are dispersed primarily by mammalian dispersal agents (e.g. *Sciurus carolinensis, Peromyscus spp.* and *Tamias striatus*). Patterns of seed dispersal were determined by a series of behavioural and field experiments in which we followed the fate of metal-tagged seeds under various conditions. These studies provided clear evidence for a markedly different pattern of acorn dispersal between species of red oak (*RO*; subgenus Erythrobalanus) and white oak (*WO*; Quercus), due primarily to the differences in the physical and chemical characteristics of the acorns.

*RO* species were dispersed and cached at distances of ten to thirty metres from their source, while *WO* showed little or no dispersal, under a range of conditions. We tested whether this differential pattern of dispersal resulted in similar dispersion patterns of seedlings. Seedling shadows were estimated through DNA fingerprinting by amplifying polymorphic STRs for ten identified primer pairs and then identifying the closest potential parent to each seedling based on individual fingerprints (n = 260 seedlings and 105 parents). Results indicate direct measures of seed dispersal for *RO* species (using metal-tagged acorns) are comparable to estimates of parent-seedling distances. *WO* species (*Q. alba*), however, establish considerably farther from parents (thirty to forty metres) than predicted by any studies on seed dispersal (less than five metres). These results suggest that methodological limitations in measuring seed dispersal of *WO* may underestimate dispersal distances, and that rare long distance dispersal events, followed by high seedling mortality at shorter distances, may contribute to patterns of *WO* oak regeneration.

# John Kanowski<sup>1</sup>, Carla P. Catterall<sup>1</sup>, Grant Wardell-Johnson<sup>2</sup> and Terry Reis<sup>1</sup>

### FRUGIVORES AND PLANT RECRUITMENT IN DIFFERENT TYPES OF REFORESTATION IN CLEARED RAINFOREST LANDSCAPES OF TROPICAL AND SUBTROPICAL AUSTRALIA.

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There is increasing interest in the reforestation of cleared land in former rainforest landscapes. At present, little is known of the value of different forms of reforestation for wildlife, or the trajectory of succession on reforested sites. In this study, we surveyed plants and birds in a range of reforestation types in tropical and subtropical Australia. Sites included monoculture and mixed species timber plantations, diverse ecological restoration plantings and unmanaged regrowth, as well as reference sites (pasture and rainforest). Each treatment was represented by five to ten replicate sites in each region. Plants were classified by dispersal mode and seed size, and birds by seed dispersal potential.

Overall, there was a correspondence between, 1) the availability of fleshy fruited plants in reforested sites, 2) the abundance of frugivorous birds using those sites, and 3) the richness of fleshy-fruited plants recruited to those sites. Ecological restoration plantings and regrowth forests were generally dominated by fleshy-fruited plants, whereas timber plantations were dominated by wind-dispersed trees. Assemblages of frugivorous birds in all reforested sites tended to be dominated by small-gaped birds. However, large-gaped birds tended to be more abundant in ecological restoration plantings than timber plantations, especially monocultures. Correspondingly, most plants recruited to reforested sites were small-seeded species, and plants with medium and large diaspores were particularly uncommon recruits in timber plantations.

In summary, different types of reforestation vary widely in their capacity to 'catalyse' the recruitment of native forest. For conservation purposes, timber plantations could be made more attractive to frugivorous birds.

# Wendy Neilan<sup>1,2</sup>, Carla P. Catterall<sup>1,2</sup>, John Kanowski<sup>1,2</sup> and Stephen McKenna<sup>1,2</sup>

# FRUGIVOROUS BIRDS AND RAINFOREST REGENERATION IN CAMPHOR LAUREL-DOMINATED SUBTROPICAL REGROWTH.

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In recent years, regrowth dominated by the bird-dispersed exotic tree *Cinnamonum camphora* (camphor laurel) has spread rapidly across the landscape once occupied by rainforest in subtropical Australia. There is debate over the values of this weedy regrowth, including whether it may facilitate or hinder rainforest succession. The present study assessed the potential for rainforest regeneration in 24 patches of camphor laurel-dominated regrowth in the Big Scrub region of northeastern New South Wales.

Sites were stratified by distance from large rainforest remnants in the Nightcap Range. We conducted standardised surveys of frugivorous birds and floristic composition in each site. Overall, 34 frugivorous bird species were recorded, including a number of rainforest specialists. Medium to large-gaped (more than 10mm) birds that regularly consume fruits without destroying seeds were considered important dispersers of rainforest plants and were moderately abundant throughout the landscape. Over 110 species of potentially bird-dispersed rainforest plants were recorded with more recruitment of rainforest tree species closest to the Nightcap Range. While bird-dispersed exotic plants dominated the adult tree layer, there was no difference between the number of native and exotic tree species recruited to the sites. Comparisons between the composition of the adult tree layer and recruits suggested regeneration was largely facilitated by birds and was increasingly dominated by later successional species. Managing the succession of rainforest plants recruited to camphor laurel-dominated regrowth may be a more cost-effective alternative for restoring rainforest to the Big Scrub region than tree planting.

Louise A. Shilton<sup>1,2</sup>

### THE ROLE OF FRUIT BATS (*MEGACHIROPTERA, PTEROPODIDAE*) IN REBUILDING AND RECONNECTING THE TROPICAL FORESTS OF THE KRAKATAU ARCHIPELAGO, INDONESIA.

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Since a cataclysmic volcanic eruption in 1883, the Krakatau archipelago has represented a natural experiment for the rebuilding of rainforest communities after major disturbance. The arrival and establishment of plants and animals on these islands has been well-documented, but the role of pteropodid bats in introducing zoochorous plants has almost certainly been under-estimated, and their early arrival on these islands has been overlooked. During field studies between 1995 and 1997, I identified five pteropodid bat species as resident on the archipelago, and a sixth, the Large Malay Flying Fox, *Pteropus vampyrus*, as a visitor to the islands.

I present a reappraisal of their role as seed dispersers in the ecosystem succession on Krakatau, based on recent findings and reinterpretation of early records. I further indicate that pteropodids had a distinctive and critical role at an early stage in the establishment and succession of this tropical forest ecosystem, both in introducing small-seeded zoochores from mainland areas and also moving their seeds locally, within islands and between islands in the group. Today, foraging pteropodids create a diverse seed rain around focal fruiting trees and continue to play a role in connecting these forests with a distributed network of mainland and island forests.

#### **Zhishu Xiao and Zhibin Zhang**

# THE ROLE OF SCATTER-HOARDING RODENTS IN FOREST RESTORATION: A CASE STUDY IN RODENT-DISPERSED OIL TEA *CAMELLIA OLEIFERA* IN A FRAGMENTED FOREST.

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Many forests have been fragmented by agricultural and industrial development, leaving only small remnants of natural forests. Forest fragmentation impacts on conservation, biodiversity and wildlife management. During the past several decades, huge efforts have been made to restore and regenerate forests for environmental protection, biodiversity conservation and sustainable development. Animal seed dispersal, a dominant mechanism of dispersal in many temperate and tropical forests, has the potential to accelerate forest regeneration and restoration. However, few studies have evaluated the role of natural seed dispersal by animals in forest restorations (especially by scatter-hoarding rodents).

Oil tea (*Camellia oleifera*, Theaceae), an economically important evergreen shrub, grows in southern and southwestern China where its populations have been reduced by severe logging. Oil tea seeds are strictly rodent-dispersed; its natural regeneration is dependent on seed-caching rodents. To assess the potential benefits to oil tea from natural dispersal by scatter-hoarding rodents in forest restoration, we tracked individual seeds marked with coded tin tags. We established artificial seed sources (mimicking natural seedfall) in both *Camellia*-rich and *Camellia*-poor stands in a subtropical evergreen broadleaved forest in southwest China. Our results showed that no seeds survived to establish a seedling in the *Camellia*-poor stand. In contrast, 3.2% established seedlings in the *Camellia*-rich stand despite high seed caching (over fifty percent) in both stands. This indicates that poor regeneration may be associated with a low abundance of seeds relative to the rate of rodent predation in the *Camellia*-poor stands but populations can effectively recruit when seed sources are abundant, like that of the *Camellia*-rich stands. Seed-caching rodents could help restore natural populations of oil tea if we increase oil tea seed sources in the *Camellia*-poor stands.

#### Sandra Bos Mikich and Rafael Fernando da Silva Possette

# DO ARTIFICIAL BIRD PERCHES IMPROVE SEED RAIN AS NATURAL ONES DO? A FIELD TEST IN THE BRAZILIAN ARAUCARIA FOREST.

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Since birds are important seed dispersers and they usually defecate from a perch, perches must be a keystone resource for forest regeneration. Nevertheless many degraded areas do not have natural perches such as trees or bushes. It has been suggested that artificial perches may act as effective nucleation sites. However, literature lacks information on the effectiveness of artificial perches compared to that of natural perches.

Such a comparison was the main objective of a study conducted between 2002 and 2004 in southern Brazil. The study area was 301 hectare of Araucaria Forest remnants, tree plantations and some open areas in which six experimental units were established. Each unit was composed of three seed traps of  $1.5m \times 1.5m$  distributed under one natural perch (*NP*), one artificial perch (*AP*) and under a no-perch control (*OP*). An isolated tree represented the *NP*, while the *AP* was composed by two crossed wood perches each a metre long, fixed at the top of a two-metre wood pole. All material deposited in the eighteen seed traps (six of each type) was collected weekly, while 8.5 kilometres of trails were walked in order to collect botanical samples and phenological data on all zoochoric species. Fruits and seeds were preserved for comparison with material found in the seed traps. The *AP* samples produced 27,308 seeds of several species, the *NP* 5,841, and the *OP* only 14, demonstrating the efficiency of the perches, particularly the artificial ones, in the improvement of ornithochoric seed rain.

#### Ken L. Tinley

# PERCH-BASE THICKETS AND BERRY BIRDS: KEYSTONES OF ARID AUSTRALIA.

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As recorded from air and ground surveys across the western and central part of the Australian Arid Biome, berry bird formed thickets are the major archipelago habitat (ecotope) pervasive as a dot pattern across most landscapes. The bushclumps, or thickets, develop beneath perch trees and scrub whose seeds are typically dispersed by wind, water or ants. They also occur on or around rock outcrops, pool margins, fence poles and windmill perches. Bushclumps vary from a few small shrubs to six metre tall dense thickets as wide as the perch-tree canopy (up to ten metres). They are composed predominantly of woody plants with brightly coloured, smallish, round, fleshy fruits or seeds attractive to birds. These include berries, drupes and arillate seeds that range in size from three millimetres (rhagodias) to thirty millimetres (sandalwood). A partial list of berry plants from the region comprises 26 families, 33 genera and 64 species, of which 45 species (70%) are browsed by stock and feral ungulates (26 spp. or 40% are highly preferred).

Berry birds and perch-base thickets are the prime mover components in ecosystem dynamics involving progressive successional tendencies of increasing clump size and ecodiversity in the absence of reversals caused by overgrazing and erosion, too frequent fire or extreme droughts. They enhance diversity of habitat structure and form, species composition as well as productivity and hence carrying capacity for berry feeders (a feedback loop) and browsers. Their presence and condition is used by the E.M.U. Process as indicators of landscape health, integrity, carrying capacity status and trend. The perch-base thickets are important archipelagos of stepping-stone connectives in the biogeographic dispersal of berry birds and berry plants. Bushclump thickets are the foundation habitats of patch-interpatch dynamics and are core habitats as seed sources for the recovery of damaged or eroded terrain, particularly where isolated living scrub plants remain. In their absence the simple expedient is to surround a dead tree or pole with brushwood, which can entrain a re-seeding recovery.

In summary this progressive berry bird mediated successional tendency results in enhanced changes of cover, pattern and structure, function, composition, productivity and resilience. An enrichment process in the development of keystone habitats by guilds of keystone species in scrub country otherwise dominated over vast areas by a relatively few scrub canopy species.

#### Pablo R. Stevenson

# ESTIMATES OF THE NUMBER OF SEEDS DISPERSED BY A POPULATION OF PRIMATES IN A LOWLAND FOREST IN WESTERN AMAZONIA.

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The purpose of this study was to describe seed dispersal patterns of the woolly monkeys at Tinigua Park (Colombia) in terms of dispersal quantity. These results are based on two sources, 1) the potential number of seeds dispersed, based on direct observations of feeding time in fruiting trees, feeding rates and handling behaviour, and 2) the number of seeds recovered in faecal depositions of focal animals, which were followed for sixty hours per month for two (non-sequential) years. A total of 1,562 depositions were collected during the study.

Each dropping contained seeds from an average of 2.53 different species (range: 0 to 9). These seeds belong to 147 different plant species. Collected depositions contained a total of 106,869 seeds greater than one millimetre. Perhaps a more realistic calculation, correcting for the seeds that I was not able to recover and including seeds dropped at night, produced an estimate of 2,780,838 seeds dispersed by the focal animals. Given that population densities have varied between 41 and 50 individuals/km<sup>-2</sup>, the woolly monkeys in the study area were observed dispersing at least 33,000 seeds km<sup>-2</sup>/day<sup>-1</sup>. However, the corrected estimates were much higher (860,025 and 1,268,586 seeds km<sup>-2</sup>/day<sup>-1</sup> for the two study years). These estimates are, in general, lower than expected based on the manipulation of fruits on trees, and, in particular, the large differences can only be explained by active seed predation. Woolly monkeys consistently act as seed predators for about 7% of plant species they consume. However, a significant positive slope (0.7) for the regression line predicting the number of dispersed seeds from the estimated number of manipulated seeds indicated that the woolly monkeys disperse the majority of the seeds that they manipulate.

I conclude that woolly monkeys at Tinigua Park are very efficient seed dispersers in terms of dispersal quantity, being responsible for about a third of the mass of dispersed seeds in the community.

### Bette A. Loiselle<sup>1</sup> John G. Blake<sup>1</sup> and Pedro Blendinger<sup>2</sup>

# SEED DISPERSAL BY MANAKINS (AVES: PIPRIDAE) IN A SPECIES-RICH TROPICAL WET FOREST.

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Fleshy-fruited plants dominate the understory of Neotropical wet forest, and birds are their principal seed dispersal agents. Neotropical plant and bird species richness arguably reach their greatest local diversities in western Amazonia, where 1,104 species of trees (greater than 10cm dbh) have been recorded in a 50 hectare tree plot, and over 525 species of breeding birds have been recorded within a 650 hectare biological station.

Forests of western Amazonia are approximately three to four times more species-rich than well-studied wet forest sites in Meso-America. From the perspective of frugivory and seed dispersal processes, one might predict that ecological roles of fruit-eating animals overlap more broadly (i.e. are more substitutable) in the species-rich forests of western Amazonia when compared to wet forest sites in Meso-America. Here we investigate this hypothesis by comparing overlap in fruit and habitat use by manakins (Aves: Pipridae) in wet forests of eastern Ecuador and Costa Rica. In the former site, six species of 'true' manakins regularly co-occur in upland terra-firme habitats, whereas in the latter site, two species, one of which is an altitudinal migrant, co-occur in undisturbed upland forest. Support of the hypothesis that diversity affects ecological overlap in seed dispersal function would suggest that species-rich forests in western Amazonia may be more resilient to population variation or even local extinction of frugivores than are forests in Costa Rica.

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# WHAT HAPPENS TO A SEED WHEN IT TRAVELS THROUGH A DIGESTIVE TRACT?

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The time and rate at which seedlings emerge are essential factors that determine the reproductive and regeneration success of a plant. In the case of fleshy-fruited species, it is thus important to examine the causes and consequences of different germination responses of seeds ingested by frugivores. Although a great number of studies have compared the germination patterns between ingested and uningested (manually depulped) seeds, we still know very little about the mechanisms by which seeds that have been retained in the guts of a frugivore can germinate either in different proportions or at different rates compared to uningested seeds.

In this study, we investigate some of such possible mechanisms in two fleshy fruited species very common in the Mediterranean, *Phyllirea angustifolia* and *Myrtus communis*. We evaluate the seed coat modification after seeds of these two species are ingested by birds by, 1) measuring seed coat thickness, 2) examining the levels of seed permeability, 3) quantifying changes in the seed coat ultra-structure, by means of SEM photographs, and 4) measuring the resistance of the seed coat to breakage.

Significant variation in these traits is found both within a plant species and within a frugivore species, and thus the inspection of these mechanisms may shed light for the first time on the inconsistent results often found in this type of studies.

#### **Richard T. Corlett**

# POLLINATION AND SEED DISPERSAL: WHICH SHOULD CONSERVATIONISTS WORRY ABOUT MOST?

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Failures of pollination and seed dispersal mutualisms could accelerate the erosion of biodiversity in disturbed and fragmented tropical forests, and slow its recovery when human pressures are reduced. However, pollination and seed dispersal are very different processes, so the implications for conservation management of their vulnerability are also very different. Theoreticians argue that the potential for tight coevolution between plants and pollinators is greater than between plants and seed dispersal agents, which could potentially make pollinator mutualisms more vulnerable. However, there is surprisingly little direct evidence for the effectiveness of either flower visitors in pollination or frugivores in seed dispersal, so specialist pollination or seed dispersal relationships may be obscured by more generalized patterns of flower visitation and frugivory. Furthermore, most tropical studies have been too brief and too localized to assess the true diversity of animals interacting with a single plant species and *vice versa*.

A comparison between the available data on pollination and seed dispersal in the Oriental Region (tropical and subtropical Asia) provides little evidence that pollination relationships are, in general, significantly more specialized than seed dispersal relationships. Most plants are dispersed by fruit-eating vertebrates, which must be generalist feeders because of their long life spans, but specialization is also precluded in long-lived colonies of social bees, the major pollinators. The most specialized pollination mutualisms are one-to-one, but most flowers attract a diversity of visitors. The most specialized dispersal mutualisms are those involving large-seeded, large fruits, which depend on a very few large vertebrate species, although these vertebrates do not show a similar dependence on the plants. In comparison with seed dispersal agents, the much smaller sizes of most pollinators make them less vulnerable to fragmentation and exploitation. The genera with the most specialized known pollination mutualisms in the region, Ficus and Glochidion, are both well-represented in disturbed and successional vegetation. By contrast, the large vertebrates that disperse the largest fruits (primates, large fruit bats, elephants, rhinoceroses, hornbills and fruit pigeons in the Oriental Region) are highly vulnerable to both hunting and fragmentation, and have already been eliminated from the majority of their natural ranges. On current evidence, there are likely to be more vulnerable dispersal than pollination mutualisms in the Oriental Region.

#### Katrin Böhning-Gaese

#### DO SEED DISPERSERS MATTER? A BIOGEOGRAPHICAL APPROACH.

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One of the main questions in current ecological research is to understand the relationship between biodiversity and ecosystem processes. Does the diversity of seed dispersers have consequences for the seed dispersal rate, spatial distribution, genetic structure and reproductive success of trees? To answer these questions we took a biogeographical approach.

We compared two tree species in the genus *Commiphora* from Madagascar (which has only few frugivorous bird species) with South Africa (which is rich in frugivorous birds). While seeds of the Malagasy species were dispersed by basically one bird with a dispersal rate of only 8%, seeds of the South African tree were dispersed by twelve species with a dispersal rate of 71%. Correspondingly, seedlings and trees had a clumped spatial distribution in Madagascar, and a random distribution in South Africa. Gene flow in the Malagasy species was limited to distances up to three kilometers, with high genetic differentiation between local populations. In the South African species, gene flow covered up to thirty kilometres with little genetic differentiation at the corresponding scale. Reproductive success into the early seedling stages was lower in the Malagasy than in the South African species. Finally, tree communities in Madagascar, where lemurs are important seed dispersers, are dominated by tree species with typical 'primate fruits', while in South Africa they are dominated by trees with 'bird fruits'.

These results demonstrate that the loss of seed dispersers can have far-reaching consequences for the spatial distribution, genetic structure and reproductive success of trees – and even the composition of tree communities.

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#### COMPLEX NETWORKS OF PLANT-FRUGIVORE INTERACTIONS: PREDICTING THE EFFECTS OF EXTINCTIONS IN THE ATLANTIC FOREST OF SOUTHEASTERN BRAZIL.

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Plant-animal interactions are a key process in the maintenance of diversity in many habitats and, particularly, frugivory and seed dispersal play a role in many tropical forest communities. The analysis of interaction matrices of fruit-frugivores interactions has led to the view of these systems as complex networks, in which species (plants and animals) are nodes, and links between two nodes occur when species interact. The network approach allows the description of the macroscopic structure of plant-animal interactions, as well as investigates their robustness in case of local extinction of interacting species. The predictive value of such a procedure is useful for conservation plans in ecological communities that, despite having a high number of interacting species, are highly threatened by habitat loss or species extinction, as is the case for the Atlantic forest in Brazil.

From 1999 to 2002, we recorded fruit-frugivores interactions in Intervales State Park, a 49,000 hectare preserved area in southeastern Brazil. We investigated the effects of the extinction of threatened frugivore species to overall network topology. While these extinctions did not markedly change the global structure of the network, five percent of plant species lost all recorded seed dispersers. We predict that the implications of local extinction of threatened frugivores will not affect the large-scale organization of this plant-animal network, but will markedly affect some plant species, pointing to the necessity of species-specific management plans.

#### Ronda J. Green

# APPLICATION OF RESEARCH TO BIODIVERSITY CONSERVATION: AN AUSTRALIAN PERSPECTIVE.

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Frugivory and seed dispersal research, in Australia as elsewhere, has expanded greatly over the past two decades. In terms of broad answers for the development of general biodiversity conservation strategy, and for practical guidelines in specific situations, what is now needed?

Theoretical and applied literature, plus additional data, are explored for three major conservation aspects of frugivory and seed dispersal:

- 1. Conservation of rare and threatened plants (How important is dispersal to long-term persistence? Are they lacking dispersers? Which extant dispersers are most likely to take them to the right places? What do these dispersers need?);
- 2. Conservation of rare and threatened frugivores (Do the threatening factors include food shortages? Do they need management for seasonal or nomadic movements or for year-round fruit supply?); and
- 3. Restoration of disturbed landscapes (Can dispersers significantly assist restoration? How do we achieve a reasonably natural mix of species, both plant and animal? How do we avoid an influx of weedy species? Which dispersers are most useful for habitat restoration and management, and how do we attract and sustain them?).

#### S. Joseph Wright

### THE IMPACT OF HUNTERS ON SEED DISPERSAL IN A TROPICAL FOREST.

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Hunters kill forest vertebrates that eat seeds, browse leaves and disperse seeds, and can be the only primary dispersal agents for large seeds. Along a gradient of hunting pressure, we identified about one thousand seedlings (less than 50cm tall) and about five hundred trees (greater than 10cm dbh) from each of twenty one-hectare plots. The resemblance between seedling and tree communities differed strongly with hunting pressure with failed dispersal being the dominant signal.

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### POTENTIAL EXTINCTION OF KEY FRUGIVORES IN HABITAT FRAGMENTS: THE IMPORTANCE OF FRUIT AVAILABILITY AND DIVERSITY TRENDS IN DIFFERENT NEOTROPICAL ECOSYSTEMS.

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White-lipped and collared peccaries (*Tayassu pecari* and *T. tajacu*, respectively) are abundant and highly frugivorous mammals in Neotropical rain forests. White-lipped peccaries form large herds (fifty to three hundred individuals), so their effects on forest habitats can be dramatic. Local extinctions of white-lipped peccary, due to habitat fragmentation and hunting, have been reported throughout its vast geographical range. Fruits may be reduced in habitat fragments, so documenting fruit availability and use is critical to peccary conservation efforts.

We compared these factors in two different Brazilian ecosystems - the highly fragmented Atlantic Forest and the natural forest mosaics of the Pantanal wetland. In addition to providing baseline information about the fruits and frugivores of the ecosystems, we gained insights about area use, diet, habitat preferences, and the vulnerability of peccaries to habitat fragmentation. Fruit availability, diversity, and peccary frugivory during dry and wet seasons differed between the two ecosystems. Overall fruit diversity and availability were lower in an Atlantic Forest fragment, but fruit scarcity periods were more extreme in the Pantanal. Scarcity periods in the Atlantic Forest were characterized by lowered fruit diversity, but not lowered fruit quantity. In the Pantanal, both diversity and quantity were dramatically reduced during fruit scarcity periods. Extreme fruit scarcity periods and a more open landscape portend even more serious consequences for Pantanal peccary populations if ongoing deforestation and habitat fragmentation of the region continue. Total fruit availability, seasonal fruit availability and distribution, and other resource-related factors specific to regional ecosystems, should be considered during development of peccary conservation efforts. This portends even more serious consequences for Pantanal peccary populations if ongoing deforestation and habitat fragmentation of the region continue.

#### Norbert J. Cordeiro<sup>1,2</sup>

# FOREST FRAGMENTATION AFFECTS MIXED SPECIES FORAGING FLOCKS: A HYPOTHESIS ON IMPLICATIONS FOR SEED DISPERSAL.

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Qualitative observations in an African forest indicated that some fleshy-fruiting plant species might occasionally have their fruits consumed, and therefore have their seeds dispersed in large quantities by frugivorous members of mixed species foraging bird flocks. If habitat fragmentation disrupts the species composition and/or abundance of seed dispersing bird species that are integral to mixed species foraging flocks, one can predict several consequences on plant species dependent on these vectors for seed dispersal.

I conducted a preliminary evaluation on the consequences of forest fragmentation on mixed species foraging flocks by undertaking a census of birds in mixed species flocks in five small, isolated fragments (less than 31 hectare), and five widely spaced continuous forest sites in the East Usambara Mountains, Tanzania. Results showed that the small forest fragments had significantly fewer species and reduced densities of several omnivorous bird species (most of which are seed dispersers) compared to continuous forest.

I use these results to predict potential effects of habitat disturbance or loss in recruitment of plant species in different guilds, suggesting that plant species with typically low visitation are most vulnerable to losses of their bird mutualists.

# Cath Moran<sup>1,2</sup>, Carla P. Catterall<sup>1,2</sup> and Ronda J. Green<sup>1,2</sup>

### DIFFERENCES BETWEEN FRUGIVORES IN DIET SELECTION HAVE IMPLICATIONS FOR SEED DISPERSAL IN A FRAGMENTED SUBTROPICAL RAINFOREST LANDSCAPE OF EASTERN AUSTRALIA.

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The dispersal of seeds between remnant forest patches and to previously-cleared land contributes to plant regeneration patterns. In Australian subtropical rainforests, 70-80% of rainforest plant species are considered to be primarily dispersed by frugivorous birds and bats. Hence, changes in the distribution of these fauna (e.g., associated with habitat loss and fragmentation) may affect patterns of seed dispersal and regeneration of many rainforest plants. We have quantified the distribution of frugivorous birds and bats in the subtropical Sunshine Coast region of south east Queensland, Australia. We surveyed the abundance of each frugivore species in three site types: extensive forest (N=16), remnant forest (N=16) and patches of rainforest regrowth (N=16). We detected three distinct abundance responses, including (i) reduced abundance in remnant and/or regrowth forest, compared with extensive forest ('decreaser' abundance response); (ii) increased abundance in remnant and/or regrowth than extensive forest sites ('increaser' abundance response); and (iii) no marked difference between site types ('tolerant' abundance response). Here, we integrate these abundance responses of the frugivorous bird and bat species occupying rainforest habitats of the study area, with information on diet selection, to predict likely differences in seed dispersal patterns resulting from forest fragmentation and disturbance. Diet information was sourced from a comprehensive search of published and unpublished literature, as well as opportunistic field observation of frugivory in the Sunshine Coast. In particular, we examine differences between the three response groups in terms of the plant taxa and sizes of fruit selected.
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### PATTERNS OF AVIAN FRUGIVORY IN A FRAGMENTED AFRO-MONTANE CLOUD FOREST: A CASE STUDY FROM SOUTH-EAST KENYA

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Loss, degradation and fragmentation of tropical forests impose a severe threat on global biodiversity. Although the relative effects of habitat loss, degradation and fragmentation on the persistence of individual species (both plants and animals) have been well documented, possible impacts on plant-animal interactions and ecosystem processes remain largely unknown. We here study how fragmentation of afro-montane cloud forest affects the interaction between fruit-bearing tree species and a suite of frugivorous birds that act as the main seed dispersers in the study area. We predict that between-fragment differences in abundance of avian frugivores affect the fruit removal rate of *Xymalos monospora*, a common bird-dispersed tree species in the study area. In smallest forest fragments, however, some bird species seem to act as 'substitute species' for real forest species, possibly resulting in a zero difference in number of seeds dispersed. Results of this study are discussed in the light of the presumed importance of seed dispersal and natural forest regeneration.

### Jennifer M. Cramer, Rita Mesquita, and G. Bruce Williamson

# DIFFERENTIAL EFFECTS OF FOREST FRAGMENTATION ON SEED DISPERAL OF TWO RAINFOREST TREES.

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In ecosystems where mutualistic interactions are prominent, forest fragmentation may affect plant populations secondarily because fragmentation reduces populations of animal pollinators and seed dispersers. We hypothesized that tree species that rely on dispersers that are sensitive to fragmentation, such as large mammals and specialist birds, will experience dramatic changes in their seed shadows as a result of fragmentation whereas trees that rely on generalist birds and bats will be only mildly affected by fragmentation. Bocageopsis multiflora (Annonaceae) is an understory tree found throughout the Amazon with small orange fruits characteristic of the "generalist bird-dispersal" syndrome. Duckeodendron cestroides (Solanaceae) is an emergent tree endemic to the Central Amazon and dispersed by medium to large terrestrial and arboreal mammals. Dispersal was censused using seed traps (B. multiflora) or by counting seeds in wedge-shaped transects (D. cestroides). Results showed that seed dispersed past the crown was not different between fragments and continuous forest for *B. multiflora*. However, dispersal of *D. cestroides* beyond its crowns was drastically reduced in forest fragments. Also, we compared estimated dispersal kernels, using a random coefficient regression with sample area as an offset variable. Seed distributions for *B. multiflora* were not different between continuous forest and fragments. In contrast, the intercepts of regressions for mammal-dispersed D. cestroides were higher in continuous forest, indicating that in fragments fewer seeds are dispersed to all distances These results demonstrate that in tropical rainforests where biotic beyond the crown. interactions are prominent, the effects of forest fragmentation on species involved in mutualisms is highly variable and species dependent.

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#### CONSEQUENCES OF FOREST FRAGMENTATION ON SEED DISPERSAL AND POPULATION GENETIC STRUCTURE OF *PRUNUS AFRICANA* IN KENYA

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Forest fragmentation can have consequences for species diversity and ecosystem processes such as seed dispersal and, in the long-term, may reduce genetic diversity. In the fragmented Kakamega Forest, Kenya, we studied seed dispersal and the population genetic structure of adults and seedlings of Prunus africana (Rosaceae). In the main forest and five forest fragments we quantified the overall frugivore community, the frugivores on 28 fruiting P. *africana* trees and estimated seed dispersal. Using six microsatellite markers, we analysed the adults' (N = 105) and seedlings' (N = 58) genetic structure. Although the overall frugivore species richness was 1.1 times lower in fragments than in main forest sites, P. africana experienced 1.1 times higher numbers of frugivores in fragments than in main forest sites. Correspondingly, seed dispersal was 1.5 times higher in fragments than in main forest sites. Genetic differentiation of adult trees between populations was very low ( $F_{ST} = 0.03$ ) with ~96 % of the genetic variation within populations, reflecting extensive gene flow before the forest was fragmented. Genetic variation of seedlings between populations was somewhat higher  $(F_{ST} = 0.08)$  with ~91 % of the variation within populations. We recorded no isolation by distance pattern for adults but did so for seedlings. The increased differentiation among populations from adults to seedlings is a first signal of restricted gene flow in the seedling population caused by habitat fragmentation. To conclude, while quantitative seed dispersal still works as well or even better in fragments, genetic analyses revealed a diminished gene flow.

#### **Jacqueline Weir**

# PATTERNS OF SEED DISPERSAL BY BIRDS IN THE DEGRADED UPLAND LANDSCAPE OF HONG KONG, CHINA

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Bulbuls (Pycnonotus sp.) are the major seed dispersal agents in Hong Kong's degraded upland landscape. Radio telemetry showed that most bulbul movements were short (<100 m) and within woody habitat patches, but that they also make longer flights (>1 km) across open areas. These long flights are likely important for dispersing seeds between habitat fragments and into degraded areas. Visual observations were made to quantify frugivore movements, particularly across open areas. This had the advantage over radio tracking in rugged terrain that final destinations of flights could usually be observed. Light-vented and red-whiskered bulbuls (Pycnonotus sinensis and P. jocosus) accounted for over 75% of observed frugivore movements. Most movements across open areas (65.2%) were by P. sinensis. Frugivore movements peaked in November-December, the winter fruiting high and a time of migratory bird influx. Smaller peaks occurred corresponding to the fruiting periods of two common shrub species. P. sinensis appeared to use forest patches marginally more than P. jocosus, relative to shrubland, but to use isolated perches further from the forest edge. P. sinensis appeared less constrained by habitat patches. Both bulbuls used isolated trees and long grass stems as perches. Most seeds deposited by bulbuls probably arrive in forest patches or shrubland. However seeds could be transported over 1 km and deposited under isolated perches, especially by *P. sinensis*. Patterns of seed rain in open areas, for fruits within its gape limit (14mm), will be determined largely by this species. Movement patterns of frugivores should be considered in reforestation strategies.

### Angel Y. Y. Au

# PATTERNS OF SEED DEPOSITION IN THE DEGRADED UPLAND LANDSCAPE OF HONG KONG, CHINA

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Hong Kong is an extreme example of a degraded tropical landscape, with no substantial remnants of the original forest cover and an impoverished disperser fauna. The seed rain into the major upland habitats (grassland, shrubland, and secondary forest) was assessed using 100 seed traps (total trap area =  $18 \text{ m}^2$ ). Birds (particularly bulbuls, *Pycnonotus* spp.) are known or inferred to be the major dispersal agents for 87% of the seed taxa that entered the seed traps, 99% of the total number of seeds trapped, and 99.8% of the seeds trapped at the grassland site. Few taxa and < 1% of the total seeds were dispersed by wind and no seed taxa were definitely dispersed by fruit bats. The spatial pattern of seed deposition in the grassland site generally matched the observed behaviour of the bulbuls, including their willingness to cross open areas to isolated perches. Seed dispersal by non-flying mammals was assessed separately. Civets (*Paguma larvata* and *Viverricula indica*) disperse some large-seeded taxa from forest into grassland, while macaques (*Macaca mulatta*) and a muntjac (*Muntiacus* sp.) disperse some species within forest. Two species of habitat-generalist rats (*Rattus sikkimensis* and *Niviventer fulvescens*) disperse some very small seeds.

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# SEED DISPERSAL AND NATURAL REGENERATION OF SECONDARY RAINFORESTS IN THE WET TROPICS

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Due to loss and fragmentation of primary rainforests, it is now vital to understand the ecology of secondary rainforests and their regeneration. This project relates plant regeneration in secondary and adjacent, intact, rainforests to: 1) spatial distributions of rainforest plants, 2)mechanisms of seed dispersal, and 3)species ecological traits, of reproductive lifespan, seeds, stems and leaves. Community-level studies quantify species composition and the representation and diversity of plant traits from understorey to canopy, and their changes with distance from intact rainforest. Secondly, spatial models of dispersal and early seedling regeneration were developed for a diverse set of 13 focal species. 'Regeneration shadow' models employ Bayesian or Likelihood methods to estimate fecundities, and probability functions for dispersal-distances, from observed distributions of source-plants and seeds/seedlings. For several species, this requires 'mixture-models' to represent dispersal via two or more mechanisms, for example hypsi and cassowary. Finally, direct estimates of fecundities and distance-distributions for seed dispersal events are given for four species, via genetic parentage analysis using highly polymorphic microsatellites. As seedling distributions result from combined processes of seed-production, dispersal, and seed-seedling survival, hypotheses on these transitions will be generated by comparing 1) statistical 'regeneration shadow' models for 3 early-seedling age-classes, and 2) process-models of frugivory, seed deposition and predation, based on observed animal movements and behaviour (D.Westcott, A.Dennis, CSIRO). Finally, these results will form the basis of simulation models, to give projections for the abundance and distribution of regeneration of rainforest species representing a range of dispersal spectra and ecological traits

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### SPATIAL PATTERNS OF SEED RAIN IN A PRISTINE RAINFOREST IN FRENCH GUIANA: HOW FAR ARE FRUGIVORES RESPONSIBLE FOR SEED SHADOW?

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Seed dispersal mechanisms play a crucial role in the maintenance of diversity in tropical plant communities. Directed dispersal by frugivores typically results in a discontinuous spatial pattern of seed rain. By contrast, wind-dispersal of seeds results in a continuous pattern. Hence, seed rain pattern in animal-dispersed species should be more heterogeneous and dispersal-limited than for wind-dispersed species. To examine the extent to which dispersal limitation and spatial patterns of seed rain are determined by dispersal syndrome, life form and habitat characteristics, we carried out a field study in a tropical rainforest in French Guiana. Seeds were collected in 160 seed traps twice a month from February 2001 to December 2004. We restricted our analyses to the 65 most abundant species (60% animaldispersed). Seven species represented 50% of the total seed production, and three of these were lianas. Only 4 (out of 39) animal-dispersed versus 14 (out of 26) wind-dispersed species were spatially autocorrelated at distances < 50 m. Nevertheless, patterns in similarity decay with distance and are comparable for animal- and wind-dispersed species (Mantel correlogam). Forest type was not an important factor in determining similarity (partial Mantel test). There was no difference in the arrival probability of seeds into seed traps between animal- and wind-dispersed species, both in terms of frequency (P=0.83) and abundance (P=0.48). In conclusion, seed rain patterns of animal- and wind-dispersed species did not differ markedly. This implies that frugivores and wind may play a similar role in the seed dispersal process.

### Matthew J. Ward and David C. Paton

## LOCAL MOVEMENT PATTERNS OF THE MISTLETOEBIRD, *DICAEUM HIRUNDINACEUM*: IMPLICATIONS FOR MISTLETOE SEED SHADOW

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Movements of mistletoebirds (Dicaeum hirundinaceum) in a temperate eucalypt woodland were determined using radio-telemetry, to understand the role of the birds in mistletoe seed dispersal. Adult mistletoebirds had a mean home range of 20 ha, with core activity areas (30%) kernel) of approximately 2 ha. Breeding males and females had core activity areas of only 0.3 and 0.01 ha respectively. Habitat compositional analyses demonstrated that mistletoebird movements and activity were strongly correlated with mistletoe abundance. Seed shadows of box mistletoes were estimated by combining movement data from 14 individual mistletoebirds over 83 tracking days, with gut retention time data previously collected for Amvema seeds. Seed shadows were leptokurtic, with a 20%, 40% and 25% percent probability of mistletoe seed being deposited 0 m (same host tree), 1-50 m and 51-100 m from the host tree respectively. Although rare, long distance dispersal of mistletoe (> 500m) can occur. These movement patterns are in keeping with previous studies of mistletoe dispersal, which demonstrate that avian vectors primarily deposit mistletoe seeds on previously infected hosts. By promoting an aggregated mistletoe distribution and to some extent facilitating long distance dispersal, mistletoebirds play an important role in shaping plant community structure in temperate eucalypt woodlands.

#### **Glenn Hoye**

# KAMAKAZI FLYING FOXES AND THEIR POTENTIAL ROLE IN SHAPING THE BIOTA OF REMOTE ISLANDS

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Lord Howe Island is a remote volcanic island approximately 480 kilometres east of Port Macquarie, New South Wales. It supports diverse forest communities with a high level of species endemism. Records of vagrant flying-foxes (*Pteropus sp.*) reaching Lord Howe Island were recorded during interviews with island residents and from published literature. Evidence of at least four records of individual flying-foxes being present on the island exist from the last 150 years. No evidence of colonisation of the island by flying-foxes exists and several factors are likely to preclude the establishment of surviving populations. Resident and visiting megachiropterans have been acknowledged as important seed dispersers for plants to islands in the Pacific and Indian Oceans. The role of non-surviving vagrant flying-foxes in shaping remote island vegetation communities has been appreciated less. A number of plants present on Lord Howe have close relatives on the adjacent mainland that are regular food plants of the Grey-headed Flying-fox. The potential for substantial input to island plant diversity is discussed.

#### **Orr Spiegel and Ran Nathan**

#### DISPERSAL EFFECTIVENESS AS A FUNCTION OF SPATIAT SCALE IN A FLESHY-FRUITED DESERT PLANT DISPERSED BY TWO AVIAN FRUGIVORES

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Although fleshy-fruited plants are relatively uncommon in desert ecosystems, they are disproportionately important as source of water, sugars and nutrients for a variety of frugivores. In this study, we compare the effectiveness of two resident bird species, Tristram's grackle (Onychognathus tristramii) and yellow-vented bulbul (Pycnonotus xanthopygos), in dispersing fleshy fruits of the desert shrub Ochradenus baccatus. Experiments in the laboratory showed minor or no difference between the two species in two dispersal qualities: in both species, passage through the gut did not affect seed survival (mean $\pm$ S.E: %94.5 $\pm$ %1.3 vs. 92.7%±1.8% respectively) and had positive effect on the probability of germination, as compared to control seeds (+31%±3.3% vs. +29%+3.6%). Video photography in the field also showed minor differences between the two species in the quantity of seeds dispersed. Yet, the two species differ markedly in the spatial scale of their movements, measured for both species at small scales (10-100 m) by laser rangefinder and, for grackles only, at large scales (1-10 km) by radio telemetry. The two species also differ in gut retention times, measured in the laboratory (mean: 2.01±1.3h vs. 0.52±0.21h; max 6.5h vs. 2.2h). Our results suggest that the two avian dispersers switch role as a function of spatial scale. The majority of the seeds dispersed in small scales (tens of meters) are transported by the bulbuls; the impact of the two species is relatively equal at scales of few hundreds of meters. The grackles are exclusively responsible for dispersal at larger spatial scales larger, up to 8 km.

#### Kara L. Lefevre and F. Helen Rodd

# DOES HUMAN DISTURBANCE OF TROPICAL RAINFOREST INFLUENCE FRUIT REMOVAL BY BIRDS?

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Anthropogenic habitat degradation is a serious threat to global biodiversity, especially in tropical forests, yet the ecological consequences of this disturbance are poorly understood. One potential impact is alteration of key plant-animal interactions that play a role in structuring ecosystems, including seed dispersal. We are investigating the influence of disturbance on avian frugivory in the lower montane rainforest of Tobago, West Indies. In 2004, we conducted a fruit removal experiment in three forest treatments: primary forest, neighbouring cultivated forest, and forest at the edge of these two habitats. We mounted displays of rainforest fruits at sunrise, and quantified the number of fruits removed by sunset, repeating the experiment five times throughout the dry season. Because our disturbed plots have higher bird abundance and diversity, we predicted that removal rates would be higher in cultivated forest. In contrast, disturbed plots had the lowest rates of experimental fruit removal, possibly because of higher fruit availability. We will discuss the implications of fruit removal rates for seed dispersal and tropical rainforest ecology.

#### Alon Lotan and Ido Izhaki

# THE IMPACT OF ENVIRONMENTAL CONDITIONS ON FRUIT NUTRITIONAL VALUE OF A DESERT PLANT (OCHRADENUS BACCATUS)

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It is well established that fruit traits are marginally affected by biotic constrains, such as seed dispersers, whereas the effect of abiotic factors on fruit traits has been widely overlooked. We predicted that abiotic factors e.g. soil minerals, climate and water availability, have an important role in shaping fleshy-fruit nutritional attributes. The impact of abiotic factors might be even greater in the desert where water and some minerals are limited. We investigated the effect of abiotic factors on the nutritional profile of the fruit of a desert shrub (Ochradenus baccatus) in four sites along climatic gradient in the south of Israel and through field and greenhouse manipulations including fertilization and irrigation. The four sites were significantly different in soil mineral content (e.g., nitrogen, phosphorus and sulfur) and in soil moisture. Several nutritional traits of the fruit were also significantly different among the four sites. For example, pulp water content in the northern site was the lowest but its sugar, fat and Mg contents were the highest among the four sites. Our secondary compound analysis indicated that the fruit pulp was rich in glucosinolates with the highest concentration in the southern site. Several nutritional traits were significantly correlated with abiotic conditions. For instance, fat and sugar content in the pulp were negatively related to the plant water potential. Likewise, pulp glucosinolate concentration was negatively correlated with soil sulphur. However, several fruit traits, such as pulp nitrogen and potassium, were similar among the four sites despite the marked differences in their abiotic conditions. In sum, as we predicted, several fruit nutritional attributes were significantly associated with abiotic environmental conditions. We will also discuss the results of our greenhouse and field manipulations as well as the possible evolutionary consequences of our findings.

Palitha Jayasekara<sup>1</sup>, Udayani Rose Weerasinghe<sup>1</sup>, Siril Wijesundara<sup>2</sup> and Seiki Takatsuki<sup>1</sup>

# VARIATION IN SPACE AND TIME OF FRUIT USE BY BIRDS AND MAMMALS IN SINHARAJA TROPICAL RAIN FOREST IN SRI LANKA

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Spatial (arboreal/ground) and temporal (day/night) variation in consumption by birds and mammals of the fruit and seeds of 22 large, fleshy fruits and large-seeded, fleshy fruits was studied in 2000 and 2001 in the Sinharaja tropical rain forest in Sri Lanka. Bait fruits were placed on the ground and in the canopy. A system of automatic cameras was set up to record the consumers. A total of 1628 photographs were taken during the study period and 19 different animal species were identified. Among them, 42% were entirely canopy specialists and 37% were ground specialists. Some, like the grey hornbill, the jungle squirrel, the golden palm civet and some murids (rats and mice) visited both layers. Recorded animals visited the fruits either during day (N = 7 species) or night (N = 8 species) but no species appeared during both day and night. All fruit species were visited in the arboreal layer as well as on the ground. In the arboreal layer some plant species were visited exclusively at night (Cullenia cevlanica, Pometia tomentosa and Garcinia hermonii) and others only during the day (Dysoxylum ficiforme, Glenniea unijuga, Myristica dactyloides, Podadenia thwaitesii and Prunus walkeri). On the ground some species were visited exclusively at night (Garcinia cambogia and Syzygium firmum) and others only at daytime (Podadenia thwaitesii, Prunus walkeri and Terminalia zevlanica). These data highlight the necessity of studying a range of layers and different times of day to get a complete picture of the frugivore assemblage with respect to target fruits. Neglecting one layer or one period of time may lead to the complete missing of some animals that could prove to important frugivores or seed dispersers.

#### Wangworn Sankamethawee and George A. Gale

# FRUGIVORY AND SEED DISPERSAL IN EVERGREEN FOREST VEGETATION, EASTERN THAILAND

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While frugivory and seed dispersal by larger birds (hornbills) and gibbons as well as dispersal data for common fruiting trees such as Ficus spp. (Moraceae) have been documented in Thailand, there is a lack of information on general frugivory by smaller birds and visitation to other fruiting plants. We studied frugivory by smaller birds from March 2003 to February 2005 in the 30 ha Mo Sinto Long-term Biodiversity research plot. This forest supports over 300 species of trees and woody climbers, of which more than 50% produce fleshy fruits. Data was obtained primarily from faecal samples by mist-netting birds and from 800 hours of direct observations of 11 tree species conducted in conjunction with phenology surveys. Additional data was collected from casual observations. A total of 46 bird species were recorded feeding on 114 plant species. As expected, the defecated/regurgitated seed size was small (0.5-16 mm). The puff-throated bulbul (Alophoixus palidus) consumed the largest number of species (n=77). Frugivore activity was highest in October (14.33 visit/hr) and lowest in April (1.76 visits/hr) at the watched trees. Overall, visitation rate varied from 0-53.2 visits/hour. Fruit removal rate was highest in Litsea monopetala which had all their fruits removed within 10 days by 14 bird species based on diurnal observations. Fruit removal rate of the 11 observed tree species was negatively correlated with the density of conspecific trees on the plot. Our preliminary results indicate that the plant-animal interactions here are generalized, although Saurauia roxburghii seems to be dispersed almost entirely by flowerpeckers (Dicaeum ignipectus).

#### Johanna Choo and Edmund Stiles

### A FIELD-BASED COMPARISON OF AVIAN FRUGIVORY IN SARAWAK AND THE PERUVIAN AMAZON: IS THERE REALLY LESS FRUIT AVAILABLE FOR FRUGIVOROUS BIRDS IN THE ASIAN-TROPICS COMPARED TO THE NEOTROPICS?

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It is generally known among fruit biologists that the neotropical forests have a higher diversity of frugivorous animals compared to the Asian tropics. This difference was attributed to the dominance in Asian forests of dipterocarps that produce fruits generally not eaten by frugivores. However, this conclusion was based on information collected from different studies conducted in different locales in both regions. We believe that a systematic fieldbased comparison will provide us with a more quantitative analyses of the differences in fruit production and frugivory in the Asian tropics and neotropics. We present the first field-based comparison of avian frugivory in the rainforests of Sarawak and Peru. We conducted fruiting phenology surveys to determine variations in fruit production, and analyzed the nutritional contents of fruits from both sites. Mist-net sampling of understorey birds and focal tree and liana observations were conducted to determine avian frugivory in the understory and canopy respectively. We will show that our study sites have resource bottlenecks at different time scales that potentially have repercussions on the diversity of frugivores at each site. We will also examine whether understorey avian frugivores time their breeding and molting cycles to coincide with periods of high fruit abundance. We will examine whether fruit traits can predict the diversity of canopy avian frugivores that visit fruiting trees and lianas. And lastly, we will compare our findings with the literature-review based conclusions obtained by other authors.

# Ruhyat Partasasmita<sup>1</sup> and Keisuke Ueda<sup>2</sup>

# THE ROLE OF BULBULS AS SEED DISPERSAL AGENTS IN A TROPICAL SHRUBLAND OF JAVA, INDONESIA \*

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Java has been experiencing heavy deforestation since the 16<sup>th</sup> century. Combined with a dense human population, most forests have been converted into open land with shrubs and secondary vegetation. Seed dispersal agents, e.g. birds, are important in rehabilitating disturbed vegetation. Bulbuls are a large group of frugivorous birds that are effective seed dispersers. However, the role of bulbuls in seed dispersal in shrubland is not described. We investigated the role of two sympatric bulbul species as seed dispersers in 80 ha of tropical shrubland ecosystem in a tea plantation that had been abandoned for 5 years in West Java, Indonesia. In this study we focus mainly on eighteen individual plants of four species (focal plant species method). Foraging observations were conducted by a behaviour sampling method. We found differences in foraging method and the proportional use of patchy resources between bulbul species. The Sooty-headed Bulbul Pycnonotus aurigaster used more patchy resources as a place for feeding on fruits, while the Yellow-vented Bulbul Pycnonotus goiavier used it for foraging on insects. Sooty-headed Bulbuls stayed at each patchy resource longer than the Yellow-vented Bulbuls did. The Sooty-headed Bulbul stayed at Sambucus javanica for 119 sec / visit and the yellow-vented bulbul did 103 sec / visit. The highest feeding rate (10 fruits / min) was recorded by Sooty-headed Bulbuls at Breynia microphylla. Yellow-vented Bulbuls also foraged at Sambucus javanica, Breynia microphylla, and Polygonum chinense with a similar rate (6 fruits / min.). In the study area Polygonum chinense appeared with the highest frequency (66%). It was dispersed the shortest distance (22 m) by Sooty-headed Bulbuls and Yellow-vented Bulbuls. This is explained by the presence of the bulbul's nearest perch (within 22 m) where they returned to rest and digest fruits. They defecated while perching at this site. Both Sooty-headed Bulbuls and Yellowvented Bulbuls seemed important seed dispersal agents for these plants in this area.

### Dave Kelly, Alastair W. Robertson, Jenny J. Ladley, and Sandra H. Anderson.

#### IS DISPERSAL EASIER THAN POLLINATION? NEW ZEALAND AS A TEST CASE

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In New Zealand a number of native plants depend on birds for pollination and dispersal. A review in 1989 stated that in this country, dispersal was more likely to be at risk than pollination. We update this prediction and test it against recent theory and field data. A number of theoretical factors suggest that in general, dispersal may be both easier to service, and less critical to the plants, than pollination. Quantitative data for bird-pollination service to 13 native plant species (many at multiple sites), and bird dispersal service to 10 fleshy-fruited species, shows that failure of the pollination mutualism is more frequent and more emphatic than failure of the dispersal mutualism. In many cases, the same three species of birds are largely responsible for maintaining both mutualisms. This greater failure in pollination is contrary to the 1989 prediction, but is consistent with more recent theoretical evaluations.

# Camila Iotte Donatti<sup>1,2</sup> and Mauro Galetti<sup>1,2</sup>

## CONSEQUENCES OF DEFAUNATION ON SEED DISPERSAL, SEED PREDATION AND SEEDLING RECRUITMENT OF THE BREJAÚVA PALM (*ASTROCARYUM ACULEATISSIMUM*) IN THE ATLANTIC FOREST

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The palms are among the most important plant species to Neotropical frugivorous animals, because their fruits are nutritive and available in periods of fruit scarcity. Palm species with big fruits show, however, limitation in seed dispersal because only a few animal species can act as dispersers. The tropical forest has suffered the "Empty Forest Syndrome", where mutualistic and agonistic interactions between animals and plants have been lost due to the absence of seed dispersers, predators and large herbivores. Here we evaluate the defaunation effect, measured as agouti abundance, on seed dispersal and seed removal. The principal hypothesis was that in areas with low agouti abundance, seed removal and seed dispersal were lower while seed predation by invertebrates was higher. The most defaunated study site showed less seed removal, seed dispersal and seed predation. The proportion of intact endocarps predated by invertebrates was higher in the study site with lower agouti abundance. The study showed that the decrease in agouti population, decrease the *Astrocaryum aculeatissimum* seed removal, dispersal and predation. Our results indicate that a large fraction of Atlantic forest palms that rely on scatter-hoarding rodents may become regionally extinct due to defaunation.

# Alfredo Valido<sup>1</sup> and Jens M. Olesen<sup>2</sup>

### THE IMPORTANCE OF LIZARDS AS SEED DISPERSERS

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Since Ridley's compilation of seed dispersal around the world, birds and mammals have received most of the attention. This can be related to the traditional notion that herbivory/frugivory in lizards is an uncommon observation, in contrast, early lizards are recognized as important seed dispersers of the first gymnosperms and angiosperms. However, the importance of fruits in the diet of lizards, and lizards' role as seed dispersers, has begun to emerge more recently. Recently it been observed that saurochory is more common in poorarthropod habitats (oceanic islands, deserts, high mountains). However, these mutualistic interactions have been generally underestimated in recent specific reviews of plant-animal interactions, possibly because the majority of observations are from the local-regional natural history literature. In the present contribution we reviewed evidence of fruit-eating lizards around the world to show: i) the geographical distribution of this mutualistic interaction; ii) morphological characteristic of fleshy fruits which lizards eat; and *iii*) taxonomic affiliation of both lizard and plant species. This information is useful for identifying i) any common ecological characteristics of the habitats in which these lizards live that might account for the geographical pattern, *ii*) to determine if there are fruit characteristics which might define a saurochory syndrome and, *iii*) to investigate if specific phylogenetic clades account for the taxonomic distribution. The results obtained show us that the phenomenon is widespread and distributed over several independent plant and lizard clades. There are no specific common fruits traits which together could be termed a saurochory syndrome since lizards are extremely generalized in diet including fruits irrespectively of fruit type, color, and size.

#### **Daniel Bennett**

## DIET OF A GIANT FRUGIVOROUS MONITOR LIZARD (VARANUS OLIVACEUS) IN THE PHILIPPINES AND IMPLICATIONS FOR THE DISPERSAL OF PANDANUS SEEDS

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Frugivory is apparently a rare strategy among lizards and very few species can be described as obligate frugivores. In the Philippine Islands two large (>9kg) species of Varanus lizard (V. *olivaceus* and *V. mabitang*) have diets that are composed largely of fruits. Here I report on the diet of Varanus olivaceus on Polillo Island, Quezon province, as determined from faecal samples collected from the forest floor and from captured individuals and describe initial attempts to investigate the foraging behaviour of the lizards and ongoing attempts to gather quantitative data on their role in the dispersal of the seeds they consume. The most common items in faeces were seeds from seven genera of fruiting plants and two species of snails. Only one of over 600 fecal samples did not contain fruit, whereas over 40% of samples did not contain animal remains. Most of the variation in fruits consumed can be explained by local and seasonal availability, one fruit (Pinanga) was only eaten when alternative fruits were unavailable and another fruit (Pandanus sp.) was most abundant during the coolest part of the year when lizard activity was very low. Overall the two most important genera of fruiting plants were Pandanus and Canarium. Despite the wide distribution and great species richness of Pandanus few animals are recorded as feeding on it and most of them appear to act as seeds destroyers rather than dispersers. Because Varanus olivaceus habitually deposits large piles of viable *Pandanus* seeds considerable distances from the parent plant it has been hypothesized that the lizards have a marked effect of *Pandanus* distribution within the forest. This hypothesis is currently under investigation.

### Jane Marhsall, Adrienne S. Markey and Janice M. Lord

### FURTHER STUDIES ON THE POSSIBLE INFLUENCE OF LIZARD FRUGIVORY ON THE EVOLUTION OF FRUIT COLOUR WITHIN THE NEW ZEALAND FLORA

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Like most temperate and tropical communities, the majority of fruit colours in the New Zealand flora are red and black. New Zealand is no exception, where most fruit are predominantly red - orange or purple – black. However, relative to other regions, New Zealand has a relatively high frequency (21.5 %) of white or blue fruited species (Lord & Marshall 2001). Fruit colour has been long thought as an adaptive response to natural selection by frugivorous seed dispersers, although empirical evidence for this is scant. The flora of New Zealand has evolved largely in the absence of terrestrial mammals, the predominant frugivores being birds and reptiles. Within this context, the role of lizard frugivory may be relatively more important in this Oceanic ecosystem than in other regions where there are mammalian frugivores.

It this talk, we will discuss the work to date which has attempted to address the evolutionary significance of fruit colour in New Zealand, and discuss the possible role of lizards as agents of selection. We will cover our research into lizard colour preferences, fruit feeding trials in a laboratory and field context, the significance of fruit in the diet of lizards. As predicted by Whitaker (1987) field trials suggest that skinks do have a preference for translucent white and blue coloured fruit. We will also discuss research on *Coprosma*, the most speciose, fleshy fruited genus within New Zealand.

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### **Thomas R. Engel**

# LONG-TERM LATRINE USE BY VIVERRIDS AND HERPESTIDS: DISPERSAL THEORY AND ITS APPLICATION ON VANISHING FORESTS

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African civets as well as sympatric genets and mongooses together can deposit diaspores for about 10% of over 1100 local plant species at regularly visited latrine sites. A long-term study (almost one decade in length) and confirmation by camera-trapping has revealed that civets and genets are much more frugivorous than previously realised. Inter-specific use of shared latrines was also confirmed for the first time. Endozoochory by viverrids and herpestids has synergetic effects and is in accordance with the escape, colonisation and the new found nonspecialised directed dispersal theory, described by the author as *coprochory*, and contradicts the clumped dispersal theorem. As known from large-scale dispersal screenings for 37 animal and 549 plant taxa, African viverrids and herpestids are currently not the sole seed dispersers for most of the plants in their diet. However, as much as more 'effective' and more prominent dispersers vanish from African ecosystems, the importance of African civets and relatives as dispersers increases. Endozoochory by African civets includes numerous pioneer and late forest stage species. Due to high quality and quantity dispersal over long-distances, even across habitat boundaries, a wide fruit diet spectra, the support of secondary coprochory and dispersal to disturbed, vegetation free sites, African civets play an important role in the complex spatio-temporal dynamics in the natural regeneration of vanishing African forests and their biocoenoses.

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# Juliet Vanitharani<sup>1</sup> and V. Chelladurai<sup>2</sup>

# *LATIDENS SALIMALII* (SALIM ALI'S FRUIT BAT) A RELIABLE SEED DISPERSER OF SOUTHERN WESTERN GHATS; INDIA.

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Throughout the tropics, most species of trees and shrubs rely on vertebrates for seed dispersal and pollination. Among mammals the plant - visiting bats focus their feeding and foraging efforts on fruits, nectar and pollen. Owing to their mobility they play an important role as seed dispersers. Morphology and behavioural attributes of fruit bats mediate resource partitioning among them. They are not opportunistic feeders. Each species focuses their feeding and foraging efforts on specific 'core' plant species. *Latidens salimalii* (Salim Ali's fruit bat), an endemic and endangered fruit bat, confines its activity above 1000m elevation of southern Western Ghats, India. It is morphologically adapted to play a major role as a seed disperser of economically important fruit trees; some of which are endemic to the southern Western Ghats. This bat primarily eats ripe fruits and the seeds are often swallowed (if small) and excreted unharmed or dropped (if big) during fruit processing. Thus *Latidens* help to replenish and restore evergreen forests.

# Marie T. Murphy<sup>1</sup>, Mark J. Garkaklis<sup>2</sup> and Giles E. St. J. Hardy<sup>1</sup>

## SEED-CACHING BY THE WOYLIE (*BETTONGIA PENICILLATA*) IMPROVES RECRUITMENT AND REGENERATION OF SANDALWOOD (*SANTALUM SPICATIM*) IN WESTERN AUSTRALIA

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The role a small marsupial, the woylie (Bettongia penicillata) might play in the recruitment and regeneration of Western Australian sandalwood (Santalum spicatum) through its seed caching behaviour was investigated in this study. Cotton thread, attached to the large seeds, was followed to determine the fate of the seeds once they were removed. A total of 25 seed caches were located. All of the seeds were found in separate caches, consistent with scatterhoarding behaviour. The average distance from the source of the seeds to the cache was 43.1  $m \pm 5.8$  m at Dryandra and 29.1 m  $\pm 3.8$  m at Karakamia Sanctuary. The mean cache depth was 4.3 cm  $\pm$  0.2 cm at Dryandra compared with 4.6 cm  $\pm$  0.3 cm at Karakamia Sanctuary. Significantly more seedlings and saplings grew away from sandalwood trees at sites with woylies than at sites with no woylies. In contrast, significantly more seedlings and saplings grew under adult trees at the site without woylies than where they were present. Significantly more whole, undisturbed seeds were found under the parent trees at the woylie-free site than at the two with woylies. These findings strongly suggest that little seed dispersal or regeneration of sandalwood occurs in the absence of woylies. Through scatter-hoarding, woylies have the potential to disperse and cache sandalwood seeds away from the source and significantly alter the subsequent regeneration of sandalwood. Furthermore, by caching seeds large distances away from a source, woylies could modify the distribution of sandalwood in an area.

#### Shernice Soobramoney and Colleen T. Downs

## LIPID-RICH VERSUS SUGAR-RICH FRUITS: EFFECTS ON DIGESTIVE EFFICIENCY AND FOOD CHOICE OF THE RED-WINGED STARLING ONYCHOGNATHUS MORIO

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Digestive processes determine whether the particular diet of a bird is used efficiently and whether energetic demands are met. Assimilation efficiency is often used as an index of whether a diet is digested effectively. Red-winged Starlings *Onychognathus morio* are avian frugivores and have a diverse fruit diet. This study compared the digestive efficiencies of Red-winged Starlings on two different diets, apple (sugar-rich) and palm fruit (lipid-rich), by measuring transit times and assimilation efficiency. Nutrient contents of the two diets varied considerably and so required different digestive processing. Red-winged Starlings lost body mass when fed sugar-rich fruit and gained body mass on lipid-rich fruit. Energy assimilated on the lipid-high fruit was significantly greater than sugar-high fruit. Red-winged Starlings had a relatively high assimilation efficiency on both diets. They were also able to adjust transit time to maximise the rate of energy gain per gram of food in order to maintain energy balance. When given a choice of diets, Red-winged Starlings selected the lipid-rich fruit which was most efficiently digested and yielded the greatest energetic reward. The feeding trials further showed that Red-winged Starlings regulated daily energy intake.

Ella Tsahar<sup>1</sup>, Carlos Martínez del Rio<sup>2</sup>, Ido Izhaki<sup>3</sup> and Zeev Arad<sup>1</sup>

# CAN BIRDS BE AMMONOTELIC? NITROGEN BALANCE AND EXCRETION IN FRUIT AND NECTAR EATING BIRDS

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The minimal nitrogen requirements (MNR) of fruit and nectar feeding birds are lower than those of omnivorous birds. This notion is supported by an allometric equation we have created. This equation indicates that the MNR of nectarivorous-frugivorous birds are lower than those of omnivorous birds by an average factor of 4. The phylogenetic comparison of the studied species suggests that frugivory and nectarivory have developed independently in several bird families. Hence, it is expected that their ability to lower nitrogen requirements may result from different operating mechanisms. We measured the MNR and the effect of protein and water intake on the nitrogenous waste composition in two frugivorous bird species: yellow-vented bulbuls (Pycnonotus *xanthopygos*) and Tristram's grackles (Onychognathus tristrami), and on an omnivorous bird, the European starling (Sturnus vulgaris). The MNR of the species followed the expected pattern; the frugivorous species had lower MNR than the omnivores. Interestingly, the species differed in the composition of the nitrogenous waste that they produced. The grackles and starlings were uricotelic (excreting over 50% of the nitrogen waste as uric acid), and the chemical composition of their nitrogenous waste products was relatively independent of water and protein intake. In contrast, the bulbuls were "apparently ammonotelic". Their ammonotely (excreting over 50% of the nitrogen waste as ammonia) was related to low protein intake and high water flux, and was the result of post-renal urine modification. We suggest that the post-renal modification of nitrogenous compounds contribute to the nitrogen balance of the bulbuls. The mechanisms underlying the low MNR of the grackles remains unknown.

### H. Martin Schaefer and Veronika Schaefer

### FRUIT COLOURS AS SIGNALS TO SEED DISPERSERS

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Fruit colour changes during ripening are often interpreted as an adaptation to attract diurnal seed dispersers. However, the mechanisms of attraction remain contentious because seed dispersers rarely show consistent preferences for certain colours. We argue that the evolution of fruit colours is more easily understood using the framework of signal theory. Two principles drive the evolution of signals: the conspicuousness of a signal that influences its detectability and, second, the reliability of a signal in indicating its message. Red and black, the most common colours of temperate fruits are also the most conspicuous fruit colours but they do not indicate fruit contents. Experiments with captive birds document that seed dispersers favour highly conspicuous signals over other fruit signals regardless of the colour involved. Other fruit colours, however, are more reliable in indicating fruit contents. Yellow to orange fruits have high protein contents, whereas blue fruits have high sugar and high tannin contents. Signalling specific nutritional rewards might be a strategy that increases seed dispersal. Consequently, distinguishing between the conspicuousness and the reliability of a fruit signal might advance our current understanding of the evolutionary ecology of fruit colouration. However, fruit colours are more than a signal. At least some fruit pigments possess strong antimicrobial activities. Because these pigments increase during ripening, colour changes might also function as a defence against fruit pests.

### Keisuke Ueda and Hirosi Arima

#### INCONSPICUOUS DRY FRUITS DISPERSED BY RESIDENT BIRDS IN JAPAN

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In natural environments there are many conspicuous coloured fruits, e. g. red, orange and black. Although these fruits effectively display to frugivorous birds, there are also many inconspicuous fruits with dull colour. We ask whether these dull coloured fruits advertise less effectively to birds. We studied the fruit preference of two species of crows, Corvus macrorhynchos and C. corone and a grey starling Sturnus cineraceus both of which are resident in central Japan. We collected faeces and pellets containing seeds in pre-gathering site neighbouring winter roosts in 1986 and 1988 identified the seeds found in them. Crows mostly preferred Rhus spp. fruits. Of the seeds identified, ca. 66 % were seeds of Rhus spp.. The pulp of *Rhus* spp. fruits contain plenty of fat which would make it a highly nutritious and valuable food for animals during winter. This is likely the reason why crows are especially fond of *Rhus* spp. The preferred fruits of gray starlings was Chinese tallow-tree Sapium sebiferum. Four other fruit species, Melia azedarch, Cinnamomum camphora, Diospyrus kaki, and Ligustrum lucidum were also common in the samples. Fruits of Chinese tallow-tree have a white sarcocarp and dehisce in autumn. The sarcocarp dries on the branch after dehiscence. We took additional data on direct observation at the tree. Again crows and gray starlings were frequent visitors to the tree. We analyzed the nutritional value of these fruit and found that these are also lipid-rich fruits. Lipid-rich fruits are important food for wintering birds. These inconspicuous fruits might be sending an honest message to birds. We also examine and discuss here the importance of ultraviolet reflection for these fruits.

### Kevin C. Burns

# ECOLOGICAL DRIFT PREDICTS FRUIT-FRUGIVORE INTERACTIONS IN A TEMPERATE RAINFOREST

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After decades of searching for adaptive relationships between fruits and frugivores, there is a growing consensus that seed dispersal mutualisms are rarely structured by deterministic processes. I developed two simple null models to generate random patterns in fruit-frugivore interactions. In both models, frugivore species foraged randomly for identical fruit species, but fruit phenologies and frugivore migration schedules were allowed to fluctuate. Theoretical predictions were then tested with two years of observations in a temperate rainforest in British Columbia, Canada. The first null model predicted that fruit removal rates from each fruit species are determined by their relative abundances. The second null model predicts that the species composition of frugivores interacting with each fruit species is determined by their relative abundances during the each fruit species' phenology. Observations documented four migrant bird species dispersing seven fruit species. Strong interspecific differences in fruit phenologies and bird migration schedules were also observed. Analyses of field data supported both null model predictions. Weekly rates of fruit removal from all 7 fruit species were correlated with the relative abundances of their fruits. The number of fruits each bird species dispersed from each plant species was correlated with the relative abundances of each bird species during each plant species' fruit phenology. Overall results indicate that bird fruit-interactions are structured randomly at this site and illustrate how simple null models based on ecological drift can be usefully applied to seed dispersal mutualisms.

### Tatyana A. Lobova and Scott A. Mori

#### **BAT-FRUIT SYNDROME: MYTHS AND REALITY IN THE NEOTROPICS**

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The characters of species known to be dispersed and potentially dispersed by bats in an undisturbed lowland tropical rain forest in central French Guiana (CFG) are described and analyzed. In this area with 133 native flowering plant families, species from 29 families are dispersed by bats, and from additional 20 are potentially dispersed by bats. Piperaceae (19 of 44 species dispersed by bats), Araceae (16 of 51), and Solanaceae (12 of 26) possess the greatest number of species utilized by bats. There are 1,918 native species known from CFG and 104 (5.4%) of them are documented to be bat-dispersed while an additional 161 (8.4%) are potentially bat-dispersed. Thus 13.8% of species in CFG may depend on bats for seed dispersal. Bats feed mostly on infructescences (47% of the bat-dispersed species) and fruits (47%), or on fleshy seed appendages (6%). The types of fruits of bat-dispersed species are mostly berries (66%), drupes (17%), or capsules, achenes, and syncarps (17%). Bats preferably feed on green coloured plant parts (46%) but also consume yellow (13.5%), brown, black, and purple (13.5%), white (11%), orange and red (8%), or of unknown colour (8%). Usually bats digest the entire pericarp (67%), part of the pericarp (18%), part of the seed (4%), or other fruit parts (11%). The diaspores are mostly seeds (74%), stones and pyrenes (17%), or entire fruits (9%). Bats disperse species endozoochorously (77%) or exozoochorously (22%), and rarely epizoochorously (1%). Endozoochorously dispersed diaspores vary in length from 0.45 to 9 mm, exozoochorously dispersed from 10 to 60 mm.

# Alastair W Robertson<sup>1</sup>, Amy P. Trass<sup>1</sup>, Jenny J. Ladley<sup>2</sup> and Dave Kelly<sup>2</sup>

# ASSESSING THE BENEFITS OF FRUGIVORY FOR SEED GERMINATION: BARKING UP THE WRONG TREE?

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The germination enhancement by gut passage through birds or other vertebrates has been the subject of numerous studies and summarised recently in two comprehensive reviews. However, most of these studies are of limited use in assessing the importance of frugivory as a seed germination cue, because of two serious methodological flaws. The testing environment is generally inappropriate, and the wrong treatments have been tested. In this paper we will present data from several New Zealand fruiting species that have been assessed with an alternative design that overcomes these flaws and allows much more powerful predictions of what will happen if fruit-dispersers stop feeding.

#### Nicole D. Gross-Camp

# MONITORING CHIMPANZEE SEED DISPERSAL: TEMPORAL ASPECTS OF SEED PERSISTENCE AND GERMINATION

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I monitored large seeds (> 5 mm) dispersed by chimpanzees at their site of deposition for seed persistence and germination over a period of six months. Ten large-seeded tree species were found in chimpanzee faecal samples though never in combination of more than two seed species. Three tree species accounted for 78% of the samples containing seeds. Chimpanzees also dispersed the seeds of a single mature forest tree species, Syzygium guineense (Myrtaceae), in an orally-processed fruit mass or 'wadge.' Six microhabitat variables were used to describe the sites in which seeds were deposited including slope, elevation, distance to an adult conspecific, distance to a fallen log, canopy cover, and herbaceous vegetation cover. Multivariate analyses indicate that while faecal and wadge samples were not clustered into particular microhabitats, there was little overlap in the microhabitats in which wadges and faecal samples were deposited. The difference in the proportion of seeds persisting and germinating in wadges and faeces changed through time. Significantly more seeds persisted in wadges than in faeces up to day 49. In contrast, the proportion of seeds that had germinated in wadges (9.7%) versus in faeces (1.6%) became significant on day 49 through day 197. Elevation was the only microhabitat variable determined to have a significant influence on seed persistence whereas slope was determined to have a significant influence on germination.

# Soumya Prasad<sup>1</sup>, Jagdish Krishnaswamy<sup>2</sup> and Ravi Chellam<sup>3</sup>

### DISPERSAL OF SEEDS THAT RUMINANTS REGURGITATE: *PHYLLANTHUS EMBLICA* LINN. (EUPHORBIACEAE) AT RAJAJI NATIONAL PARK, INDIA

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Fruits of *Phyllanthus emblica* Linn. (Euphorbiaceae), a tropical Asian tree, are an important non-timber forest product. Prior to this study, little was known about the fate of P. emblica fruit in the absence of extraction. At Rajaji NP, P. emblica fruits were consumed by two deer (chital Axis axis, barking deer Muntiacus muntjak), a colobine monkey (langur Semnopithecus entellus) and a rodent (Indian gerbil Tatera indica). Chital and barking deer swallowed fallen fruits, retained them in their rumen, and later regurgitated them. Langur dropped fruits under parent trees, making vast quantities of fruit-crop available to deer. At Rajaji, deer-regurgitated cocci (seeds within endocarps) of P. emblica, together with Terminalia belerica, Zizyphus *mauritiana* and Z. xvlopyra, in clusters at chital bedding sites. We investigated the role played by ruminants in dispersal of large-seeded plants via the chital-P. emblica interaction using captive feeding trials and germination experiments. Chital swallowed fruits whole, and regurgitated 78% as intact cocci within 7-27 h. Though rumen retention lowered germination success, it was not very low (22%), implying some probability of seeds surviving rumen passage. In large-seeded species regurgitated by deer at Rajaji, fruit traits that could influence rumen retention time were less variable than others. These might maximize dispersal while keeping predation risk low. Ruminants are among the few dispersers known for many largeseeded plants and are more liable to be affected by habitat degradation than smaller frugivores. Local extinctions of ruminants can leave plants like *P. emblica* without effective long-range dispersers.

### **Richard T. Corlett**

# INTERACTIONS BETWEEN EXOTIC PLANTS AND NATIVE FRUGIVORES IN HONG KONG, CHINA

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Both of Hong Kong's fruit bat species and all the common urban and agricultural frugivorous birds consume the fruits of planted and spontaneous exotic plant species. Almost all small (< 20 mm diameter), unprotected fruits are eaten, but larger or protected fruits are generally avoided, with the exception of *Syzygium jambos* and *Psidium guava*, which are consumed by fruit bats. The presence of reliable, phenological gap-filling, exotic fruit sources probably increases the density of frugivores in urban and agricultural habitats. Several cultivated exotics with fleshy fruits are naturalizing or are already naturalized as a result of dispersal by native frugivores, as are some species that were probably introduced by accident. However, 90% of the naturalized exotic flora produces non-fleshy fruits with seeds that are dispersed by wind or other means. The invasion of natural or semi-natural plant communities by exotic plant species is not currently a major conservation problem in Hong Kong, but the main consumers of exotic fruits (*Pycnonotus* spp. and *Zosterops japonica*) are wide-ranging habitat-generalists that would be ideal dispersal agents for invasive species, as indeed they have proven to be where introduced on oceanic islands.

#### **Carl Gosper and Gabrielle Vivian-Smith**

# WEEDS AND FIGBIRDS – DIETARY IMPORTANCE AND DISPERSAL IN BRISBANE

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A high proportion of the most invasive plants in south-east Queensland, Australia, have fleshy fruits that are consumed by vertebrates. Little is known, however, of the importance of these new food sources in the diets of native frugivores, or how these frugivores contribute to weed spread. We have studied the diet of figbirds (*Sphecotheres viridis*) in suburban Brisbane through the collection of faecal samples and dropped food beneath a communal roost. Seeds of invasive plants were present in all samples, and formed the bulk of the non-*Ficus* spp. component of the samples in some months. We also tested the ability of figbirds to disperse viable seeds of two emerging invasive plant species, *Murraya paniculata* and *Ochna serrulata*, by comparing germination rates of seeds collected from the roost with seeds collected and sown whole or with the pulp manually removed. In both cases, seeds dispersed by figbirds had similar rates of germination to seeds collected directly from plants. Figbirds in suburban Brisbane consume substantial quantities of weed fruits and are an effective dispersal agent for the species examined.

### Sandra Anderson, S. Heiss-Dunlop and J. Flohr

# A MOVING FEAST: BIRD DISPERSAL OF WEEDS INTO CONSERVATION AREAS.

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Active re-planting of degraded sites is commonly undertaken in an attempt to redress native biodiversity decline. The aim is to benefit native flora and fauna, and eventually restore the site to a semblance of the ecosystem formerly occupying it. However continual input from the surrounding unmanaged area, and the impact of this on the restoration process, is rarely acknowledged. Failure to assess the influx of weedy species by seed vectors from adjacent land prejudices the ability of such systems to be self-sustaining once active management is withdrawn. In this study, we compared the seed influx from starling flocks arriving to roost on two offshore New Zealand islands managed for conservation purposes. The land adjacent to one island (Tiritiri Matangi) is predominantly regional park and actively weed-controlled, while the land adjacent to the other (Motuihe) lacks any weed control. Observations of fruiting weed species confirmed that starlings frequently visit them to feed. Seedfall traps on both islands at roost and control sites also confirmed that seed rain was significantly higher at starling roost sites. Identification of seeds showed that starlings disperse some native fruiting species, but the proportion of exotic seeds in the seed rain was 70% on Motuihe, compared with only 30% on Tiritiri Matangi. The results suggest that surrounding land use should be an important consideration in prioritising sites for restoration. They also suggest that native plant species attractive to bird dispersers utilising the area should be established in the early stages of restoration, to favour native regeneration. In the New Zealand context, the results highlight that attention to weed control of coastal land may be a cost-effective means of preventing continual weed export to valuable island reserves via mobile bird seed dispersers.
#### David A. Westcott and Andrew J. Dennis

# CAN WE PREDICT DISPERSAL CHARACTERISTICS OF INVADERS BEFORE THEY INVADE?

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Knowing the dispersal characteristics of an invasive species in a habitat before it has actually invaded that habitat is potentially a handy bit of information for management. For example, it could provide insights into the scale and rate of spread and may contribute to decisions on how much effort should be invested in preventing the invasion. Similarly, once an outbreak of a novel weed is detected being able to predict it's dispersal behaviour without extensive field observation can guide containment activivity by providing clues to the spatial scale of eradiction required. Here we provide a framework for assessing the dispersal characteristics of potential and novel invasive species and guiding first-response containment activities.

# Melissa Setter<sup>1,4</sup>, Matt Bradford<sup>2,4</sup>, Bill Dorney<sup>1,4</sup>, Ben Lynes<sup>5</sup>, Jim Mitchell<sup>3,4</sup>, Stephen Setter<sup>1,4</sup> and David Westcott<sup>2,4</sup>

# ANIMAL DISPERSAL OF POND APPLE, A WEED OF TROPICAL AUSTRALIAN WETLANDS

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Pond apple (Annona glabra) is one of Australia's 20 Weeds of National Significance. This small-medium tree invades wetlands and associated ecosystems along the north-eastern coast of tropical Queensland. Fruit production peaks over two to three months, usually between December and March, often coinciding with high rainfall or flooding events. Pond apple dispersal occurs primarily via fresh and saline water movement and, to a lesser extent, through animal movement. The large aromatic fruits (diameter 8-10 cm) contain up to 250 seeds (approximately 1 cm long) and are used as a food source by several animal species. Our research to date has focussed on quantifying the role of the endangered native cassowary and the introduced feral pig as potential dispersers of pond apple. Field observations and collections at several locations have confirmed that both species consume the fruit in the wild, and pass viable seed. Highest seed numbers found in a single dropping were 842 for cassowaries and 288 for feral pigs. Captive feeding results showed maximum gut retention times of 28 hours for cassowaries and 8 days for feral pigs. In conjunction with animal movement data from other studies, these results suggest that cassowaries could distribute seed up to 1200 m from the ingestion site, and feral pigs may transport it 10 km or more. Animals can disperse pond apple beyond the range achieved through water dispersal, for example, upstream and between catchments. This has implications for detection and control of pond apple plants. Cassowary dispersal, in particular, may affect weed management. In certain areas, members of the community perceive pond apple to be an important cassowary food, and so land managers may need to stagger the timing of pond apple control and revegetate with other cassowary food species.

# Gabrielle Vivian-Smith<sup>1</sup>, Carl R. Gosper<sup>1</sup>, Anita Wilson<sup>2</sup> and Kate Hoad<sup>3</sup>

# THE FRUIT- AND SEED-DAMAGING FLY, *OPHIOMYIA LANTANAE*: SEED PREDATOR, RECRUITMENT PROMOTER OR DISPERSAL DISRUPTER OF THE INVASIVE PLANT, *LANTANA CAMARA*?

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One suggested strategy for controlling the spread of bird-dispersed invasive plants is the introduction of biological control agents that infest fruits to either deter frugivores from dispersing seeds, or that act as pre-dispersal seed predators, to prevent recruitment. We tested this by examining the effectiveness of the Agromyzid fly, Ophiomyia lantanae, an early biological control agent that infests the fruits and seeds of the invasive plant, Lantana camara. We determined the effects of O. lantanae infestation on fruit removal rates of L. camara. We also examined the effects of O. lantanae on seed mass and investigated the recruitment responses of two common *L. camara* biotypes, pink and pink-edged red (PER). As a final component of our investigation we examined seed bank densities under L. camara infestations to determine whether recruitment was likely to be seed limited. The rate that infested fruits were removed was significantly lower than for non-infested fruits, suggesting that frugivores select against infested fruit. O. lantanae infestation only reduced seed mass in the smaller seeded PER biotype. In all recruitment experiments, the responses to infestation were biotype dependent; with reduced recruitment of infested PER seeds and neutral to increased recruitment of infested pink seeds. In the larger seeded pink biotype, O. lantanae may have promoted seedling emergence by interfering with dormancy mechanisms. In situ seed banks at L. camara populations prior to peak seed production demonstrated mean viable seed densities ranging from 78.6 - 402.8 seeds m<sup>-2</sup>, suggesting that recruitment is unlikely to be seed limited. We conclude that while O. lantanae influences recruitment and dispersal processes, the magnitude of the responses measured may not greatly influence plant densities in south-east Queensland infestations.

#### **Yvonne M. Buckley**

#### MODELLING THE SPREAD OF INVASIVE PLANTS BY FRUGIVORES

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The emergence of mutualisms between invasive plants and frugivores in their exotic range has implications for a number of areas in the ecology and evolution of invasives. I am particularly interested in how this interaction contributes to the spread of invasive plants. It has been shown that the speed of spread of invading plants seems to be most sensitive to the shape of their dispersal kernels. I will review available data on the dispersal of invasive plants by frugivores and modelling strategies for estimating speed of spread.

# POSTER ABSTRACTS (Alphabetical by first author)

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#### ROLE OF APODEMUS SPECIOSUS IN THE SEED DISPARSAL, RECRUITMENT AND REGENERATION OF *CAMELLIA JAPONICA L.*, IN THE ISLAND ENVIRONMENTS

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Role of *Apodemus speciosus* in the seed dispersal of *Camellia japonica* was investigated in an abandoned vegetable field adjacent to an evergreen broad-leaved forest. Seed dispersal by *A.speciosus* was confirmed by taking photographs of animals that removed seeds experimentally deposited on the forest floor. Camellia seeds hoarded beneath the soil were protected from drying. Mother trees of 28 seedlings were identified by examining multilocus genotypes of microsatellite DNA loci. Distance of seedlings from the nearest mature tree was significantly positively correlated with the actual dispersal distance of seeds from mature trees as revealed by DNA analysis. Seeds were dispersed from 0m to 29m with an average distance of 5.79m±5.96SD. Moreover, 54% of seeds were dispersed from mother trees in the nearby evergreen broad-leaved forest to the area of successional stage rather than around the mother trees in the forest. These results suggest that seed dispersal by *A.speciosus* contribute to expanding the distribution of *Camellia japonica*.

#### Laurence P. Barea, David M. Watson and Gary W. Luck

# WHAT DO MISTLETOE SPECIALISTS FEED THEIR CHICKS? INSIGHTS FROM THE PAINTED HONEYEATER.

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Frugivorous birds exhibit a range of strategies when feeding chicks--some switch to an insectivorous diet, others restrict their diet to high-protein fruits, while others become partly carnivorous. Mistletoe-specific birds are found in most forested ecosystems, and many subsist entirely on mistletoe fruits. Little is known about diet selection during chick rearing however, and it is unclear whether mistletoe fruits contain sufficient protein and fat for developing chicks. We addressed this issue as part of a larger scale study on the ecology of the painted honeyeater Grantiella picta (Meliphagidae), the only obligate frugivore in the family, and one of two mistletoe specialists in Australia. Data were collected during the 2004/2005 breeding season in a semi-arid woodland near Griffith, New South Wales, Australia, where the bird specialises on the fruits on grey mistletoe Amyema quandang. Twelve hundred and sixty four food items fed to chicks at 22 painted honeyeater nests were recorded over the early, middle and late stages of the nestling period. Of these, 1213 items were identified as either mistletoe fruit or invertebrates. Painted honeyeaters in this study supplemented the basic mistletoe fruit diet with invertebrates during all nest stages and fed significantly more invertebrates during the early nest stage. In all stages, however, mistletoe berries comprised the main dietary item. Incorporating measures of protein content of mistletoe fruit, we discuss diet composition of painted honeyeaters, and compare our findings with work on other mistletoe specialist birds elsewhere.

#### Kevin C. Burns

#### MACROECOLOGICAL PATTERNS IN FRUITING SEASONS

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I evaluated macroecological patterns in fruiting seasons in a meta-analysis of data from 47 biogeographic locales. I tested whether the month of peak fruit production and monthly variation in fruit production varies latitudinally. I compared phenological patterns to temperature and rainfall data to determine whether latitude is a surrogate for climatic effects on fruiting seasons. I also compared phenological patterns between the northern and southern hemispheres to evaluate whether the migratory behaviour of birds might influence fruiting seasons, because migrants are common in the northern hemisphere but rare in the southern hemisphere. In the northern hemisphere, the month of peak fruit production typically occurred from March to May in low latitudes and from October to December in high latitudes. Conversely, the timing of fruiting seasons was unrelated to latitude in Southern Hemisphere. Monthly variation in fruit production showed similar trends. In the northern hemisphere, high latitude sites undergo stronger periods of fruit scarcity than similar latitudes in the southern hemisphere and in the tropics. Both the month of peak fruit production and monthly variation in fruit production were more closely associated with latitude than to climatic variables. Overall, results show that latitudinal trends in fruiting seasons differ between hemispheres and are more closely associated with the migratory habits of birds than to geographic differences in climate.

# Cássia S. Camillo<sup>1</sup>, Lidiamar B. Albuquerque<sup>2</sup> and Lucinei Zago<sup>1</sup>

# IS ALOUATTA CARAYA A GOOD SEED DISPERSER IN THE PANTANAL, MATO GROSSO DO SUL, BRAZIL?

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Alouatta carava is a frugivorous species and sometimes a good seed disperser. The aims of this study were to document which species were eaten by A. caraya and to determine if it is a good seed disperser for these species. This study was conducted in May 2004, in the Pantanal Miranda/Abobral, Brazil. Analysis of fresh A. caraya faeces identified 7 species of fruits: Banara arguta (87.74%), Cecropia pachystachya (6.76%), Copernicia alba (2.94%), Andira inermis (1.99%), Rhamnidium elaeocarpum (0.34%), Inga marginata (0.19%) and an unidentified species (0.04%). Germination tests were conducted for the most abundant species with 4 replicates (25 seeds each) for the following treatments: 1) seeds from faeces: intact, stained and split; 2) seeds from fruits (control): intact and stained. The results from this experiment were analyzed using Student's t-test (p<0.01). There were statistically significant differences between seed germination rates of B. arguta from fruits: 79% intact and 67% stained, and from faeces: 46% intact, 33% stained and 14% split, however mean time of germination for split seeds (3 weeks) was lower than the others treatments (6-10 weeks). The germination rates of C. pachystachya control seeds (93%) were statistically different from those of feces (68%), but there was no difference between mean times of germination (10) days). In this study, A .carava reduced the seed germination of B. arguta and C. pachystachya. In addition, to this, A .caraya defecates at latrines, a behaviour that negatively affects seedling survival. Given this we conclude that A. caraya is not good seed disperser for these species.

#### Bernardo Clausi and Claudia Baartsch

#### FRUGIVORY BY BIRDS IN THREE FORESTS REGIONS AT EASTERN PARANÁ STATE, BRASIL

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Frugivory and ecosystem interactions in the Brazilian Atlantic forests are not well understood. Singificantly, at least 144 bird species of these forests are endangered. We studied avian frugivory at two locations in the highlands (Planalto) (S 25018.517'/W49005.267'), one in the lowlands (S 25o 35.664'/W 48o41.758'), two in the first mountain range from the lowlands and one on an island near the coast. The data were collected between January 2003 and January 2005, totaling 90 observation bouts over 32 days. The 10 most common birds observed feeding, from a total of 40 species belonging to nine families, were Chiroxiphia caudata, Turdus albicollis, Tangara seledon, Trogon viridis, Tangara cyanocephala, Dacnis cavana, Platycichla flavipes, Tachyphonus coronatus, Thraupys savaca, Turdus rufiventris. The summer migrants, mainly Tyrannidae species, ate fruits of many species, mainly in areas where local resident birds weren't well established. These were *Elaenia sp, Tyrannus savana*, Tyrannus melancholichus, Vireo olivaceus, Myiodynastes maculatus, Legatus leucophaius. Procnias nudicollis and Carpornis cucultatus (Cotingidae) were also observed. Procnias males disappeared from some areas in winter months. One female was detected at Planalto in June, though males were not observed at this site from March - September. Powel et al, 2004, detected inadequacies in the Costa Rica reserves due to bellbird's migration. The most common plant families were Rubiaceae, Lauraceae, Myrtaceae, Melastomataceae, Moraceae, Nyctaginaceae, Myrsinaceae. Some fruit dependent species were not detected in degraded areas. Species that were detected in these areas included: Penelope obscura, Saltator similis, Trogon surrucura, Turdus amaurochalinus, Pipraeidea melanonota, Pachyramphus validus, Stephanophorus diadematus.

# Camila Iotte Donatti <sup>1,2</sup>, Mauro Galetti <sup>1,2</sup> and Marco A. Pizo <sup>2,3</sup>

# THE MANDUVI, TOCO TOUCAN AND THE HYACINTH MACAW: A FRAGILE CONNECTION IN PANTANAL, BRAZIL

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Manduvi trees (Sterculia apetala; Sterculiaceae) are among the tallest plants in the Pantanal where they frequently appear as an emergent tree over the forest canopy. Moreover, they often contain large holes in the trunk, making them the most important nesting site for Hyacinth Macaws (Anodorhynchus hyacinthinus) throughout the Pantanal. Focal observations were carried out on ten trees in the morning (06:30-12:00) and afternoon (15:00-18:00) at Fazenda Rio Negro, MS, Brazil. After 285 h of observations eight bird species were recorded feeding on manduvi fruits. Of these, only two species (Toco toucan Ramphastos toco, and Aracaris *Pteroglossus aracari*) were considered effective seed dispersers because they ingested seeds whole rather than destroying them. The Toco toucan was by far the most frequent visitor (79% of 523 visits) and most important as it removed the bulk of seeds (92% of 433 seeds eaten). We also focused our study on the spatial distribution of the seedlings around the adult Manduvis. We found that the distribution of the seedlings was most concentrated below the mother plant, but some seedlings were also dispersed beyond the canopy, some more than 30 meter far from the closest adult. We counted 125 seedlings around 49 adults. If a healthy population of manduvis is to be maintained, not only to keep the integrity of the Pantanal ecosystem, but also to ensure the reproduction of one of its flagship species, the Hyacinth macaw, then a healthy population of seed dispersers is essential.

#### **Thomas R. Engel**

# INTERSPECIFIC AND LONG-TERM LATRINE USE BY VIVERRIDS AND HERPESTIDS AND THE IMPACT ON NATURAL FOREST REGENERATION

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African civets and sympatric genets and mongooses deposit diaspores at civetries. In coastal Kenya a high density of latrine sites exist and some are even used inter-specifically as confirmed by long-term latrine analyses and camera trapping. Numerous sites have been in permanent use for years whereas some have ceased to be used and others had moved some metres or were started as a new latrine some distance away. Yet, even after flood-like precipitation with a thorough wash-away effect, many sites remained stable, giving an inkling of the autecological orientation and synecological communication of these sites. Intra- and inter-specific latrine use provides initial natural forest regeneration. Latrines found along roads resembled disturbed terrain or gaps that require diaspores for plant regeneration. Most of the viverrids and herpestids involved disperse plant diaspores. Fruit diet variation and latrine sharing by several species and/or individuals resulted in a synergetic accumulation of different locally deposited plant diaspores. Clumped diaspore deposition at latrines causes spotted initiation of forest regeneration. At an observable time scale, shared latrine use and its variation combined with secondary seed dispersal can also result in plant regeneration over wide areas. An impact on natural forest regeneration appears considerable, since germinating seeds, seedlings, some saplings and even a few fruiting plants actually have been recorded at such shared latrine sites – and this although mortality in plant offspring is generally high. The observed variation in diversity, space and time at shared latrine sites allows an improved understanding of the complex spatio-temporal dynamics of natural plant regeneration in Africa.

#### Akiko Fukui

# **RELATIONSHIP BETWEEN SEED RETENTION TIME IN BIRD'S GUT AND FRUIT CHARACTERISTICS**

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Seed retention time (RT) of 16 fruit species in the guts of the Brown-eared Bulbul (Hypsypetes amaurotis), a major fruit consumer in Japan, was studied to examine the relationship between RT and fruit characteristics, i.e. fruit size, seed size, seed weight, and water content. Caged bulbuls were videotaped after being fed fruits, and the time of defecation of each seed was recorded. Seeds of all species were defecated in faecal pellets, with the exception of the largest seeded species Aucuba japonica, of which one seed was regurgitated and the rest defecated. Bulbuls defecated large seeds more rapidly than small seeds; RT of the last defecated seed, mean RT, and standard deviation of RT were all significantly and negatively correlated with seed size, fruit size, and seed weight. RT of the first defecated seed and water content were not correlated with any fruit characteristics examined. This suggests that bulbuls have the ability to eliminate bulky seeds rapidly from their guts in order to overcome gut limitation. Since fruit species whose seeds are regurgitated or have a short gut retention time are preferred by birds, these results suggest that large seeded species will have the advantage of larger quantity of seeds being dispersed. On the other hand, small seeds have the advantage of greater dispersal distances and thus can achieve a diverse range of seed destinations. The evolutionary interaction between fruit plants and seed dispersers may affect diversity of fruit characteristics mediated by the length of retention time in bird's gut.

# Juan Luis García-Castaño<sup>1,2</sup>, Jesús del Gran Poder Rodríguez-Sánchez<sup>1,3</sup> and Pedro Jordano<sup>1</sup>

# THE SPATIAL PATTERNS OF RECRUITMENT IN A BIRD-DISPERSED PLANT COMMUNITY. I: SEED RAIN

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Birds disperse the seeds of fleshy-fruited plants in a non-random way across the landscape, frequently resulting in highly-clumped, patchy seed shadows related to disperser habitat preferences. When compared across species, the landscape pattern of the seed shadow could result from species-specific interactions with different frugivores as well as from landscape characteristics and disperser habitat preferences. We test the hypothesis that interactions with generalist frugivore birds that respond to landscape-level habitat heterogeneity would result in consistent patterns of seed rain among plant species. We studied bird-generated seedfall patterns at a landscape scale for a fleshy-fruited plant community in a Mediterranean highland ecosystem of SE Spain, for 2 years and replicate sites with 6 distinct, patchily-distributed microhabitats. Seed rain was monitored with a stratified sampling using more than 700 seed traps, and considered from both a conspecific/non-conspecific and a functional structure, i.e. microhabitat, point of view. Species-specific spatial patterns in the seed shadows were analysed to test for general effects of landscape structure that overcome differences imposed by species-specific interactions with frugivore birds. The importance of the plant species\*microhabitat interaction on seed rain is discussed in the light of the variable patterns of interaction with different frugivore bird species existing in the study area.

# Juan Luis García-Castaño<sup>1,2</sup> and Pedro Jordano<sup>1</sup>

### THE SPATIAL PATTERNS OF RECRUITMENT IN A BIRD-DISPERSED PLANT COMMUNITY. II: SEEDLING EMERGENCE

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The spatial distribution of seedling emergence in bird-dispersed plant species across the landscape is known to be non-randomly distributed, i.e. seedlings are clumped in patches as result of many factors ranging from species-specific habitat preferences by frugivores to differential post-dispersal seed survival and/or germination. We studied the landscape-level patterns of seedling emergence for a fleshy-fruited plant community, in the same years (3 years) and sites (considering 6 distinct, patchily-distributed microhabitats), in a Mediterranean highland ecosystem of SE Spain. Seedling recruitment was estimated in plots adjacent to those used to estimate bird-generated seed rain (see the companion poster). Spatial variation in seedling emergence is related to the presence of conspecifics/non-conspecifics and to variation in vegetation structure, i.e. microhabitat type. We examine how consistent the spatial patterns of seedling emergence was across a variable landscape. If frugivore consumption is generalist, dispersers respond to landscape variation through habitat preferences and, additionally, there is no species-specific recruitment requirements imposing spatial differences in post-dispersal seed survival and/or germination, seedling emergence patterns are expected to be spatially heterogeneous but consistent among species. Otherwise, if the different stages considered do not counterbalance each other, we would expect less consistent patterns for different species. The relative importance of the plant species\*microhabitat interaction on seedling emergence is discussed in the light of the seed rain generated by frugivore birds and species-specific differences in the transitional stages from dispersed seed to established seedling.

#### **Regielene S. Gonzales**

# SEED DISPERSAL BY BIRDS AND BATS IN A SEMI-EVERGREEN LOWLAND FOREST IN THE PHILIPPINES

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A recent study in the Philippines found that in montane forest, birds predominate over bats as seed dispersal agents (Ingle 2003, Oecologia129:385-394). I wish to examine whether the same pattern is true in the Subic Watershed Forest Reserve, a seasonally dry lowland forest which is a component of the former US naval facility in the country. It is under legislative protection and was cited as an Important Bird Area by BirdLife International. I placed pairs of day and night seed traps in a successional area adjacent to a forested area. Traps were put at 0, 20, and 40 meters from the forest edge. Day traps were closed during the night, and night traps were closed during day. It was assumed that vertebrate-dispersed seeds that fell in day traps were dispersed by birds, and those in the night traps by bats. There were no other noteworthy animal dispersers in the study area, and seed predation experiments showed no significant seed predators. The traps were run for one week every month within a six-month period. Results showed that seed input decreased as distance from edge increased. Data also showed that more seeds of vertebrate-dispersed species fell into day traps. Moreover, there were more kinds of species found in the day than in the night traps. Overall results indicate that, based on the number of seeds as well as the number of species of seeds dispersed, birds play a more dominant role in seed dispersal over bats in the study area.

### **Carl Gosper and Gabrielle Vivian-Smith**

#### FUNCTIONAL GROUPS OF BIRD-DISPERSED WEEDS

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Bird-dispersed weeds represent a major challenge for conservation and weed management. The processes of seed dispersal and weed spread are complex and difficult to predict. Characteristics of the fruits and fruiting patterns of weed species may play an important role in weed invasiveness. The choice of fruits by fruit-eating birds, and hence the potential transport of seeds, may be influenced by fruit morphology, nutritional value of the fruit pulp and the time of year of fruit production. In this project we ask the following questions: Do more highly invasive species have fruits that are more attractive to dispersers and share key characteristics? Can functional groups of weeds be identified based on their fruit characteristics? These groups of species may exhibit similar modes of spread, which may be useful in their management. We present our preliminary findings for measured aspects of fruit morphology for a range of weed species in subtropical south-east Queensland. The most invasive species had smaller fruits (width 5-10 mm), fewer seeds (one to two), and seeds intermediate in size (width 3-7 mm).

#### Ronda J. Green

#### COLOUR SPECTRA OF SOME SUBTROPICAL AUSTRALIAN FRUITS

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Hypotheses relating avian and other frugivore behaviour to colours of fruits are deficient without knowledge of wavelengths beyond our own colour vision. Very little is yet known of the colour spectra of Australian fruits. This paper presents early stages of such investigation. Questions being investigated include: (1) Do some fruits which appear inconspicuous to human eyes reflect ultraviolet to a degree likely to make them conspicuous to birds? (2) Do fruits with wavelengths that maximize their conspicuousness to particular groups of dispersers or minimize conspicuousness to non-dispersers have other features consistent with such adaptation? (3) Do the spectra of red *Solanum* fruits that appear to be avoided differ in consistent ways from other red fruits readily sought by frugivores? (4) Do spectra of fruits tend to maximize conspicuousness against their own foliage and the background spectra of their usual habitats?

## Kazuhiko Hoshizaki<sup>1</sup>, Yasue Yamamoto<sup>1</sup>, Midori Abe<sup>1,2</sup> and Hideo Miguchi<sup>2</sup>

# SEEDS OF DIFFERENT QUALITY COMPLICATE THE RODENT RESPONSE TO VARIABLE SEED RESOURCE IN TEMPERATE FORESTS

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Large seeds are attractive food resource for rodents, and masting of large seeded species often affects annual rodent population size. Since rodents have generalist food habits, their response to seed resources is likely to be complex in multi-species forests. Many large seeds, oak acorns and horse chestnuts for instance, contain defensive secondary compounds (tannins and saponins, respectively). These traits may lead to differential response of rodents to variable seed resources. We monitored annual production of large seeds and rodent populations over 8 vears or more in beech mono-dominant and beech-horse chestnut-oak mixed forests in temperate Japan, and compared rodent numerical responses. In beech mono-dominant forests, annual seed resource was highly pulsed, and rodent numbers were accordingly predictable. In contrast, in the mixed-species forest, annual seed resource was relatively constant. However, rodent populations varied unpredictably among years, but the effect of beech masting was still distinct. These patterns suggest that lipid-rich beechnuts serve as high-quality foods for rodents but other seeds with defensive compounds do not, despite their large seed size. To test the hypothesis that tannins and saponins may be toxic for rodents, those seeds were fed to captive wood mice. While beechnuts maintained rodent daily body weight, oak acorns and horse chustnuts caused reduction of body weight. Artificial formula diet with a horse chestnut-saponin constituent also showed similar pattern of body-weight change and moreover resulted in death of most individuals, indicating toxicity of the sapoin. Such effects might be a mechanism underlying the complex pattern of rodent population fluctuation in mixed species forests.

#### Isaac S. Suthakar, J. Deepa and J. Balasingh

# THE ROLE OF FRUIT BAT CYNOPTERUS SPHINX IN SEED DISPERSAL AND EARLIER GERMINATION OF PLANT TERMINALIA CATAPPA.

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Bat-plant interactions are restricted to tropical parts of the world. Fruit bats are partially or fully dependent on plants as a source of food. Plants use fruit bats as pollination and seed dispersal agents. The objectives of this study were to observe the behaviour of the fruit bat, Cynopterus sphinx as a disperser of seeds of Terminalia catappa and to demonstrate the germination success of bat dispersed seeds. The study was carried out in and around St.John's College campus, Palayamkottai, (8° 44'N; 77° 42'E), India from July to December 2003. Visual observations were made on the foraging behaviour of the bat. Feeding roosts were identified by the food remnants, such as chewed fruit pellets and seeds found on the ground discarded by the bats. The dispersed seeds were collected and categorized as pericarp fully chewed (PFC) and pericarp partially chewed (PPC) fruits. Fruits with pericarp unchewed (PUC) were treated as controls. These seeds were dried and subjected to germination in mud pots. The observations reveal that C. sphinx disperse the seeds of T. catappa. While foraging, the bats plug the fruit, carry it to a nearby feeding roost, mostly, Cocus nucifera located 50 – 100 m away. They chew the pericarp, suck the juice and discard the fibre and seeds. The germination success of bat-dispersed seeds was demonstrated by sowing PFC, PPC and PUC seeds. The results show that the germination percentage of PFC was 68%, PPC 60% and PUC is 40%. The mean germination period for PFC seeds was 28.4 days ( $\pm 3.13$ ; n = 25), PPC seeds 29.8 days ( $\pm$  3.97; n = 10) and PUC 49.6 days ( $\pm$  4.66; n = 20). Plant growth parameters were significantly higher in PFC and PPC when compared to PUC control seeds. Thus C. sphinx disperses the seeds and promotes earlier and high percentage of seed germination of T. *catappa*. This reflects the mutual interactions that occur between the bat and plant species.

#### Carolina Jorge dos Santos<sup>1</sup> and Renata Cristina Batista Fonseca<sup>2</sup>

#### SEASONAL VARIATION IN FRUIT PULP CONSUMPTION AND FRUIT REMOVAL OF SYAGRUS ROMANZOFFIANA- (ARECACEAE) BY NON-FLYING TERRESTRIAL MAMMALS IN A SEMI-DECIDUOUS FOREST FRAGMENT IN BOTUCATU, SAO PAULO, BRAZIL.

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The tropical forest palm Syagrus romanzoffiana is considered an important species for the diet of several animals due its phenological features (fruition for long and distinct periods in comparison to other zoochorics species). The study aims to evaluate: (1) medium and large sized terrestrial mammals as potential dispersers of *Syagrus romanzoffiana*; (2) the fruit pulp consumption and removal seasonality. For the experiment, 15 open plots were installed, each measuring 1,5 x 1,5 m (minimum of 40 m between each plot) within Semidecidual Stational Forest fragment, located in Botucatu, Sao Paulo, Brazil. Field studies were conducted between March 2004 and March 2005. Over monthly intervals, six individual fruits of Syagrus romanzoffiana were placed within each plot, to attract frugivorous mammals; two nights after the placement of fruit, evaluation was conducted for footprints of animals, removal of fruit and amount of fruit pulp ingested. Data was analysed by the Friedman Test. Test analysis did not show a significant difference for fruit removal, however there was a period, from March to August 2004 (dry season), that the fruit pulp consumption was significantly greater and when the fruit availability was scarce within the community. Eleven mammal species were registered over the 15 sites: Didelphis sp., Lutreolina crassicaudata (Didelphidae), Dasypus novencinctus (Dasypodidae), Nasua nasua, Procyon cancrivorus (Procyonidae), Eira barbara (Mustelidae), Leopardus pardalis, Puma concolor (Felidae), Mazama sp. (Cervidae), Coendou sp. (Erethizonthidae), Dasyprocta azarae (Dasyproctidae). Among these, agoutis (Dasyprocta azarae) are considered the only fruit dispersers of Syagrus romanzoffiana due to their visiting frequency and scatter-hoarding behaviour.

#### Dave Kelly, Alastair W. Robertson, Jenny J. Ladley and Sandra H. Anderson

# ARE INTRODUCED BIRDS IMPROTANT FOR DISPERSAL OF NATIVE FRUIT IN NEW ZEALAND?

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We review the importance of introduced birds for fruit dispersal of New Zealand native plants. The major shift since human arrival in New Zealand is towards reliance on the recently-arrived native silvereye, which makes 38% of all visits to native plants and is the single most important frugivore mutualist. Four natives (silvereye, bellbird, tui, kereru) make 84% of all visits to fruit. Introduced bird species make up 32% of the species lists of visitors to native fruits, but only make 5% of all visits. The blackbird is the most important introduced bird to native fruits, but only makes 4% of all visits. This is about the same share of total visitation made by the endemic and rare stitchbirds and saddlebacks, despite these birds being absent from 80-90% of sites. This review shows that while introduced birds have been listed as visitors to fruits on native plants, overall their importance as frugivores is negligible.

### Kazuya Kimura<sup>1</sup>, Takakazu Yumoto<sup>2</sup> and Kihachiro Kikuzawa<sup>3</sup>

# FRUITING PHENOLOGY OF FLESHY-FRUITED PLANTS AND SEASONAL DYNAMICS OF FRUGIVOROUS BIRDS IN FOUR VEGETATION ZONES ON MT. KINABALU, BORNEO

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An altitudinal survey of correspondences between the fruiting phenology of fleshy-fruited tree species and the seasonal dynamics of frugivorous was carried out for 50 weeks across four vegetation types on Mt. Kinabalu in Borneo. In hill forest, a large fruiting peak during October-November in 1996, following the general flowering phenomenon, and a fruitless period during February-April in 1997 were observed. A bimodal fruiting pattern was observed in lower montane forest. A large number of frugivorous temperate migrants were present during the fruiting peak. The number of resident frugivorous birds increased and several lowland bird species appeared, when the number of resident birds decreased in the hill forest. In upper montane forest and subalpine forest, more continuous and irregular fruiting patterns without outstanding peaks were observed and the number of resident frugivorous birds was more stable throughout the year. These results suggested 1) there was a strong relationship between fruiting seasonality and seasonal dynamics of temperate migrants in the lower montane forest; 2) seasonal altitudinal movements of lowland bird species to montane vegetation zones might occur during the fruitless period in the lowland forest; and 3) the continuous fruiting pattern in the higher vegetation zones might be related to the scarcity of available frugivorous birds. The hypothesis that the influx of temperate migrants into the montane vegetation zones of Mt. Kinabalu is affected by density and habits of resident frugivorous birds was supported. Montane vegetation zones in Borneo play an important role as temporal refugia for temperate and altitudinal migrants by supplying fruit resources.

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#### DISPERSAL OF *CANARIUM EUPHYLLUM* (BURSERACEAE), A LARGE-SEEDED TREE SPEICES IN A MOIST EVERGREEN FOREST IN THAILAND

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We investigated the dispersal of a large-seeded tree species, *Canarium euphyllum* (Burseraceae), in the moist evergreen forests of the Khao Yai National Park in Thailand. By combining direct observations of fruit consumption in tree canopies (543 h) and camera-trapping observations of fallen fruit consumption on the ground (175 d), we identified the frugivore assemblage that foraged on the fruits of *C. euphyllum* and assessed their role in seed dispersal and seed predation. In the canopy, our results showed that seeds were dispersed by a limited set of frugivores, one pigeon and four hornbill species, and predated by two species of squirrel. On the ground, seven mammal species consumed fallen fruits. A combination of high fruit removal rates and short visiting times of mountain imperial pigeons (*Ducula badia*) and hornbills lead us to conclude that these large frugivorous birds provide effective seed dispersal for this tree species, in terms of quantity. These frugivorous species often have low tolerance of negative human impacts, yet loss of these dispersers would have severe deleterious consequences for the successful regeneration of *C. euphyllum*.

#### Joanna E. Lambert

#### FRUIT REMOVAL: THE RELATIVE ROLE OF PRIMATES IN THE FRUGIVORE COMMUNITY OF KIBALE NATIONAL PARK, UGANDA

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Because many primates are highly frugivorous and can comprise the majority of arboreal mammalian biomass, they are increasingly recognized for their roles as seed dispersers. Yet, evaluations regarding the impact of primate dispersers are often made without reference to the wider frugivore community. This shortfall hinders a full understanding of plant-frugivore and forest regeneration dynamics. Here, I evaluate the relative role of primates in fruit removal from three common tree species in Kibale National Park, Uganda. Focal trees of Ficus exasperata (n = 30), Uvariopsis congensis (n = 6) and Celtis durandii (n = 6) were observed for 12 days/month, June 2001 - June 2002. Fruit removal by birds, non-primate diurnal mammals (primarily squirrels), and primates (including Pan troglodytes, Lophocebus albigena, Cercopithecus ascanius, C. mitis, C. l'hoesti, Procolobus badius, Colobus guereza) was monitored. Data were collected on frugivore visitation (frequency, duration), feeding rates, fruit-processing, and seed removal. Preliminary analysis of a sub-set of 1,150h of observational data indicates that primates removed more fruit than birds as a consequence of greater frequency and duration of visitation. Feeding rates among the frugivore species were highly consistent, regardless of taxon. Cercopithecines were the most common visitors, followed by chimpanzees and colobines. C. ascanius was the most reliable frugivore, in part due to their high relative density. These preliminary results have implications for interpreting forest-wide patterns of seed dispersal. Moreover, given that primates are particularly vulnerable to population declines, these findings have conservation implications for forest regeneration in the face of declining seed dispersers.

#### Ya-Ling Lin and Ling-Ling Lee

# ROLE OF DUNG BEETLES AS SECONDARY SEED DISPERSERS IN A SUBTROPICAL MONTANE FOREST IN NORTHERN TAIWAN

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The role of dung beetles in affecting the fate of seeds dispersed by Taiwan macaques (Macaca cyclopis) was studied at Fushan Experimental Forest, a subtropical montane forest in northern Taiwan. Macaque faeces were visited by 16 species of dung beetles, including tunnellers, rollers and dwellers. Species richness and abundance of beetles were significantly different among different habitat types. Time needed to process macaque faeces and the ratio of seeds in faeces buried by dung beetles varied with season and habitat, and the results were related to the dung beetle community. Dung beetles buried macaque faeces faster and buried more seeds (73.4%) underground in warm seasons than in cold seasons (55.4%). Regardless of the sizes of mimic seeds in faeces, more seeds were buried in forest (2mm: 89.0%, 4mm: 80.8%) than in grassland (2mm: 52.5%, 4mm: 47.7%). However, smaller seeds were buried at a higher ratio and deeper than larger seeds. Seeds buried more than 5 cm below ground failed to germinate. Our results indicate that dung beetles may have a negative impact on germination of the small seeds that are often found in macaque's faeces, because small seeds are often buried at a depth that is unfavourable for germination. However, further studies are needed to examine if seed-burial by dung beetles would decrease other selection pressure against survival of seeds, e.g. predation by rodents or infection by fungi.

# Pei-Jung Lin<sup>1</sup>, Yue-Joe Hsia<sup>1</sup> and Ling-Ling Lee<sup>2</sup>

# THE POTENTIAL EFFECTIVENESS OF SUBTROPICAL FRUGIVORES IN DISPERSING SEEDS OF LAURACEAE TREES

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Fruit consumption by animals visiting 37 individual trees of five Lauraceae species (Lindera communis, Litsea acuminate, Machilus thungbergii, M. mushaensis, and M. zuiboensis) was observed and recorded for a fixed interval of time in the morning, afternoon, and at night during the fruiting season of October 1998 to July 1999 to determine the potential effectiveness of animals in dispersing seeds of these dominant trees. When animals visited a tree, the duration, the amount of fruit removed, and the way seeds were handled were recorded. At least 13 animal species were identified to consume fruits from the sample trees. Macaca cyclopis, Callosciurus erythraeus, Hypsipetes madagascariensis, Megalaima oorti, and Petaurista petaurista were the dominant fruigivores consuming more than 80% of fruits removed by all animals. The Taiwan macaque consumed more ripe fruits from 3 tree species than did other frugivores. They often stored the fruits in their cheek pouches and spat out the seeds as they moved away from fruiting trees. Therefore, they have the greatest potential of dispersing seeds for these Lauraceae trees. Large arrays of bird species, including some migratory species, are also potential seed dispersers, because they often swallowed the fruits and defecated intact seeds away from the fruiting tree. Squirrels (*Callosciurus erythraeus*) and flying squirrels (Petaurista petaurista, P. alborufus, and Belomys pearsonii) were less effective in seed dispersal, because they often fed on the pulp and dropped seeds close to fruiting trees.

#### Silvia Lomáscolo

# FIG CONSUMPTION BY MAMMALS AND BIRDS IN RELATION TO FRUIT COLOR, ODOR, AND SIZE

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Studies of fruit evolution try to explain the tendency of brightly coloured fruits to be odourless and small based on the Dispersal Syndrome Hypothesis (DSH). This hypothesis predicts that, because birds have acute colour vision, a poor sense of smell, and commonly swallow fruits whole, they should select for brightly coloured, odourless, small fruits. Because mammals rely more heavily on odour than on visual cues for finding fruits, and often eat fruits piecemeal, they should select for dull-coloured, odorous, large fruits. But, do mammals and birds really prefer fruits with the combination of fruit traits predicted by the DSH? I explore this question on fig trees (Ficus, Moraceae) of a lowland forest in Papua New Guinea by videotaping fruiting trees during the day and night (using an infrared light source) to record tree visits by frugivores. This non-intrusive method permits unbiased, uninterrupted observations under natural conditions unlike previous studies, which have used captive animals in non-natural situations, or have largely ignored nocturnal mammals due to the difficulty of their observation. Preliminary results suggest that frugivores prefer fruits with the combination predicted by the DSH, although they emphasize the importance of odour for mammals. Mammals most commonly feed on large, dull-coloured, odorous figs, but they may also feed on small, red fruits if they have a strong odour. Birds consume only small, red figs, whether they are odorous or not. Understanding frugivore choice is essential to elucidate the importance of seed dispersers in the evolution of fruit traits.

#### A. S. Markey, D. A. Orlovich<sup>-</sup> and J. M. Lord

# THE EVOLUTION OF FRUIT TRAITS WITHIN COPROSMA AND THE COPROSMINAE.

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The Rubiaceae is a pan-tropical family in which fleshy fruitedness is a common trait. However, one austral tribe, the Anthospermeae, is typically dry-fruited. Within this tribe, fleshy fruit have reappeared in the subtribe, the Coprosminae. The greatest species diversity of this subtribe is within New Zealand, from which members may have subsequently dispersed throughout the South Pacific and Australasia. It is within *Coprosma*, the predominant genus within the subtribe, that the greatest diversity of fruit traits have evolved. This genus, and its respective subtribe, the Coprosminae, have been used a model to explore the evolution of fleshy fruit. I resolved a phylogeny of the subtribe Coprosminae, and *Coprosma*, using the 16 rps chloroplast intron and nuclear markers from the ITS region. From this, I was able to speculate on how fleshy fruit have arisen within a predominantly dry-fruited tribe. It also appears that fruit colour is a labile trait which has changed throughout the evolution of the genus, and co-varies with vegetative and fruit traits in a manner predicted by a putative dispersal syndromes within New Zealand.

#### Takashi Masaki

#### SPATIO-TEMPORAL PATTERNS OF SEED DISPERSAL OF SWIDA CONTROVERSA: ANNUAL VARIATION DURING TWELVE YEARS

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Since 1987, I have been monitoring the seedfall of Swida controversa, a tall tree species with fleshy fruits, using 143-263 seed traps over a 1.2-ha area in a Japanese temperate forest. By using the data during 1987-2000, I assessed the following questions: 1) how does fruit production fluctuate annually?, 2) how does the proportion of fruits eaten by birds fluctuate annually?, and 3) How does the spatial distribution of bird-dispersed seeds fluctuate annually? S. controversa produced fruits every 2-3 years. In intervening years, few fruits were produced. The proportion of fruits eaten by birds varied annually from 15% to 80%. This variation depended on the temporal pattern of bird dispersal; the fruits of this species ripened at early September every year, and the time of the intense bird-dispersal occured at early September (denoted as the "early dispersal") or in late October ("late dispersal") or at both times, probably reflecting temporal change in frugivore abundance. When early dispersal was dominant, 40-80% of seeds were dispersed by birds in total, and when the late dispersal was dominant, 10-30% of seeds were dispersed because most of mature fruits were already fallen. Early-dispersal of seeds by birds was unsuccessful (distributed locally around the mother trees), but the distribution of late-dispersed seeds was much wider (up to 50 m). There was an optimum balance between the early and late dispersal which maximized the probability of a seed dispersed successfully. The spatially pattern of seed dispersal varied unexpectedly, and was closely related to its temporal pattern in each year.

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# HOW CAN THE ESSENTIAL OILS OF CHIROPTEROCHORIC FRUITS CONTRIBUTE TO FOREST RESTORATION?

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Since fruit-eating bats can defecate while they are flying in and between forest remnants, they are particularly important for the restoration of large open degraded areas. In order to locate their preferred food items these bats rely mainly on olfaction, focusing specifically on the essential oils released by fruits. Such oils can be extracted by headspace or hydrodistillation and we have demonstrated that fruit-eating bats can be attracted by the odour alone, both inside and outside forest isolates. The tests were conducted between 2001 and 2005 in southern and northern Brazil, using mist-nets baited with artificial fruits embedded in oil (test) and water (control). However, when set inside forest remnants the oils of *Piper* and *Ficus* mature fruits attracted mainly the expected species, i.e. those which exhibit preference for the oil used (*Carollia* and *Artibeus*, respectively), but when set outside the remnants both oils attracted almost exclusively Artibeus spp. So, we believe that in food-limited areas the odour of a potential food source will attract mainly those species that are used to flying over these hostile habitats in order to reach other forest remnants. We also verified that most bats attracted outside the forests (like those inside) defecated variable amounts of seeds, indicating that they had already fed. Consequently, we conclude that the use of essential oils of chiropterochoric fruit species in an open area which needs to be restored will attract foraging frugivorous bats and will consequently increase local seed rain through defecation, accelerating the successional process.

#### Tatsuya Otani

# EFFECTS OF MACAQUE INGESTION ON SEED DESTRUCTION AND GERMINATION OF *EURYA EMARGINATA*

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The effect of macaque ingestion was examined with respect to both seed destruction during passage through the gut and germination enhancement after defecation, using the typically endozoochorous fruits of a fleshy-fruited tree, Eurya emarginata. Mechanical and chemical actions associated with the ingestion were also examined. A fruit-feeding experiment found that 4.4% of ingested seeds could pass intact through the gut of Japanese macaques. No significant difference was detected between the seed passage percentages of six Eurva emarginata trees despite individual variation in seed weight and hardness, implying that mastication is a major factor in the severe seed mortality during the gut passage. Seeds in intact fruits showed lower germination percentage and longer germination delay than seeds with the flesh removed artificially. In contrast, no enhancement in germination was observed after passage through the gut. A series of seed treatment experiments indicated that seed abrasion did not affect germination percentage, though acid and heat-exposure enhanced germination. The two factors, severe seed destruction and germination enhancement by flesh removal, opposed each other. With the survival proportion of uningested seeds taken as 1.0, the survival proportion of ingested seeds was estimated as 0.49 (95% confidence interval of 0.14-1.46), which indicated no significant difference between the proportions of ingested and uningested seeds. This result suggests that reconsideration of the effectiveness of primate's endozoochory for relatively small-seeded plants is required, because mastication is common feature in the foraging behaviour of primates.

### Ruhyat Partasasmita<sup>1</sup> and Keisuke Ueda<sup>2</sup>

# THE ROLE OF BULBULS AS SEED DISPERSAL AGENTS IN A TROPICAL SHRUBLAND OF JAVA, INDONESIA

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Java has experienced heavy deforestation since the 16<sup>th</sup> century. Combined with a dense human population, most forests have been converted into open land with shrubs and secondary vegetation. Seed dispersal agents, e.g. birds, are important in rehabilitating disturbed vegetation. Bulbuls are a large group of frugivorous birds that are effective seed dispersers. However, the role of bulbuls in seed dispersal in shrubland is not described. We investigated the role of two sympatric bulbul species as seed dispersers in 80 ha of tropical shrubland ecosystem in a tea plantation that had been abandoned for 5 years in West Java, Indonesia. In this study we focus mainly on eighteen individual plants of four species (focal plant species method). Foraging observations were conducted by a behaviour sampling method. We found differences in foraging method and the proportional use of patchy resources between bulbul species. The Sooty-headed Bulbul Pycnonotus aurigaster used more patchy resources as a place for feeding on fruits, while the Yellow-vented Bulbul Pycnonotus goiavier used it for foraging on insects. Sooty-headed Bulbuls stayed at each patchy resource longer than the Yellow-vented Bulbuls did. The Sooty-headed Bulbul stayed at Sambucus javanica for 119 sec / visit and the yellow-vented bulbul did 103 sec / visit. The highest feeding rate (10 fruits / min) was recorded by Sooty-headed Bulbuls at Breynia microphylla. Yellow-vented Bulbuls also foraged at Sambucus javanica, Breynia microphylla, and Polygonum chinense with a similar rate (6 fruits / min.). In the study area Polygonum chinense appeared with the highest frequency (66%). It was dispersed the shortest distance (22 m) by Sooty-headed Bulbuls and Yellow-vented Bulbuls. This is explained by the presence of the bulbul's nearest perch (within 22 m) where they returned to rest and digest fruits. They defecated while perching at this site. Both Sooty-headed Bulbuls and Yellowvented Bulbuls seemed important seed dispersal agents for these plants in this area.

# Virginia Sanz<sup>1</sup> and Ronda J. Green<sup>2</sup>

# THE ROLE OF PARROTS AS SEED PREDATORS ON ACRONYCHIA OBLONGIFOLIA (RUTACEAE), AN AUSTRALIAN WINTER FRUITING TREE.

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Achronychia oblongifolia is a subtropical Australian rainforest tree which fruits in winter, the season with lowest fruit abundance, and the season when one might thus expect higher consumption of available fruits. Our objective was to find out if a high seed predator population affected the reproductive efficiency of this tree at the Green Mountain section of Lamington National Park. In this area the parrot population is high because hand-feeding of parrots is a popular tourist attraction. We conducted focal observations on eight trees located in three different areas totaling 120 hours of observations from June to September 1998. Five visiting bird species were seed dispersers: Ailuroedus crassirostris, Strepera graculina, Lopholaimus antarcticus, Sericulus chrysocephalus, and Ptilonorhynchus violaceus, and two psittacids were seed predators: Platycercus elegans and Alisterus escapularis. P. elegans made the longest visits ( $6.8 \pm 5.7$  min, n= 81), consumed more fruits, and at the highest rate  $(3.4 \pm 3.6 \text{ fr/min}, n= 44)$ , but *P. violaceus* was the most frequent visitor (1.35 visits/h). The ratio seeds dispersed:predated from the parent trees was 0.5. In spite of the high levels of seed predation, A. oblongifolia does not seem to be negatively affected as many juveniles are found under parent trees, at forest edge and in gaps. The studied population has several seed dispersers, primarily P. violaceus, but this may be due to its location at the edge of the nation's largest reserve of subtropical rainforest. In other areas, however, there could be potential problems, e.g. if parrot populations were artificially increased in severely fragmented areas.

#### Veronika Schaefer and H. Martin Schaefer

#### THE DUAL ROLE OF UV REFLECTANCE: ATTRACTION AND PROTECTION

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Although seed dispersers are viewed as the primary selective agents on fruit colour, their role remains contentious. Seed dispersers may influence fruit colour evolution either by preferring one colour (Preference hypothesis) or by being more likely to detect a colour because it is more conspicuous (Contrast hypothesis). We tested these hypotheses by presenting UVreflecting and non-UV-reflecting blueberries (Vaccinium myrtillus) against backgrounds of foliage and sand to crows (Corvus ossifragus) in a large flight cage. Against foliage, UVreflecting berries had higher contrast than non-UV-reflecting berries, while on sand the two fruit types had similar contrasts. Against foliage, crows consumed more UV-reflecting blueberries and discovered them from a larger distance than non-UV-reflecting berries, thereby corroborating the Contrast hypothesis. When berries were displayed against sand, crows consumed both fruit types equally. Because the waxy UV-reflecting bloom of blueberries and other temperate fruit species develops in still unripe fruits and at a stage, when signalling to seed-dispersers is presumably irrelevant, we hypothesized that the bloom may also have a physiological function. To test this hypothesis, we removed the epicuticular waxes responsible for the bloom from unripe blackthorn fruits (Prunus spinosus) and compared their fate during ripening to control fruits. Removing the waxes resulted in a 56% increase in fruit loss due to desiccation during ripening. After ripening, the presence of the bloom had no effect on the likelihood of a ripe fruit being consumed and its seeds dispersed. We suggest that epicuticular waxes function both to maintain water balance and to signal efficiently to seed dispersers.
#### Ian R. Smith

#### BUNYA PINES (ARAUCARIA BIDWILLII) - SPREADING SEEDS BY RATS

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The bunya pine (*Araucaria bidwillii*) has very large cones and large seeds. Now extinct relatives with similar cones and seeds appeared during the Jurassic and were likely dispersed by megafauna. *Araucaria bidwillii* now has a very limited distribution within Australia, which is likely due currently poor dispersal or its seeds. Although there are no reported dispersal agents for the seeds of *A. bidwillii*, macropods and various rats are known as predators.

To begin to examine the extent to which seeds are destroyed or dispersed by extant native fauna, I conducted a pilot study in two natural stands of *A. bidwillii*. I monitored the fates of 100 seeds placed at each site, 25 of these were protected by mammal exclosures (controls) at each site. From 63 to 92% of control seeds germinated, whereas from 30 to 48% of those exposed to mammals germinated. Much of the difference was explained by the number eaten and killed by rodents. Rodents frequently moved the seeds they handled (35 to 96%), some as far as 16 to 20 m (11% at one site). Between 9 and 46% of the seeds moved by rodents subsequently germinated, some in open sites away from conspecific adults. This pilot study indicates that small rodents may be important in maintaining local populations of bunya pines. More work is required to confirm this and to better understand the relationship and its impact on bunya recruitment.

Orr Spiegel and Ran Nathan

#### DISPERSAL EFFECTIVENESS AS A FUNCTION OF SPATIAI SCALE IN A FLESHY-FRUITED DESERT PLANT DISPERSED BY TWO AVIAN FRUGIVORES

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Although fleshy-fruited plants are relatively uncommon in desert ecosystems, they are disproportionately important as source of water, sugars and nutrients for a variety of frugivores. In this study, we compare the effectiveness of two resident bird species, Tristram's grackle (Onychognathus tristramii) and yellow-vented bulbul (Pycnonotus xanthopygos), in dispersing fleshy fruits of the desert shrub Ochradenus baccatus. Experiments in the laboratory showed minor or no difference between the two species in two dispersal qualities: in both species; passage through the gut did not affect seed survival (mean $\pm$ S.E: %94.5 $\pm$ %1.3 vs. 92.7%±1.8% respectively) and had positive effect on the probability of germination, as compared to control seeds (+31%±3.3% vs. +29%+3.6%). Video photography in the field also showed minor differences between the two species in the quantity of dispersed seeds. Yet, the two species differ markedly in the spatial scale of their movements, measured for both species at small scales (10-100 m) by laser rangefinder and, for grackles only, at large scales (1-10 km) by radio telemetry. The two species also differ in gut retention times, measured in the laboratory (mean: 2.01±1.3h vs. 0.52±0.21h; max 6.5h vs. 2.2h). Our results suggest that the two avian dispersers switch role as a function of spatial scale. The majority of the seeds dispersed in small scales (<300 m) are transported by the bulbuls; the impact of the two species is relatively equal at scales of 300-600 m. The grackles are exclusively responsible for dispersal at larger spatial scales (2-3 km, and up to 10 km).

#### **Richard J. Staniforth and Susan A. Collins**

## FRUGIVORY BY THREE LARGE MAMMAL SPECIES IN THE CANADIAN ARCTIC

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The diversity of fruit-bearing plant species in the central Canadian arctic is low (3.8% of 342 spp.), however fruit densities may be locally high (up to 200 fruits and 3,600 seeds per  $m^2$ ). The ability of herbivorous mammals to disperse seeds of such fruits was examined by analysing the viable seed content of faecal pellets from barren-ground caribou (Rangifer tarandus), Arctic hare (Lepus arcticus) and Arctic ground-squirrel (Spermophilus parryi) from four mid-arctic tundra plant communities, near Baker Lake, Nunavut, Germination tests were conducted on fragmented pellets after a period of stratification (4°C). Arctic hare and Arctic ground-squirrel were both effective seed dispersers with 15.8 and 43.6 viable, germinable seeds per 10g of dry fecal pellets, respectively. The majority of seeds (87.4%; hare, 94.3% squirrel) were from the soft-fruited species, Vaccinium uliginosum (northern blueberry), with small amounts for V. vitis-idaea (rock cranberry) and Empetrum nigrum (black crowberry). Fruits of each species were different in color (blue, red and black, respectively), but were otherwise similar in shape (spherical), diameter (0.7 cm) and possessed numerous small seeds. Dispersion of hare pellets was widespread on the tundra and assisted by anemochory, but squirrel pellets were confined to the vicinity of their burrows, nevertheless, numerous seeds of all three species were abundant in the dormant soil seed bank. Caribou were not proven to be responsible for the dispersion of any viable seeds, even though their migratory behaviour would suggest that they are potentially effective agents.

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# WHO DISPERSE SEEDS OF MYRICA RUBRA? – A COMPARISON OF THE FRUGIVORE FAUNA AND FRUIT CONSUMPTION BETWEEN YAKUSHIMA AND TANEGASHIMA ISLANDS

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What will happen in the forest when the main frugivores are exterminated / extinct ? If plant species depend only on a few frugivorous animals for their seed dispersal, their disappearance could lead to a failure in seed dispersal. In this study, we conducted a series of field observations on feeding behaviour of frugivores on Yakushima and Tanegashima Islands; islands with and without Japanese macaque, respectively. In addition, we developed 13 microsatellite loci for the shrub *Myrica rubra*, and used them to estimate the gene flow among populations on both islands. A total of 25 species of animals were recorded on the two islands, 48% of which were frugivores. Frequent visitors to the tree were Macaca fuscata *yakui*  $(4.7 \pm 1.4 \text{ times / day})$  and *Hypsipetes amaurotis*  $(3.2 \pm 0.9 \text{ times / day})$  on Yakushima Island but Hypsipetes amaurotis  $(3.8 \pm 0.9 \text{ times / day})$  only on Tanegashima Island. In a single day, these animals remove approximately 730 fruits on Yakushima Island and 11 fruits on Tanegashima Island. This suggests that *M. fuscata* should be a much more efficient seed disperser than H. amaurotis, and that most M. rubra fruits drop under the tree on Tanegashima Island due to the absence of *M. fuscata* despite consumption by *H. amaurotis*, which also take over the vacant role of macaque. However, estimates of gene flow among populations suggest that dispersal happens quite often.

#### Yasuhiro Yamaguchi

#### SHORT RANGE MOVEMENT OF BROWN-EARED BULBULS INFLUENCED BY AMOUNT OF BERRIES AND MIGRATION PATTERN

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Brown-eared bulbuls (*Hypsipetes amaurotis*) are one of the main frugivores and seed dispersers in Japan. A part of the population migrates in fall from the northern part of Japan to central and western Japan while others stay same area all year round. Eight study sites were set up in the range of the 10-840m altitude and 30 km long from north and south. Bulbuls numbers and berry abundance were investigated twice each month from October to April of the following year. The number of bulbuls increased in autumn, during the migration period, and there ware no relationship with berry abundance in high altitude areas. Increases and decreases in the abundance of berries and the number of bulbuls corresponded in the low altitude areas, particularly in the areas in which berries were abundant. These results suggest that bulbuls used high altitude areas as a passage route during migration and low altitude areas for settlement. Observational information on migration by bulbuls was collected from across all of Japan in fall to reveal the pattern of migration. When Japan is divided into ten zones, the earliest migration was detected in southern zones and continued there longest than elsewhere. This suggests that bulbuls in southern zones start migration first and are followed through the south by bulbuls from the north.

#### Masatoshi Yasuda, Shingo Miura and Nor Azman Hussein

# FALLEN FRUITS AND TERRESTRIAL VERTEBRATE FRUGIVORES IN A MALAYSIAN TROPICAL RAINFOREST

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A study of frugivory on the forest floor was carried out using camera traps in a Malaysian lowland tropical rainforest, the Pasoh Forest Reserve. Over 50 plant species were studied in a three-year non-masting period, and nearly 4000 photos of animals were obtained. Sixteen animal species including representatives of the classes Mammalia, Aves and Reptilia were considered common vertebrate frugivores in the forest. The pig-tailed macaque (Macaca *nemestrina*) was the most common visitor, using 89.8% of the plant species studied. Rodents consumed a variety of fallen fruits and seeds: *Leopoldamys sabanus*, *Maxomys* spp. (Muridae) and Lariscus insignis (Sciuridae) used 53.1% of the plant species studied, while two species of porcupines (Trichys fasciculata and Hystrix brachyura) used 38.8% and 32.7%, respectively. These common rodents showed different food utilization patterns among them. The murids consumed a wide range of fruits including those whose edible part was well protected by hard fruit wall or seed coat. The sciurids preferred rather soft and juicy fruits. The porcupines showed strong preference for nutritionally rich fruits including the families Myristicaceae, Clusiaceae and Fabaceae. Two classification methods, Morisita's similarity index and TWINSPAN, divided the plant species into four major groups according to the dominance of consumers: Macaca, Leopoldamys, Lariscus, and Trichys, Results suggest that fruit chemistry and fruit morphology are important in determining frugivore food preferences and in organizing the frugivore community, while fruit colour is not important in the fruitfrugivore relationship on the forest floor in a Malaysian lowland rainforest.

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#### HOW TO COLLECT BIRD DISPERSED SEEDS IN FOREST

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Although recent advances in genetic analysis enable us to identify parent trees of a single seed by use of DNA sequences in the seed, effective methods to collect bird dispersal seeds still remain undeveloped. Here we introduce our perch-and-trap method, which consists of a wooden perch with artificial fruits and a seed-trap beneath the perch. The artificial fruits were made of both red and black coloured glass beads (6 mm in diameter). The study site was in the Ogawa Forest Reserve, Ibaraki Prefecture, central Japan, an old growth forest where Fagus and Quercus were dominant. As the trees that bear fruit eaten by birds have a natural perch effect, we avoided setting the seed-traps under such trees. A pair of seed-traps was set in a site; one was with a perch and artificial fruits and the other was without them as a control. Fifteen pairs in total were set in 2003, and seeds in the seed-traps were collected at intervals of 2-4 weeks. Bird dispersed seeds could be distinguished from naturally fallen seeds by their appearance. The result was excellent. More bird dispersed seeds were collected by the perchand-trap method than in the control. Two peaks of seed dispersal by birds were recognized in a year: in mid winter (January) and in early autumn (August-September). The species collected were Celastrus orbiculatus, Euonymus fortunei (Celastraceae), Cornus controversa (Cornaceae), Ilex macropoda (Aquifoliaceae), Phellodendron amurense (Rutaceae), Phytolacca americana (Phytolaccaceae, introduced sp.), Prunus spp. (Rosaceae), Rhus ambigua (Anacardiaceae), and Viburnum dilatatum (Caprifoliaceae).

#### E. R. Hooper<sup>1,2</sup>, P. Legendre<sup>2</sup> and S. J. Wright<sup>3</sup>

#### THE EFFECT OF DISPERSAL AND ENVIRONMENT ON TREE AND SHRUB SPECIES COMPOSITION OF 50 HA OF TROPICAL RAINFOREST ON BARRO COLORADO ISLAND, PANAMA

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The factors hypothesized to affect plant community composition in tropical rainforest are controversial. Some evidence suggests species distributions are environmentally-dependent. A contrasting view is that floristic differences result from random, but spatially-limited seed dispersal (Hubbell 2001). We contribute to this debate by partitioning the variance of tree species composition on Barro Colorado Island between three separate fractions: 1) purely environmental, 2) overlap between spatial and environmental, and 3) purely spatial. Together spatial and environmental variables explain a high percentage of the variance (76.1%). Purely spatial factors determine 41.2%, supporting the hypothesis of dispersal-limitation, while habitat factors determine 34.9% (24.3% of this is spatially-dependent) supporting the hypothesis of environmental determinism; both are important controls of species composition. The hypothesis that species composition is random, but spatially autocorreated because of dispersal limitation assumes dispersal neutrality in that species are identical in their per capita dispersal probabilities. However, species have varying seed sizes, dispersal vectors and consequent dispersal kernels which may result in differential species' distributions. We utilize a variance partitioning methodology to compare the variance explained by non-neutral (actual) dispersal kernels represented by seed trap data (Wright 2002)] to the variance explained by neutral dispersal (identical dispersal kernels) This analysis explains 70% of the variance; actual and neutral dispersal each explain 35%. Overlap is 11.8%, resulting in floristic composition conforming to neutral model predictions. In contrast, 23% of the variation is uniquely attributable to actual dispersal kernels (seed trap data), resulting in floristic composition that does not conform to neutral model predictions.

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#### SPATIAL AND TEMPORAL PATTERNS OF RESOURCE USE BY SPECTACLED FLYING FOXES (PTEROPUS CONSPICILLATUS)

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The diet and degree of specialisation of *Pteropus conspicillatus* was examined by collecting faecal material in seed traps at four camps (communal roosts) in the Wet Tropics bioregion, Queensland, Australia. This study found temporal and spatial variation in resource use by *P. conspicillatus*. At each camp, *P. conspicillatus* displayed a unique dietary signature and utilised a wider breadth of resources than has been shown before. Furthermore, *P. conspicillatus* made substantial use of habitats other than rainforest, indicating that this species is more of a dietary generalist, and is more similar in foraging habit to three other Australian flying foxes, than previously thought. As well as seeds and pollen, viable bryophytes were found in *P. conspicillatus* faecal samples, implicating *P. conspicillatus* as a dispersal agent for a wide range of plants. The results of this study have not only broadened our knowledge of the feeding ecology of *P. conspicillatus*, they also raise new questions about the dispersal role of flying foxes for angiosperms and other plants.

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