

Biodiversity and ecological function in an age of biotic redistribution

by Erick Lundgren

Thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

under the supervision of Daniel Ramp and Arian Wallach

University of Technology Sydney Faculty of Science

March, 2021

Certificate of Original Authorship

I, Erick Joseph Lundgren, declare that this thesis is submitted in fulfilment of the requirements of the award of Doctor of Philosophy, in the School of Life Sciences, Science at the University of Technology Sydney.

This thesis is wholly my own work unless otherwise referenced or acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

This document has not been submitted for qualifications at any other academic institution.

This research was supported by the Australian Government Research Training Program

Production Note: Signature removed prior to publication.

Erick Lundgren

Date: March 31, 2021

Acknowledgements

I am deeply grateful to my supervisors, Daniel Ramp and Arian Wallach, who brought invaluable insight and guidance. They constantly reinvigorated my curiosity in ecology and asked all the hardest questions–questions that demanded interior investigation of deeply held values and that revealed new ways to look at the world. I look forward to many future collaborations with both of them.

I would also like to thank my family. To my brother Michael, whose work as an artist converges with and inspires much of my thinking about our relationship to this planet, and whose company on many desert field trips and whose endless support made all of this possible. To my brother Robin, whose persistent brilliance and personal strength has always been a beacon and a reminder of human intelligence, fortitude, and humility. I would like thank my Father for the influences he brought and for the conversations about introduced species so many years ago that started all these lines of questioning. Last but not least, my Mother for always supporting my curiosity, no matter how many snakes and bugs escaped into her house.

I would like to thank Adam O'Neill for his field wisdom and companionship and showing me the Australian desert like no one else could. To Eamonn Wooster, thank you for teaching me about 'goonbags' and all the other particularities of Australian culture, and for some of the best fieldwork trips imaginable. To many more! Thank you also to Gavin Bonsen, Chris Hasselerharm, Esty Yanco, and Caitlin Austin for inspiring conversations, friendship, and help with all the incomprehensible-to-me bureaucratic hurdles.

Finally, I would like to thank all of my coauthors on these various papers, whose names would take more pages than allowed. In particular, thanks to John Rowan for endless counsel and insight and humor, and to Owen Middleton and Simon Schowanek for their friendship and for being the nucleus for all sorts of megafauna thoughts.

List of Papers and Statement of Author Contribution

This thesis is a compilation of chapters and 4 published/publishable manuscripts. Each paper is formatted for their destination journals, except for referencing styles which were standardized throughout.

Chapter 2 – Published

Lundgren, E. J., D. Ramp, J. Rowan, O. Middleton, S. D. Schowanek, O. Sanisidro, S. P. Carroll, M. Davis, C. J. Sandom, J.-C. Svenning, and A. D. Wallach. 2020. Introduced herbivores restore Late Pleistocene ecological functions. Proceedings of the National Academy of Sciences **117**:7871-7878.

Contributor	Statement of contribution
	Conceptualization (50%)
Production Note:	Investigation (100%)
Signature removed	Formal analysis (100%)
prior to publication.	Visualization (50%)
	Writing (100%)
	Conceptualization (25%)
Production Note:	Visualization (25%)
Signature removed prior to publication.	Review and editing (50%)
Production Note: Signature removed prior to publication.	Conceptualization (25%) Visualization (25%) Review and editing (50%)

Chapter 3 – Accepted

Lundgren, E. J., D. Ramp, J. C. Stromberg, J. Wu, N. C. Nieto, M. Sluk, and A. D. Wallach. 2020. Equids engineer of desert water availability. *Science*.

Contributor	Statement of contribution
	Conceptualization (100%)
Production Note:	Investigation (100%)
Signature removed	Formal analysis (80%)
prior to publication.	Visualization (50%)
	Writing (100%)
	Formal analysis (10%)
Production Note:	Visualization (25%)
Signature removed prior to publication.	Review and editing (50%)
Production Note: Signature removed prior to publication.	Formal analysis (10%) Visualization (25%) Review and editing (50%)

Chapter 4 – In Preparation

Lundgren, E. J., D. Ramp, O. Middleton, E. Wooster, C. Hasselerharm, M. Mills, W. J. Ripple, J. Sanchez, and A. D. Wallach. 2020. Echoes of the late Pleistocene in a novel trophic cascade between cougars and introduced donkeys.

Contributor	Statement of contribution
	Conceptualization (50%)
Production Note:	Investigation (100%)
Signature removed	Formal analysis (100%)
prior to publication.	Visualization (75%)
	Writing (100%)
	Conceptualization (25%)
Production Note:	Review and editing (50%)
Signature removed prior to publication.	
Production Note:	Conceptualization (25%)
Signature removed	Visualization (25%)
prior to publication.	Review and editing (50%)

Chapter 5 – In Preparation

Lundgren, E. J., A. D. Wallach, D. Ramp 2020. The inadvertent arks: the potential for introduced species to alter conservation priorities.

Contributor	Statement of contribution
	Conceptualization (33%)
Production Note:	Investigation (100%)
Signature removed	Formal analysis (75%)
prior to publication.	Visualization (50%)
	Writing (100%)
	Conceptualization 33%)
Production Note:	Formal analysis (25%)
Signature removed	Visualization (50%)
prior to publication.	Review and editing (50%)
Production Note:	Conceptualization (33%)
Signature removed	Review and editing (50%)
prior to publication.	

Table of Contents

Certificate of Original Authorshipi
Acknowledgementsii
List of Papers and Statement of Author Contributioniii
Table of Contentsv
List of Figures and Tables
Figuresvii
Tablesxi
Thesis Abstract1
Chapter 1: Introduction
Conservation biology in an age of biotic redistribution3
Nativism in conservation biology4
Thesis overview
References
Chapter 2: Introduced herbivores restore Late Pleistocene ecological functions
Abstract22
Significance Statement23
Introduction24
Results
Discussion
Materials and Methods
Supplemental Information45
References
Chapter 3: Equids engineer desert water availability
Abstract
Main Text67
Supplementary Materials
References
Chapter 4: Echoes of the late Pleistocene in a novel trophic cascade between cougars and introduced donkeys
Abstract
Introduction

Results	106
Discussion	
Methods	117
Supplementary Materials	125
References	139
Chapter 5: The inadvertent arks: the potential for introduced populations to alter	
conservation priorities	145
Abstract	145
Introduction	146
Methods	148
Results	
Discussion	159
References	

List of Figures and Tables

Figures

the Sturges algorithm, which finds natural breakpoints in continuous distributions. Three species introduce novel groups to Australia and Europe. Points indicate species and are jittered randomly for visualization within each cell.

Chapter 3

Chapter 4

Figure 4......109

Predation on feral donkeys was associated with increased utilization of wetlands by other mammal species. **a.** Duration of activity by other mammal species at wetlands increased with maximum daily temperature (χ^2 =210.25, p<0.001), but to a greater extent at sites with active donkey predation (interaction term: t-ratio=-6.42, p<0.001). **b.** Daily activity duration of other mammals had a negative relationship to the activity of donkeys on that day, across all sites (z=4.5, p<0.001). Durations were log-transformed

to reduce over dispersion. **c.** Richness of other mammal species at sites with and without donkey kills (W=37.5, p=.045). Given unequal trap nights, richness was interpolated following (Chao <u>*et al.*</u> 2014)

Chapter 5

Tables

and relativist scenario) affected prioritization simulations both by removing species (if delisted) and by changing priority weighting (see text).

Thesis Abstract

The human-assisted dispersal of species through introductions is a form of anthropogenic change that has received significant attention in conservation biology research and in conservation policy. Until recently, introduced biodiversity has been considered by most to be synonymous with anthropogenic harm. However, the empirical premises supporting this have been criticized as evidence has falsified or qualified the claims about introduced species as biodiversity threats and as the underlying normative value of *nativism* has come increasingly into focus. This thesis asks how suspending the value of nativism might alter how we understand biodiversity change, the ecology of introduced species, and conservation policy. This thesis focuses primarily on introduced herbivores, a globally endangered functional group that has experienced significant human-caused declines since prehistoric extinctions in the Late Pleistocene.

I begin by analyzing how the twin anthropogenic forces of extinction and introduction have shaped herbivore functional diversity since the Late Pleistocene, finding that introduced herbivores restore many lost ecological functions and make assemblages more similar to the pre-extinction past than native ones. I then describe ecosystem engineering by introduced equids, who dig wells to groundwater in desert drainages. In doing so, introduced equids restore a capacity to buffer desert water availability and facilitate plant and animal communities. While introduced herbivores are functionally similar to extinct species and can have facilitative relationships with native species, little is known about whether the small-bodied predators that survived the Late Pleistocene extinctions can influence them. In Chapter 4, I report on a trophic cascade driven by cougar (*Puma concolor*) predation on wild donkeys (*Equus africanus* asinus) which significantly altered their behavior and their effects on desert wetlands.

Finally, I synthesize this work by asking to what extent broadening our value systems changes conservation priorities. I empirically test several value scenarios, including *nativism* and more inclusive alternatives, by conducting spatial prioritization simulations to find optimal solutions to protect threatened species. I find that while the scale of global endangerment overshadows the scale of introductions, including introduced species as biodiversity provides new opportunities to prevent extinctions and shifts conservation priority into overlooked landscapes.

Like any applied scientific discipline, conservation biology is comprised of both normative values and empirical facts. It is, however, imperative that conservation biology interrogate its values as robustly as its facts. This thesis suggests that expanding conservation values offers new understandings of ecological change, reveals unseen ecological relationships, and provides new solutions to prevent global extinctions.