

**LOCAL-SCALE ASSESSMENT OF REGIONAL CONSERVATION PLANS:
STRATEGIES FOR THE CONSERVATION OF ANIMALS AND PLANTS IN A
TROPICAL RAINFOREST AND SURROUNDING MIXED-FARMLAND**

by

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Abstract

There is an urgent need to conserve biodiversity in human-modified landscapes throughout the tropics. Animal conservation has traditionally focused on single species, but it remains unclear whether these strategies will also protect other taxa that co-occur within the ecosystem. These uncertainties can also affect plant conservation if management interventions change plant-animal interactions. I identified steps to mitigate the effects of hunting, forest product extraction, and farming on rainforest animals and plants in Suaka Margasatwa Buton Utara (SMBU) and the surrounding mixed-farmland on Buton Island, Southeast Sulawesi, Indonesia. First, I used Bayesian Network inference to assess whether protecting anoa (*Bubalus* spp.) habitat might also benefit other animals by modelling species co-occurrences in relation to habitat and human activities. Next, I completed a pantropical Network Meta-Analysis (NMA) to identify where controlling the foraging of granivorous mammals might reduce mortality of management-sowed seeds in human-modified forests. Finally, I used the NMA to guide an experimental assessment of how seed predation might affect the regeneration of nine plant species in the reserve and mixed-farmland. Buton macaques (*Macaca ochreata*) did not co-occur with anoa and were the only species to avoid human-dominated areas. The government might consider concentrating patrols in easy-to-access areas to increase the distribution of macaques throughout SMBU and the mixed-farmland. The NMA identified that granivore control could help reduce seed mortality, but which seeds to protect depended on the type of human activity that modified the forest. At SMBU, granivore control was not required in the mixed-farmland because seed predation was very low for 78% of the studied plants. Low seed losses in the mixed-farmland suggested that forest regeneration might be enhanced by increasing macaque distribution and natural seed rain throughout those areas. My approach could be used to design projects that

conserve animals and plants in human-modified ecosystems. Local co-occurrence analyses can identify species that remain vulnerable to humans under conservation projects focused on other species. In data deficient situations, wide-scale evidence synthesis using NMA can help guide decision making, such as when to use granivore control, in human-modified ecosystems.

Lay Summary

Numerous tropical animals and plants are threatened by human activities. Although protected areas can conserve biodiversity, many species of conservation concern are also dependent on land found outside reserves in areas used by humans. I identified steps to protect animals and assist the regeneration of plants in a rainforest and the surrounding mixed-farmland areas on Buton Island, Southeast Sulawesi, Indonesia. First, I showed how reducing human activities in easily accessed areas can positively affect animal species. Next, I identified where protecting tree seeds might improve their survival and overall forest regeneration. Finally, I confirmed that seeds naturally deposited in the mixed-farmland do not require protection from seed-eating animals during regeneration. Overall, I provided evidence that mixed-farmland areas can be sustainably managed for biodiversity conservation while also supporting human livelihoods.

Preface

This dissertation is a combination of original, collaborative, and synthesis work completed by the author, A. L. Contasti. The fieldwork reported in Chapters 2 and 4 was supported largely by Operation Wallacea Indonesia and was approved by Operation Wallacea and Kementerian Riset Dan Teknologi Republik Indonesia (RISTEK). All fieldwork was covered by RISTEK research permits issued by the Indonesian Government to A. L. Contasti in 2014 (no. 143/SIP/FRP/SM/VI/2014) and 2015 (no. 168/SIP/FRP/SM/V/2015). I worked in partnership with the Universitas Haluoleo in Kendari, South East Sulawesi, Indonesia and researchers Abdul H. Mustari (2014) and Suci Barasamna (2015).

Chapter 2: original and collaborative work

I developed the research theme for Chapter 2, completed the analysis, and wrote the Chapter. I worked in collaboration with G. Z. L. Froese to design the camera trap survey and collect the data during my 2014 field season. I designed the survey and collected the data during my 2015 field season. During each season, the sampling design was modified from that developed by G. Z. L. Froese at my study sites in 2013. Chapter 2 analyses include the camera trap data collected by G. Z. L. Froese in 2013 with permission, the camera trap data collected by G. Z. L. Froese and I during 2014, and the camera trap data collected by myself in 2015.

G. Z. L. Froese completed his original B.Sc. Honours thesis using the 2013 data (University of British Columbia, Vancouver). These and the 2014 data were also used in the published work Froese, G. Z. L., A.L. Contasti, A. H. Mustari, and J. F. Brodie. 2015. Disturbance impacts on large rain-forest vertebrates differ with edge type and regional context in Sulawesi, Indonesia. *Journal of Tropical Ecology*. 31(6):509–517. G. Z. L. Froese completed the

analyses for each work, which were unrelated and completely different from the work I present in Chapter 2.

The code for the hierarchical community occupancy model used to correct for detection errors in the camera trap data was obtained and modified from Kéry and Royle (2016) Chapter 11 “Hierarchical Models for Communities” in *Applied Hierarchical Modelling in Ecology* Analysis of distribution, abundance and species richness in R and BUGS.

Chapter 3: original, collaborative, and synthesis work

I developed the research theme for Chapter 3, completed the analysis, and wrote the Chapter. Chapter 3 is a network meta-analysis of post-deposition seed predation experimental data gathered by 17 different research groups. Each of the research groups were independently responsible for designing and running their experiments. In all but two cases, the data were published by each research group in peer reviewed journals. The three-level network meta-analysis code used in the analysis was modified from that published in Saramago et al. (2012).

I requested the raw experimental data from each lead author in exchange for co-authorship on any publication arising from the meta-analysis. No manuscripts have been submitted to date, so co-authorship has yet to be provided. The research groups are listed in Appendix B by published work with co-author identities and corresponding institution tenures.

Chapter 4: original work

I developed the research theme for Chapter 4, designed and ran the experiments, completed the analysis, and wrote the Chapter.

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List of Abbreviations

BF: Bayes Factors

BN: Bayesian Network

NMA: Network Meta-Analysis

NTFP: Non-timber forest product

SMBU: Suaka Margasatwa Buton Utara

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for me

Chapter 1: Introduction

Most of the world's tropical animals and plants are threatened by human activities such as hunting, non-timber product extraction, and farming (Corlett 2016, Hughes 2017, Díaz et al. 2019). Protected areas can conserve biodiversity, but numerous species of conservation concern are also found outside reserves in areas that are used by humans (Riley 2008). There is an urgent need to sustainably manage multi-use landscapes for biodiversity conservation while also allowing for continued support of human livelihoods.

Finding efficient ways to protect animal communities is an ongoing challenge for conservationists. Some species can persist in human-modified landscapes by changing their diet (Riley 2007), activity patterns (Riley 2008), or habitat selection (Remis and Kpanou 2010), whereas more vulnerable species tend to be rare and difficult to locate across the landscape (Bodmer et al. 2018, Thompson et al. 2020). The 'umbrella conservation strategy' (Wilcox 1984) was originally designed for situations where each species cannot be separately protected. The strategy assumed that co-occurring taxa would indirectly benefit from protecting the one species that had moderate sensitivity to human activities (Fleishman et al. 2001) and a wide distribution (Berger 1997, Andelman and Fagan 2000). Despite its appeal for managers with limited time (Fleishman et al. 2001) and funding (Roberge and Angelstam 2004), it remains unclear whether the umbrella strategy might also protect the remaining animals in the community.

Uncertainties in animal conservation can also have unknown repercussions for plants. Many tropical plants interact with animals during at least one phase of their life history (Howe and Smallwood 1982, Bascompte et al. 2003, Wright et al. 2007). Behavioural changes in animals can affect plant-animal interactions when, for example, a mutualistic animal partner no longer occurs in a once occupied habitat (McConkey and Drake 2006) or when an antagonistic

partner increases in abundance (Dirzo et al. 2007, Beck et al. 2013). Any management or human induced changes in seed dispersing or seed eating animals can therefore affect the natural regeneration of plants in human-modified ecosystems.

A common approach to mitigate threats to plants is assisted regeneration such as direct seed sowing into human-modified areas (Blakesley et al. 2002, Holl and Aide 2011, Garcia et al. 2016). Evidence that some non-human primates move between protected and degraded areas (Koné et al. 2008, Estrada et al. 2012, Albert et al. 2014) suggests that primate conservation might also indirectly enhance regeneration by increasing natural seed rain (Chapman 1989, Vulinec et al. 2006, Andresen et al. 2018). However, post-deposition seed predation – which is known to dramatically alter patterns of seed deposition even in undisturbed areas (Andresen and Levey 2004, Razafindratsima 2017) – is rarely quantified for primate-dispersed seeds (Lambert 2002, but see Estrada and Coates-Estrada 1991). Efforts to control granivore populations can reduce seed loss (Garcia-Orth and Martínez-Ramos 2008, Pender et al. 2013), but variation in post-deposition predation among ecosystems and seed species (e.g., *c.f.* Holl and Lulow 1997, Lambert 2002, Chapman and Chapman 2003, Rosin and Poulsen 2016, Cao et al. 2018) makes it difficult to design an effective control methods for a particular human-modified ecosystem.

My goal was to find a way to protect animals while also assisting the regeneration of plants in a tropical rainforest and the surrounding mixed-farmland areas on Buton Island, Southeast Sulawesi, Indonesia. First, I assessed whether an umbrella species conservation strategy might benefit all species within the community of terrestrial mammals and ground birds. Next, I looked for patterns in post-deposition seed predation that suggested where granivore control (e.g., fencing or burying sowed seeds) might improve seed survival in assisted forest regeneration projects. Finally, I investigated how changes to animal species after successful

management might affect assisted forest regeneration in the mixed-farmland areas. I completed these steps in three different analysis chapters as follows:

Chapter 2: Umbrella species conservation: what can we learn from modelling small-scale co-occurrence patterns? A case study from the rainforests of Buton Island, Indonesia

In Chapter 2, I answered the question: ‘could protecting one animal species and its habitat also protect other co-occurring animals from human activities’? To do this, I used Bayesian Network inference to model co-occurrences among all species in relation to local habitat and human activities.

Chapter 3: Assisted regeneration of human-modified tropical forest ecosystems: where might seed predator control improve the survival of sown seeds? A hierarchical network meta-analysis

In Chapter 3, I answered the question: ‘where and for what seeds might granivore control mitigate seed losses in assisted regeneration projects’? To do this, I completed a pantropical hierarchical Bayesian Network Meta-Analysis that quantified the probability of post-planting predation on seeds of a given size in tropical forests that had been modified by a specific type of human activity.

Chapter 4: Will post-deposition seed predation affect the regeneration of mixed-farmland at a tropical rainforest reserve boundary

In Chapter 4, I answered the question: ‘in addition to human-sowing, could increasing the distribution of a seed-dispersing animal contribute to the regeneration of human-modified

habitats’? To do this, I used the NMA results from Chapter 3 to inform an experimental assessment of the probability of post-deposition seed predation in forest and mixed-farmland areas at my site that were used and avoided by non-human primates.

Chapter 2: Umbrella species conservation: what can we learn from modelling small-scale co-occurrence patterns? A case study from the rainforests of Buton Island, Indonesia

2.1 SUMMARY

The umbrella and other focal-species conservation strategies were designed to protect co-occurring biota indirectly from human-mediated disturbances. Many have questioned the validity of these approaches after identifying fine-scale discrepancies in habitat requirements and vulnerabilities among co-occurring species. Here I investigated how local-scale human activities affect the efficacy of ‘umbrella’ species as indicators of ecosystem integrity. I did this using a Bayesian Network (BN) of interspecies co-occurrences that estimated the probability that sets of species would be found together in different habitats depending on the accessibility of those areas to humans. The BN serves as a visual aid for selecting an ‘umbrella’ species by confirming co-occurrence relationships, determining in which habitats species co-occur, and identifying which co-occurrences are vulnerable to human activities. I demonstrated how to use the BN for an assemblage of rainforest vertebrates by asking whether the Strategy and Action Plan for Conservation of Anoa (*Bubalus quarlesi* and *depressicornis*) 2013–2022, developed by the Indonesian Ministry of Forestry, would also serve to protect other focal species in the area. The BN identified two subnetworks of co-occurring species along an elevation gradient. I found no empirical evidence that anoa or any of their co-occurring species (red junglefowl *Gallus gallus*, Malay civet *Viverra zibetha*, and Murid rodents) were affected by human activity. On the other hand, the Buton macaque (*Macaca ochreata*) and Sulawesi warty pig (*Sus celebensis*) were more likely to co-occur in forested and mixed-farmland areas that were less accessible to humans. Small-scale differences in habitat selection among anoa and macaques therefore

rendered anoa an ineffective umbrella species for the community. In addition to the current steps to protect anoa, my results indicate that a separate conservation action plan is required for macaques. Overall, the BN of co-occurrences provides additional evidence that ignoring small-scale discrepancies in habitat selection and avoidance of human dominated areas could lead to the failure of umbrella species conservation strategies.

2.2 INTRODUCTION

Human activities are causing rapid species loss from communities worldwide (Murphy and Romanuk 2014, Martínez-Ramos et al. 2016, Díaz et al. 2019). The umbrella (Wilcox 1984) and other focal-species (Lambeck 1997, Caro 2010) conservation strategies (hereafter ‘umbrella’) were developed under the assumption that protecting a single species or the habitat that it required would also protect co-occurring species in the community. The ideal umbrella species was moderately sensitive to human disturbance (Fleishman et al. 2001), had wide distribution patterns (Andelman and Fagan 2000), and a large home range size (Berger 1997). Conservation decisions could therefore be made by ‘casting a wide net’ to protect biodiversity without the need to directly model small-scale co-occurrence patterns. Although criticized for simplicity (Mills et al. 1993, Simberloff 1998, Lindemayer and Fischer 2003), the umbrella strategy remains an appealing tool for managers with limited time (Fleishman et al. 2001) and funding for research (Roberge and Angelstam 2004).

Despite its appeal, the extent to which umbrella strategies effectively protect biodiversity remains unclear. Identifying umbrella species using wide-scale distribution patterns ignores subtle differences in occurrence patterns among species, which can change in different environmental conditions (Bertness and Callaway 1994, Tylianakis and Morris 2017) and in

human-modified areas (Bregman et al. 2015, Pringle et al. 2019). Local habitat conditions may therefore alter co-occurrence between the protected and other species (Lindemayer and Fischer 2003, Tikhonov et al. 2017) in a way that reduces the effectiveness of an umbrella conservation strategy. For example, Carlisle et al. (2018) found that improving the nesting habitat of an umbrella species (*Centrocercus urophasianus*) had damaging effects on sympatric species with different habitat requirements. Local-scale variation in human activities can also make it difficult to identify an effective umbrella species. For example, Ficetola et al. (2007) could not identify a suitable umbrella species from a community of small vertebrates due to local-scale differences in vulnerability to human presence and vegetation trampling. These observations suggest that ignoring small-scale differences in habitat selection and avoidance of human dominated areas could lead to the failure of umbrella conservation strategies. Modelling small-scale co-occurrence patterns among species might therefore improve our understanding of the degree to which an ‘umbrella’ protects the remaining species.

Ecologists have developed several tools to model co-occurrence among species. However, many have limited use for managing the small-scale negative effects of human activities on biodiversity. Joint species distribution models (Pollock et al. 2014, Tikhonov et al. 2017) require extensive, high resolution co-occurrence data and maps of human activities including small-scale disturbances such as illegal hunting (Deith and Brodie 2020), which are often not available for threatened species (Andelman and Fagan 2000). Species \times site presence-absence matrices (Diamond 1975, Gotelli and McCabe 2002) do not control for environmental effects or account for imperfect detection, which can lead to biased estimates of presence for threatened species in an area because many are rare and elusive (Kéry and Royle 2016). Although MacKenzie et al. 2004 developed a method to estimate the fine-scale probability of co-

occurrence among species pairs, the analysis is limited to ≤ 4 species, which is unrealistic for most animal communities. A more suitable framework would estimate the joint probability of co-occurrence among all species while accounting for habitat selection and vulnerabilities to human activities.

Network theory is a flexible alternative for modelling co-occurrences across fine-scale habitat gradients in human-modified landscapes. For example, bipartite interaction networks (Bascompte et al. 2003) have been modified to guide conservation by identifying which habitats support the most co-occurring species (Marini et al. 2019). Bayesian Network (BN) inference can also identify habitat-species and species co-occurrence relationships among communities (Milns et al. 2010) and, in some cases, can outperform classic regression-methods when identifying co-occurrence patterns (Thompson et al. 2020). BNs have been used to guide conservation by identifying important habitat for threatened species (Amstrup et al. 2008) and shared habitats among species (MacPherson et al. 2018), but they have never been extended to model small-scale co-occurrences in response to environmental and human disturbance conditions.

The need for detailed, small-scale modelling approaches that assess the effectiveness of conservation strategies is urgent in the tropics where humans have altered the historic pattern of species occurrence across many communities (e.g., Peres 2000, Laurance et al. 2006). These changes are particularly concerning in Southeast Asia where many species, most of which are endemic, are threatened by extremely high rates of deforestation, conversion of land to plantations, and hunting (Hughes 2017). Although some have modelled co-occurrence among species in response to large-scale disturbances such as selective logging (Brodie et al. 2018a),

there have been few, if any, attempts to use co-occurrence patterns to design an umbrella species conservation strategy.

Here, I developed a BN of co-occurrence patterns among all terrestrial mammals and one bird making up the regional species pool of a tropical rainforest reserve on Buton Island, Southeast Sulawesi, Indonesia. I then used those patterns to calculate the conditional probability that pairs of species would be found together based on similarities in habitat selection and avoidance of areas that were easy and difficult for humans to access. Finally, I asked whether the Strategy and Action Plan for Conservation of Anoa (*Bubalus quarlesi* and *depressicornis*) 2013–2022 (Mustari et al. 2015), developed and implemented by the Ministry of Forestry, Republic of Indonesia, would also serve as an effective umbrella species conservation strategy for mitigating the local-scale effects of human activity on the occurrence of the focal species. The overall effectiveness of an ‘umbrella’ species for protecting regional biodiversity is usually assessed a much higher number of species from several different taxa including mammals, birds, reptiles, invertebrates, and plants (Wilcox 1984, Shi et al. 2019, Ward et al. 2020). However, I chose to focus only on mammals and birds from this system because I was interested in identifying small-scale co-occurrence patterns of vertebrates that are threatened by human activities as listed on the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2019).

2.3 METHODS

My objective was to identify co-occurrence patterns among all species in relation to fine-scale habitat conditions and human activities and to use those patterns to inform local-scale conservation decisions. To achieve this goal, I used new observation data and a BN to model

how multiple species use habitat in a lowland tropical rainforest reserve and in the farmland just outside the reserve boundary where farmers plant cash crop trees interspersed with native vegetation (hereafter ‘mixed-farmland’; Sorensen 1996, Pangau-Adam et al. 2006).

First, I collected new observations of terrestrial mammal and bird occurrence and habitat conditions at different sites in Suaka Margasatwa Buton Utara (SMBU) reserve and mixed-farmland on Buton Island, Southeast Sulawesi, Indonesia. Second, I used a Bayesian Network algorithm to determine similarities and differences in how each species uses the landscape and whether habitat use depended on how easily an area could be accessed by humans. I assumed that area accessibility was proportional to the level of human activity where: (i) easy to access mixed-farmland had higher levels of subsistence agriculture, hunting, and non-timber forest product (NTFP) extraction than did difficult to access mixed-farmland and (ii) easy to access forest had higher levels of hunting and NTFP extraction than did difficult to access forest. An analysis of data from years one and two (Froese et al. 2015) identified correlations between the abundance of several species and distance (Euclidian) from human landscape features. My analysis builds on this prior work by assessing potential effects of habitat and human activities on co-occurrence.

Next, I calculated the conditional probability that two or more species were found together within a certain habitat and whether those co-occurrences changed in easy vs. difficult to access areas. BN analysis is ideal for this problem because it incorporates multiple forms of uncertainty when identifying co-occurrences among species. Altogether, this approach allowed me to evaluate whether the Strategy and Action Plan for Conservation of Anoa (*Bubalus quarlesi* and *B. depressicornis*) 2013–2022, developed for the Ministry of Forestry, Republic of Indonesia (Mustari et al. 2015), would also serve as an umbrella species strategy to indirectly protect the

remaining focal animals from current human activities at my study site. The anoa is endemic to Sulawesi, is a flagship species for conservation, and meets the general criteria for an ‘umbrella’ species including wide habitat distribution patterns and a large home range size (Burton et al. 2005; Mustari et al. 2015).

2.3.1 Case study

I present data from a three-year study of a little-known rainforest animal community in the SMBU reserve and the contiguous mixed-farmland on Buton Island, Southeast Sulawesi, Indonesia. The focal community consists of all ground-dwelling mammals and birds (Table 2.1) that were captured on camera traps including: the lowland and mountain anoa (‘anoa’), Buton macaque (*Macaca ochreata*; ‘macaque’), Malay civet (*Viverra tanglunga*), Murid rodents (Muridae; ‘rodents’), Sulawesi warty pig (*Sus celebensis*; ‘warty pig’), and red junglefowl (*Gallus gallus*; ‘junglefowl’). The remaining mammals in the community were not included as their almost exclusive arboreal nature did not allow for monitoring using camera traps. These mammals included: the Sulawesi bear cuscus (*Ailurops ursinus*), Sulawesi dwarf cuscus (*Strigocuscus celebensis*), the spectral tarsier (*Tarsius spectrum*), and nine squirrel species. The anoa is the only species in the terrestrial community listed as ‘endangered’ on the IUCN Red List of Threatened Species (IUCN 2019). However, macaques are threatened by retaliatory killing for crop raiding (Harwick et al. 2017), and all other species are listed as being ‘threatened by hunting’ within their range by the IUCN (IUCN 2019).

SMBU (WDPA ID 8877; 4°57’S, 123°14’E; 820 km²) (Figure 2.1) was established in 1979. It is a federally governed reserve that is managed by the Balai Konservasi Sumber Daya Alam Sulawesi Tenggara. The area is lowland tropical forest on karst coral limestone with a high

diversity of tree species (Powling 2006). Climate is equatorial and changes with elevation from Köppen-Geiger climate zone Aw (equatorial savanna with dry winter) outside reserve boundaries to Am (equatorial monsoon) in the interior (Kottek et al. 2006, ORNL DAAC 2017). My sites were mainly Aw (4 sites Am). Rainfall (1,500–2,000 mm annual average) is greatest from April–June with a dry season from June–September (Jennings et al. 2006).

2.3.2 Conceptual Bayesian Network of co-occurrences

BNs can model species-specific responses to the environment, habitat, and human activities while also identifying significant co-occurrence patterns among species (Marcot et al. 2006, Milns et al. 2010). All species in this analysis have a unique set of habitat requirements and a unique response to human activities. Different responses could therefore drive co-occurrence patterns on the local scale, and I expect that such differences will affect the outcome of an umbrella species conservation plan.

I identified species co-occurrences in relation to habitat and human activities in SMBU and the surrounding mixed-farmland in two steps. In the first step, I designed a conceptual BN showing predicted relationships between explanatory (habitat and area accessibility for humans; hereafter ‘area accessibility’) and output (species-specific occurrence and co-occurrence) variables for my focal species. In the second step, I used a Bayesian learning algorithm to design an empirical BN that showed only the co-occurrence relationships that were supported by the field data I collected in SMBU (see 2.3.3: *Empirical Bayesian Network of Co-occurrences: learning the structure from data*).

I designed the conceptual BN using predicted habitat use and hypothesized species co-occurrence relationships from other systems containing similar species. However, it is important

to note that the empirical BN was not constructed using traditional statistical hypothesis testing of the relationships in the conceptual BN. Rather, I used the conceptual BN to guide my interpretation of the empirical BN to ensure that the habitat-occurrence and species co-occurrence relationships made biological (not just statistical) sense. The empirical BN was used for all subsequent analyses.

In BN terminology, the BN of co-occurrences is called a Directed Acyclic Graph (DAG) containing a set of nodes (the variables) connected by directed arrows (Korb and Nicholson 2010). Conditional relationships among variables are indicated by the arrows (or ‘arcs’) that start at the explanatory (hereafter ‘parent node(s)’) variables and end at the output variables (hereafter ‘child node(s)’) (Figure 2.2a upper panel). A BN can contain all continuous variables, all discrete variables, or a mixture of continuous and discrete variables. I chose to model relationships among all discrete variables.

The occurrence and co-occurrence relationships included in the conceptual BN were based on observations from similar mammals and birds in other systems. I predicted that species-specific occurrence would respond to the following environmental and habitat conditions [*habitat-occurrence predictions (HO)*]: canopy height (m), elevation (m above sea level), and distance from water. I also predicted that species-specific occurrence would be different in areas that were easy and difficult for humans to access based on the assumption that accessibility was proportional to the level of hunting and NTFP extraction in mixed-farmland and forest [*area accessibility-occurrence predictions (AAO)*]. Finally, I added arcs between the following environmental, habitat, and activity variables that were predicted to be highly correlated (see Marcot et al. 2006): elevation→area accessibility and mixed-farmland/forest area→canopy

height. Arcs between habitat and area accessibility nodes described the distribution human activities with habitat at my site (following Milns et al. 2010).

I then extended the conceptual BN to allow for co-occurrence among pairs of species following the Milns et al. (2010) method of adding arcs between species-specific occurrence nodes (Figure 2.2b upper panel). These arcs represent both positive (co-occur together) or negative (avoidance) relationships. Under this framework, habitat and area accessibility mediate co-occurrence by affecting one or both species per pair (Figure 2.2c upper panel). All arcs in a BN must be unidirectional (Korb and Nicholson 2010, Scutari 2010), so I assigned each species per pair as an ‘influencer’ (parent) or ‘responder’ (child) based on potential (but not tested) relationships that underlie co-occurrence of similar species in different ecosystems [*co-occurrence hypotheses (COH)*]. I also based co-occurrence relationships on known and predicted habitat, behaviour, and diet requirements for the focal species (Appendix A Table A.2.1). For example, I assumed that two species with similar diets would compete for resources and therefore have negative co-occurrence patterns. Predicted relationships between habitat and occurrence nodes (Figure A.2.1), between area accessibility and occurrence nodes (Figure A.2.2), and hypothesized relationships between species occurrences (Figure A.2.3) are given in Appendix A.

2.3.3 Empirical Bayesian Network of Co-occurrences

The occurrence and co-occurrence relationships included in the empirical BN were identified using the ARACNE (algorithm for the reconstruction of accurate cellular networks; Margolin et al. 2006) score-based algorithm included in the R (R Core Team 2018) package “bnlearn” (Scutari 2010). The ARACNE algorithm ‘learned’ the empirical BN structure from

field data (see 2.3.5 *Bayesian Network of Co-occurrences: dataset*) by placing lines ('edges') between all habitat, human activity, and species occurrence nodes and then sequentially removing lines without statistical dependencies. The resulting BN contained lines between nodes with statistically significant relationships without a specified direction. I converted all the lines into arcs following the Milns et al. (2010) method of forcing all arcs to begin at habitat and end at occurrence (e.g., elevation→occurrence); to begin at area accessibility and end at occurrence (accessibility→occurrence); and to begin at the 'influencer' and end at the 'responder' species (influencer→responder).

Each habitat, human activity, and species occurrence node in the empirical BN represents a conditional probability table (Figure 2.2 a–c bottom panels) indicating the probability (i.e., conditional probability distribution) that a variable takes a certain state given the state of its parents (here states are discretized variable categories). I calculated the conditional probability table for each node by fitting the empirical BN to field data using Bayesian parameter estimation and the R package 'bnlearn'. For example, in Figure 2.2 a, the occurrence of species a depends on how accessible an area is to humans (upper left panel). The conditional probability (lower left panel) that species a is present is 10% if the area accessibility is high, whereas the conditional probability that species a is present is 85% if the area accessibility is low. For any node without a parent, the conditional probability indicates the distribution of habitat types, area accessibility, or species occurrence across my study site. For example, in Figure 2.2 a, the 'habitat' node (upper right panel) does not have a parent node. Its conditional probability table (lower right panel) indicates that 70% of the habitat at my study site was habitat b whereas 30% was habitat a. The probabilities for each node state within the conditional probability tables are provided without

confidence intervals because the variables are modelled using the Dirichlet distribution (Korb and Nicholson 2010).

2.3.4 Assumptions and sensitivity analyses

The assumptions of the empirical BN are (Korb and Nicholson 2010): (1) for each node, the probability of one state was independent of all other possible states (local parameter independence), (2) for each child in all parent-child combinations, the parameter values under one parent state were independent of the parameter values for all other possible parent state, (3) for each child in all parent-child combinations, the parameter values were independent of the states of all non-descendant nodes given the value of its parents (local Markov property), and (4) the prior distribution for all parameters were Dirichlet distributed (uniform).

I completed a sensitivity analysis on the empirical BN using the imaginary sample size (iss) and the conditional/marginal probability distributions for each node. For the iss analysis, I changed the weight assigned to the prior and to the data using the imaginary sample size (iss). Higher values place more weight on the prior, which makes it easier to find parent-child relationships, whereas low (iss = 1) values rely more on the data (Milns et al. 2010, Scutari 2010). I calculated the iss required to find relationships without relying on the data (α^*) (Scutari 2010) and then compared network scores for those fit with iss = 1 (more weight assigned to data) and iss = α^* . The network with the highest score was fit using iss = 1 (following Milns et al. (2010). For the conditional/marginal distribution analysis, I compared the conditional probability distributions (listed in conditional probability tables) for each child node to their corresponding marginal probability distribution. Marginal probability distributions were calculated separately for each child without information on the state of its parent(s) (see Witten et al. 2017) and

represent the probability that a child takes a given state independent of the relationship with its parent(s). The conditional probability distribution for any node is equal to its marginal probability distribution if the state of that node is not related to the state of any other nodes in the network (i.e., the node should not be connected to any other nodes in the BN). Therefore, all relationships were removed from the BN for any node with equal conditional and marginal probability distributions for a child were equal. All diagnostic values were calculated using “bnlearn”.

2.3.5 Identifying support for relationships

The empirical BN contained relationships between only those habitat and area accessibility variables that had a statistical dependency with species occurrence and interspecies co-occurrences. Significance was based on Bayes Factors (BF), which were calculated as an empirical probability for the conditional dependence between all possible habitat/area accessibility and species occurrence nodes (Scutari 2010). $BF = 0$ indicates a relationship with no empirical support, whereas $BF = 1$ indicates complete support. The ARACNE algorithm automatically removed all relationships with BF values lower than a threshold value indicating a degree of confidence (Scutari & Nagarajan 2013) for each relationship. I identified this threshold value *post hoc* as the lowest BF for a relationship contained in the final BN structure.

Relationships representing the effect of habitat and area accessibility on species occurrence and interspecies co-occurrence were identified as having a high degree of confidence – and therefore, included in the final BN structure – when their BF values were greater than the threshold degree of confidence. Relationships with strengths below the threshold were considered to have low empirical support and were thus excluded from the BN.

2.3.6 Data set

I obtained habitat, area accessibility, and species-specific occurrence data from $n = 40$ sampling stations inside SMBU and in the mixed-farmland. I constructed station-habitat, station-accessibility, and station-species occurrence matrices and then combined each into a single data matrix for BN inference analysis.

Station-habitat matrix

The station-habitat matrix contained station-specific values for canopy height, elevation, distance to water, and location (mixed-farmland vs. forest). For each station, I obtained canopy height (Simard et al. 2013) and elevation (Jarvis et al. 2008) from online databases. I assigned distance to water as ‘near’ when an ephemeral or permanent stream could be seen or heard from the station (< 50 m from water source) and as ‘far’ when otherwise. I assigned location as mixed-farmland or forest based on the reserve boundaries and confirmation from field guides.

Station-accessibility matrix

The station-accessibility matrix contained station-specific values for average human walking speed on foot (in km per hour) from all villages within a 15 km radius of my study site. Human activities are generally concentrated in areas that are easy to access from towns or villages and occur less frequently in remote and difficult to access areas (Levi et al. 2011, Benítez-López et al. 2017, Deith and Brodie 2020). Therefore, I assumed that area accessibility was proportional to the level of human activities at a site where ‘easy access’ areas had lower levels of human activities than ‘difficult access’ areas.

For each station, I calculated walking speed as average conductance associated with the shortest distance from the villages within a 15 km radius of my study site ($n = 7$) that were visible from Google Earth (Google Earth Development Team 2017). I chose a 15 km radius based on the Levi et al. (2011) bio-demographic hunting model that identified spatial depletion of target species within 14 km of a hunting village. Conductance was calculated using a digital elevation map (Jarvis et al. 2008) and Tobler's hiking formula (Tobler 1993) for walking speed in tough terrain. I used walking speed rather than walking time because Tobler's formula incorporates effort based on elevational changes along a specified walking path. Therefore, a station that takes 1 hour to reach at 1 km/hr is assumed to take more effort to access than a station that takes 2 hours at 4 km/hr. All calculations were completed in R (R Core Team 2018) packages "gdistance" (van Etten 2017) and "raster" (Hijmans 2018).

Activity type was not included in this matrix because it can be inferred exactly from the location habitat variable. Stations located in mixed-farmland were exposed to subsistence agriculture (e.g., cocoa trees), hunting, and NTFP extraction including rattan (Widayati and Carlisle 2012; *personal observation*). Forest sites were exposed to only hunting and NTFP extraction.

Station-species occurrence matrix

The station-species occurrence matrix contained station-specific occurrence for each species. Occurrence was measured as the probability that each species was detected (present) at a given site and used as a proxy for small-scale habitat use (as in Burton et al. 2012). I did not estimate relative abundance of each species because abundance was not likely to vary reliably within my study site. I assumed that small scale differences in habitat requirements between any

generalist and specialist species would be identified as habitat or human activity nodes that are connected to only one species per co-occurring pair. For example, imagine that Figure 2.2 c represents a co-occurrence relationship between a generalist (the influencer) and specialist (the responder). In this example, the habitat requirements of the specialist influence its occurrence and, therefore, also influence its co-occurrence with the generalist. Although the generalist does not respond to different ‘habitat’ conditions, the preference of the responder for different ‘habitat’ conditions is incorporated into the co-occurrence relationship between the influencer and responder based on individual species occurrence data.

Occurrence data were collected from a camera trap survey. I set up Reconyx HC500 motion-triggered camera traps in a total of 40 random locations (hereafter ‘stations’) inside the reserve and in the surrounding mixed-farmland in 2013 (Jun–Jul; 12 stations), 2014 (May–Aug; 16 stations), and 2015 (Jun–Aug; 32 stations). Station locations were randomly chosen using a GPS before setting up the cameras. I was permitted access to a small area of mixed-farmland and, due to spacing constraints, could only place seven stations therein. The remaining 33 stations were placed in forest. I resampled a random subset of stations each year (2014: $n = 8$; 2015: $n = 6$) as new cameras became available.

Each camera was drilled into a tree between 0.4 and 0.5 m above ground and remained in place for the duration of each field season (hereafter ‘session’). The cameras were set at high sensitivity and took three consecutive photographs when triggered with no delay between photo bursts. All photographs were date and time stamped. All stations were at least 250 m apart within and across sessions. I initially aimed to space stations 1 km apart, which is the typical average spacing used in camera trap studies (range: 0.02–8 km; Burton et al. 2015), but this was not possible at my site because of challenging terrain (coral rocks, steep ridges) and lack of hiking

trails. A similar camera survey in lowland tropical forests of Peru found that camera spacing and total survey area did not affect the number of species captured (Tobler et al. 2008). In addition, I used occurrence as a proxy for habitat use (as in Burton et al. 2012), not to estimate population size or density. Therefore, I do not consider that my camera spacing will affect my ability to identify fine-scale habitat use in relation to human activities.

I organized photographs by survey, station, and species. Station-specific captures for each species were recorded into a sampling detection–non-detection occurrence Z matrix (Kéry and Royle 2016) where 1 = detected and 0 = not detected for each station. I pooled species-specific occurrence across years for analyses because I was only interested in habitat use (i.e., occurrence) during my study and did not investigate changes in density or abundance. Captures for all rodents were pooled at each station because it was not possible to distinguish between genera or species from photographs. Fully arboreal species were likely missed more often at my site than terrestrial species given that I placed cameras at knee height. However, I did not include any fully arboreal species in this analysis and so do not expect these differences to affect my occurrence values after correcting for detection errors. All cameras took photographs during the day and night, so I also did not expect any influence of diurnal vs. nocturnal species on captures.

Camera trap data are subject to detection errors if some species were not captured at a station even though they were truly present (e.g., walked behind the camera). Therefore, I corrected the camera trap detection–non-detection data for each species at each of my stations following the methods of Kéry and Royle (2016). They used a three-level (metacommunity, community, and species) hierarchical Bayesian Dorazio-Royle multispecies occupancy (hereafter ‘occurrence’) model (Dorazio and Royle 2005) with parameter expanded data augmentation (Dorazio et al. 2006, Royle et al. 2007, Royle and Dorazio 2012) to estimate station-specific

occurrence for each species corrected for detection errors. Details of the modelling procedure are listed in Appendix A.3.

Variable discretization

Before fitting the BN, I converted all variables in the data matrix to ≤ 3 states (Marcot et al. 2006, Milns et al. 2010). For habitat variables, canopy height was divided into categories by the median as: ‘low’ (≤ 26 m) or ‘high’ (> 26 m) canopy height. Elevation was categorized by the first, second, and third quartiles as: ‘low’ (< 73 m), ‘mid’ (73 to 319 m), or ‘high’ (> 319 m) elevation. Distance to water was divided into categories: ‘near’ or ‘far’ (see *Station-habitat matrix*). Habitat location was divided into categories based on station location as: ‘mixed-farmland’ (where activities are agriculture, hunting, and NTFP extraction) or ‘forest’ (where activities are hunting and NTFP extraction).

For area accessibility variables, access was divided into categories based on the median walking speed from villages as: ‘high’ ($>$ median walking speed from village) or ‘low’ (\leq median walking speeds from village) access. For species-specific occurrence variables, occurrence was assigned as ‘present’ (occurrence probability corrected for detection errors $>$ the 85th percentile) or ‘absent’ (occurrence probability corrected for detection errors \leq the 85th percentile).

2.3.7 Evaluating the effectiveness of an umbrella strategy

Evaluating if protecting the habitat of an ‘umbrella’ species might also mitigate the local-scale effects of human activities on other species in an ecosystem requires information on: (i) the distribution of easy and difficult access areas within local-scale habitat features, (ii) species-

specific habitat use in relation to area accessibility, and (iii) co-occurrence patterns among species. The BN can be used in the evaluation by answering a set of “what if” questions (Amstrup et al. 2008) for each of these requirements. For example, (i) “what is the probability that a mixed-farmland area is easy to access (i.e., low access mixed-farmland)?”, (ii) “what is the probability that anoa are present if a mixed-farmland area is easy to access?”, and (iii) “what is the probability that anoa and macaque will co-occur if a mixed-farmland area is easy to access?” I answered these questions using logic sampling (a.k.a., conditional probability queries; Korb and Nicholson 2010, Scutari 2010).

Logic sampling calculates the posterior probability of an event (the ‘what’) given a set of evidence conditions (the ‘ifs’). Events are calculated for child nodes given evidence from their parent(s). For each parent-child relationship identified in the empirical BN, I used logic sampling to calculate the conditional probability of an event given evidence for (i) habitat and area accessibility nodes, between (ii) habitat and/or area accessibility nodes and species occurrence nodes, and for (iii) habitat and/or human activity and co-occurrence relationships.

I used the R package “bnlearn” for logic sampling. One query returned a result calculated from 5,000 samples without a confidence interval. Each query produced a slightly different result because the method uses Monte Carlo simulation (Scutari 2010, Bae et al. 2017). Therefore, for each relationship, I followed the bootstrap resampling technique ($n = 5,000$) of Bae et al. (2017) to calculate the mean and 95% confidence intervals for each event described below. This step accounted for the uncertainties with model structure and sampling design that affect the probability of species occurrence and interspecies co-occurrence in the empirical BN.

For relationships between (i) habitat and area accessibility nodes, I calculated the conditional probability that the area accessibility node took the state ‘low access’ or ‘high

access' given the state of its habitat parent node(s). For example, if there was a relationship between elevation (parent) and area accessibility (child), I calculated the conditional probability of a low access area being at low elevation by setting accessibility to 'low' (event) and elevation to 'low' (evidence).

For relationships between (ii) habitat and/or area accessibility and species occurrence nodes, I calculated the conditional probability that a species (child) is 'present' or 'absent' given each possible state of its parent node. For example, if there was a relationship between location (i.e., mixed-farmland/forest; parent) and macaque occurrence (child), I calculated the conditional probability of macaque presence in mixed-farmland by setting macaque to 'present' (event) and location to 'mixed-farmland' (evidence). If there was a relationship between area accessibility (parent) and anoa occurrence (child), I calculated the conditional probability of anoa presence in low access areas by setting anoa to 'present' (event) and area accessibility to 'low' (evidence).

For relationships between (iii) habitat and/or area accessibility and species co-occurrences, I calculated the conditional probability of co-occurrence for each species pair (event) given each possible state of habitat and area accessibility variables (evidence). For example, if anoa and macaque co-occurrence was affected by area accessibility, I calculated the conditional probability of co-occurrence in low access areas by setting the anoa and macaque states to 'present' (event) and the area accessibility state to 'low' (evidence). For co-occurrence in high access areas, I set the anoa and macaque states to 'present' (event) and the area accessibility to 'high' (evidence).

I used the logic sampling results to evaluate if the Action Plan for Conservation of Anoa 2013–2022 (Mustari et al. 2015) would serve as an effective umbrella species conservation strategy for mitigating the effects of human activities on all species within my study site. I

determined (1) if anoa occurrence was affected by area accessibility within habitats, (2) the proportion of species with which anoa co-occur, and (3) if the co-occurring species have the same response to area accessibility as anoa (e.g., two species co-occur in low access forest but not in high access forest).

2.4 RESULTS

2.4.1 Empirical Bayesian Network of co-occurrences

The empirical BN of co-occurrences identified that species occurrence and co-occurrence patterns responded to canopy height, elevation, water availability, location (mixed-farmland vs. forest), and area accessibility. All conditional probabilities for occurrence and co-occurrence given habitat conditions and area accessibility were different than their corresponding marginal probability distributions (Appendix Figure A.2.4 a vs. A.2.4 b).

There was empirical support for the effect of habitat conditions and area accessibility on species occurrence and interspecies co-occurrence when these relationships had $BF > 0.4114$, as calculated by the ARACNE algorithm. There was very low confidence or empirical support for a relationship between area accessibility and the co-occurrence of any species except for macaques and warty pigs. For the effects of area accessibility on individual species occurrence, there was very low confidence for detecting a relationship for the anoa ($BF = 0.0187$), junglefowl ($BF = 0.0269$), Malay civets ($BF = 0.0632$), rodents ($BF = 0.0219$), and warty pigs ($BF = 0.0411$). However, there was empirical support for a relationship between area accessibility and macaque occurrence ($BF = 0.4540$). Even though all species were observed in the forest and mixed-farmland, there was also very low confidence for detecting a relationship between location and the occurrence of the anoa ($BF = 0.0798$), junglefowl ($BF = 0.0979$), macaques ($BF = 0.0760$),

Malay civets (BF = 0.0570), rodents (BF = 0.2376). However, there was empirical support for the effect of forest vs. farmland on the occurrence of warty pigs (BF = 0.6061).

2.4.2 Area accessibility for humans within habitats

The Bayesian algorithm detected a relationship between area accessibility and the distribution of human activities at my study site in SMBU and the contiguous mixed-farmland (green, drab green, and red nodes in Figure 2.3). At low elevation, there was essentially only high access (98.4% of stations [97.9–98.8%]) mixed-farmland areas (69.4% of sampled area; 67.6–71.2%). Mid and high elevation areas were mostly forested. It was extremely rare to find farmland at mid (0.8% [0.6–1.0%] of the surveyed area) and high (1.8% [1.3–2.4%] of the surveyed area) elevation. Low and high access areas were evenly spaced among mid (47.7% high access [46.3–49.0%]) elevation forest stations, whereas almost all high elevation forest stations were low access (only 1.8% were high access [1.2–2.3%]).

2.4.3 Species-specific habitat use

Of the six species I modelled, the distribution of only two species – the macaques and warty pigs – were correlated with human activity type and area accessibility. The distribution of the four remaining species was explained only by habitat features. These species included the anoa, junglefowl, Malay civets, and rodents.

Macaques were the only species whose occurrence responded to area accessibility within habitats (Figure 2.3). Macaques were more likely to occur in low access areas (79.3% [78.2–80.4%]), whereas their occurrence in high access areas was much more uncertain (50.0% [48.6–

51.4]). Warty pigs occurred more often in mixed-farmland (96.6% present [95.8–97.4%]) than in forest (73.0% present [72.0–74.0%]).

Anoa occurrence changed with elevation and canopy height (Figure 2.3) but did not respond to human activity or area accessibility. Anoa preferred high canopy at mid elevation (80.9% present [79.6–82.2%]) and low canopy at low elevation (74.0% present [71.2–76.8%]). They rarely occurred in high canopy areas at low elevation (17.6% [15.8–19.5%]) or low canopy areas at mid elevation (21.0% present [19.1–22.9%]). Anoa were essentially absent from high elevation, low canopy sites (1.6% present [0.8–2.5%]), but I could not confirm their preference for high canopy at high elevation (50% present [47.5–52.5%]).

Junglefowl occurrence did not respond to any of the human activity, area accessibility, or habitat features considered. Malay civet occurred slightly more often in high canopy areas (55.3% present [54.2–56.5%]) and rarely occurred where canopy height was low (27.0% present [25.6–28.5%]). Rodents occurred slightly more often in areas close to water (54.1% present [52.5–55.7%]) than they did in sites farther from water (33.0% present [32.1–34.5%]).

2.4.4 Species co-occurrences

The empirical BN (Figure 2.3) identified two sub-networks of co-occurring species along an elevation gradient. In the first sub-network, there was positive co-occurrence between macaques and warty pigs in mixed-farmland and forest. The co-occurrence of these species changed in forested areas depending on area accessibility. However, warty pigs were equally likely to occur in low and high access mixed-farmland whether macaques were present or absent (97.1% and 92.6%, respectively; Figure A.2.4 a).

In the second sub-network, there were positive co-occurrences between anoa and junglefowl, junglefowl and rodents, and rodents and Malay civets. None of these co-occurrence relationships were affected by area accessibility or human activity type within habitats. Anoa and junglefowl co-occurrence was mediated by elevation and canopy height. Junglefowl and rodent co-occurrence was mediated by availability of riparian habitat. Rodent and Malay civet co-occurrence was mediated by canopy height and availability of riparian habitat.

At low elevation, macaques and warty pigs were most likely to co-occur in low access mixed-farmland (76.9%; 60.7–91.7%; Table 2.2) and equally unlikely to co-occur in high access mixed-farmland (48.5%; 46.2–50.9%) and forest (45.2%; 41.6–48.6%). The pair had high but variable co-occurrence in low access forest (71.5%; 42.9–100%). At mid and high elevations, macaques and warty pigs were more likely to co-occur in low access forest (mid elevation: 71.7% [70.0–73.4%]; high elevation: 71.7% [69.9–73.5%]; Table 2.2) than high access forest (mid elevation: 45.2% [43.2–47.2%]; high elevation: 45.0% [29.4–61.0%]). Co-occurrence was most variable in high elevation high access forest.

Anoa and junglefowl were most likely to co-occur in high canopy sites at mid elevation (60.2% [58.5–61.9%]; Table 2.3) but rarely co-occurred in high canopy at high (37.2 [34.7–39.7%]; Table 2.3) and low (13.1% [11.4–14.7%]) elevation. Low canopy sites generally did not support anoa and junglefowl co-occurrence (high elevation: 1.2% [0.5–2.0%] and mid elevation [15.6% [13.9–17.3%]) except at low elevation (55.0% [51.9–58.3%]).

Junglefowl and rodents were generally more likely to co-occur in areas closer to water (Table 2.3) at low elevation regardless of canopy height (high canopy: 63.2% [60.6–65.9%] vs. low canopy: 59.6% [54.3–64.9%]). They were least likely to co-occur in low canopy areas far from water at high (11.8% [8.9–14.7%]) and mid (17.4% [15.3–19.6%]) elevation. At low

elevation, the pair were unlikely to co-occur in high canopy areas far from water (16.4% [14.2–18.7%]).

Rodents and Malay civets were more likely to co-occur in areas close to water across elevation and canopy heights (Table 2.3). However, co-occurrence reached a maximum of only 52.5% (49.7–55.2%) in high canopy areas close to water at mid elevation. Co-occurrence was low for all other water and canopy height combinations across elevations.

I could not confirm if anoa, junglefowl, rodents, and Malay civets co-occurred across elevations at my study site. Complete co-occurrence probability only reached a maximum of 45.3% (42.5–48.1%) in high canopy areas close to water at mid elevation (Table 2.3). However, it is very likely that these species do not co-occur in low canopy areas at high elevation (areas far from water: 0.5% [1–1.2%] and areas close to water: 0.9% [0–2.0%]).

2.4.5 Anoa as an umbrella species

I found no empirical evidence that anoa occurrence was correlated with area accessibility or human activity type at my site. Anoa had direct co-occurrence only with junglefowl (20% of species) and were identified in a subnetwork of co-occurrence with junglefowl, rodents, and Malay civets (60% of species). The occurrence of none of the species that co-occurred with anoa was correlated with area accessibility within mixed-farmland or forest habitats. Anoa occurrence was not correlated with macaque or warty pig occurrence.

2.5 DISCUSSION

2.5.1 A local-scale assessment of the umbrella species conservation strategy

I developed a BN that can be used to assess the potential success of an umbrella species conservation strategy on the local scale by identifying small-scale co-occurrence patterns in relation to human activities within habitats. The empirical BN identified changes in interspecies co-occurrence that would likely be missed when selecting an ‘umbrella’ species using regional distribution maps. My assessment involved (1) confirming which species have significant co-occurrence relationships, (2) determining which habitats support co-occurrences, and (3) identifying which co-occurrences changed in areas that were used by humans.

The overall effectiveness of an ‘umbrella’ strategy for protecting regional biodiversity is usually assessed within the boundaries of a protected area for a large number of species including mammals, birds, reptiles, invertebrates, and plants (Wilcox 1984, Shi et al. 2019, Ward et al. 2020). However, many species use habitat just outside protected area boundaries (Riley 2008) where they are at a higher risk of encountering human activity (e.g., hunting, subsistence agriculture). Using habitat outside protected areas can have negative impacts on large-bodied species that tend to be more vulnerable to human activity compared to smaller body species because of their life history (Benítez-López et al. 2017). For example, the Katavi National Park in Tanzania, which was established using large-bodied mammals as ‘umbrella’ species, has protected ungulate species within the park but not on the outside where species are at a lower abundance due to hunting (Caro 2003). Hunting on the outside of protected areas can potentially affect the abundance of target species on the interior of the reserve if individuals continue to emigrate from the interior (Robinson et al. 2008). Therefore, it is important to assess the

effectiveness of umbrella strategies both within protected areas and in human-modified areas just outside the boundaries.

2.5.2 Identifying co-occurrences among species

BNs have been used to identify habitat-species and species co-occurrence networks (Milns et al. 2010), similarities in species responses to environmental variables (Berry and Widder 2014, Thompson et al. 2020), and species richness at fine spatial scales (Grafius et al. 2019). Bayesian inference algorithms have also been used to study secondary extinctions in food webs (Eklöf and Ebenman 2006). However, this is the first time, to my knowledge, that a BN has identified changing co-occurrence patterns in response to small-scale differences in human activities within the same habitat. Previous work in the tropics has demonstrated the negative effect of human activities on species occurrence such as hunting rainforest mammals (Koerner et al. 2017), fishing reef fishes (Goetze et al. 2011), and harvesting medicinal plants (Murali et al. 1996). However, very few studies have asked how human activity directly shapes co-occurrence among species and instead have inferred effects as a by-product of their results.

Based on the threshold level of confidence calculated by the Bayesian inference algorithm, I found evidence that only a subset of co-occurring species (macaques and warty pigs) responded to the accessibility of mixed-farmland and forested areas to humans. Co-occurrence patterns among the remaining species (anoa, junglefowl, rodent, and Malay civet) could only be reliably correlated with habitat conditions. Such small-scale discrepancies in habitat requirements have limited the ability of other ‘umbrella’ species to protect co-occurring taxa (e.g., Carlisle et al. 2018). Differences in how species respond to human activities has also made it difficult to identify which species performs best as an umbrella (Lindemayer and Fischer 2003,

Ficetola et al. 2007). An improved ability to model small-scale changes in co-occurrence, such as that provided by my BN, might therefore identify vulnerabilities for specific species that would be missed when decisions are based on regional patterns.

2.5.3 Limitations and future directions

I used a discrete BN to calculate the probability that a species was present at a site after accounting for imperfect detection. Although Milns et al. (2010) demonstrated that discrete BNs can identify interspecies networks from presence/absence data, more informative results might be obtained using continuous occurrence probabilities. For example, Hradsky et al. (2017) used a continuous BN to identify species-specific occurrence probability in fire-affected landscapes. Therefore, I recommend comparing my results to those obtained from a continuous or hybrid BN with mixed continuous and discrete nodes (Scutari 2010) where at least species-specific occurrence values are continuous nodes.

I did not test potential species interactions (facilitation, competition, predator-prey) and so cannot confirm the identity of each ‘influencer’ and ‘responder’ in each co-occurring pair. However, this uncertainty should not influence the overall results because (1) the umbrella species conservation strategy does not usually infer interspecies relationships when identifying co-occurring species (Wilcox 1984), (2) arc direction in BNs represents a statistical correlation between the states of two variables that does not require causality (i.e., statistically equivalent directionality; Milns et al. 2010), and (3) co-occurrences were interpreted as similarities in selection for habitat conditions and avoidance of human dominated areas. Similarities in habitat selection tend to be more reliably identified by network methods than interspecies interactions (Berry and Widder 2014), and others have studied co-occurrence patterns based on habitat

selection within different communities (MacKenzie et al. 2004, Beaudrot et al. 2013, Steen et al. 2014, Brodie et al. 2018a).

2.5.4 Conservation implications

The anoa is endemic to Sulawesi and is a flagship species for conservation. The Ministry of Forestry, Republic of Indonesia, implemented the Strategy and Action Plan for Conservation of Anoa (Mustari et al. 2015) between 2013–2022 in SMBU and 13 other protected areas. Here I used the BN of co-occurrences to assess if this Action Plan would also serve as an umbrella species conservation strategy by indirectly mitigating the local-scale effects of human activity on occurrence of the remaining species at my site.

My results suggest that the Action Plan for Conservation of Anoa might not address the small-scale effects of humans on macaques. There was no evidence of a co-occurrence relationship between anoa and macaques, indicating that macaques did not co-occur in anoa habitat. Macaques were the only species whose occurrence was lower in easy to access mixed-farmland and forest compared to difficult to access areas. In addition, there was very little empirical support for a correlation between anoa occurrence and area accessibility in mixed-farmland or forest. This disconnect between habitat use suggests that conservation decisions for anoa would not protect macaque because they would not consider area accessibility in mixed-farmland or forest. However, the Action Plan might indirectly protect the species that co-occur with anoa (junglefowl, rodents, and Malay civets).

The Action Plan for Conservation of Anoa proposed increasing ranger patrols to control illegal hunting and identifying anoa habitat for preservation inside and outside protected areas.

My results suggested that anoa use low canopy habitat at low elevation and high canopy habitat at mid elevation.

The negative effects of humans on macaques suggest that a separate Action Plan is required to preserve this species. Macaques co-occurred more often with warty pigs in mixed-farmland and forest areas that were more difficult to access compared to easy to access areas. However, warty pigs were also observed in mixed-farmland where macaque were absent. Macaques (Hardwick et al. 2017) and warty pigs (Burton et al. 2017, Luskin et al. 2019) are common crop raiding pests. Recent interview surveys of Buton residents (Hardwick et al. 2017) confirmed retaliatory killing of macaques, which could explain their uncertain occurrence in easy to access areas. Human disturbances have also disproportionately affected the abundance of other primate communities in the tropics (Rosenbaum et al. 1998; Whitworth et al. 2019). Therefore, in addition to the Action Plan for Conservation of Anoa, an effective strategy to address current threats of human activities at my site would involve curtailing retaliatory killing of macaque in mixed-farmland and forested areas.

Chapter 3: Assisted regeneration of human-modified tropical forest ecosystems: where might seed predator control improve the survival of sown seeds? A hierarchical Network Meta-analysis

3.1 SUMMARY

Human activities threaten the regeneration of many plant species throughout the tropics. These threats can be ameliorated by assisted regeneration via direct seed sowing, but such projects must also account for the effects of post-deposition granivores. Efforts to control granivore populations can reduce seed losses, but the effectiveness of these methods varies among seeds within and between human-modified ecosystems. Previous attempts to identify trends in seed losses using frequentist meta-analyses have failed to consider within-ecosystem differences in post-deposition seed predation for specific types of seeds and human activities. This information is required to design granivore-control tactics. Here, I used a hierarchical Bayesian Network Meta-Analysis (NMA) to identify ecosystem-human activity combinations where granivore control might enhance the regeneration of human-sowed seeds. I synthesized post-deposition seed predation data from 18 experiments in four tropical forest ecosystems (dry, moist deciduous, mountain system, and rainforests) that were modified by a unique combination of five different human activities (10 combinations total). There were no overall differences in seed predation between undisturbed and human-modified ecosystems. However, within particular ecosystems, I identified several seed size \times activity interactions that indicate where and when to use granivore-control methods. In tropical moist deciduous forests, granivore control could help to reduce loss of large seeds in edge areas where hunting and logging activities occur. However, smaller seeds would benefit more from granivore-control than large seeds in moist deciduous forest, mountain system forest, and rainforest edges that are not otherwise modified by human

activities. Granivore-control efforts could also protect small seeds sowed in rainforest edges where hunting and non-logging product extraction occur. Many conservation projects, especially assisted forest regeneration, might benefit from considering wide-scale evidence synthesis using NMA when designing tactics to combat the effects of human activities on plants.

3.2 INTRODUCTION

A large portion of the world's vulnerable and endangered plants are found in the tropics (Corlett 2016, Stévant et al. 2019). There is a growing concern that the natural regeneration of many tropical plants may be compromised by human activities such as timber and non-timber forest product extractions (NTFP; Sabogal et al. 2013) and agroforestry and agricultural expansion (Tschardt et al. 2005, Perfecto et al. 2007). Human activities suppress the natural regeneration of plants by reducing animal-mediated pollination (Quesada et al. 2003) and seed dispersal (Brodie et al. 2009). But less is known about whether human activities also alter antagonistic interactions such as seed and seedling predation (see meta-analyses by Magrach et al. 2008, Markl et al. 2012, Neuschulz et al. 2016).

A major tactic for mitigating these threats to plant regeneration is assisted regeneration, such as direct seed sowing into human-modified areas. Such projects are ongoing throughout much of the tropics, usually entailing careful consideration of the type of human activity that has modified the ecosystem and the characteristics of the plant species (Blakesley et al. 2002, Holl and Aide 2011, Garcia et al. 2016). What works for a tropical rainforest might not work for a tropical dry forest (*c.f.* Vieira and Scariot 2006, Fajardo et al. 2013). Specifically tailored methods are often required for logged lowland dipterocarp rainforests (Kettle 2010), overhunted Neotropical rainforests (Fernandez et al. 2017), abandoned agricultural plots (Chapman and

Chapman 2003), and burned tropical savannas (Gashaw et al. 2002). Direct seed sowing is appropriate for some species and ecosystems (Blakesley et al. 2002, Kettle 2012), whereas high rates of seed predation render this technique futile in other areas unless granivore control methods are also implemented (Garcia-Orth and Martínez-Ramos 2008). Therefore, the same care that went into designing ecosystem-specific seed sowing projects should also be used to design granivore control methods that might enhance the regeneration success of planted seeds.

Efforts to control granivore populations can help reduce the loss of sown seeds that are at the highest risk of predation. But where, and for which seeds, might granivore control measures reduce seed losses? Control measures might not be required in ecosystems where hunting has decreased the abundance of large-bodied granivores (e.g., *Tayassu pecari*; Silman et al. 2003) or where granivores with high intrinsic rates of population growth are unaffected by hunting (Bodmer et al. 1997), such as the wild boar *Sus scrofa* (Servanty et al. 2011) or rodents (Effiom et al. 2013a). However, granivore control might protect seeds in ecosystems where hunting has indirectly increased the abundance of small-bodied granivores after extirpating large-bodied mammals (Dirzo et al. 2007, Rosin and Poulsen 2016). For human activities that affect plants, control measures might reduce seed losses in ecosystems where logging has facilitated the invasion of small-bodied granivores (Loveridge et al. 2016) but might have no effect where small-scale modifications to vegetation structure reduce granivore foraging. For example, NTFP extraction (Widayati and Carlisle 2012) and livestock grazing (Legge et al. 2019) reduce understory vegetation, and some granivores are less likely to remove seeds from areas with low vegetation cover where their own risk of predation is high (Gutiérrez-Granados et al. 2011, Perea et al. 2011). A final complication is granivore preference for seeds of a certain size (Wang and Chen 2009), which can change in different ecosystems (Brewer 2001, Cao et al. 2018) and under

different activities such as fragmentation (Chen et al. 2017b) and vegetation removal (Perea et al. 2011). Overall, variation in post-planting seed predation among ecosystems, human activities, and seed species makes it difficult to determine which ecosystems and seeds might benefit from granivore control.

Identifying reliable patterns in post-planting seed predation across ecosystems and species can help design granivore control methods. For example, large-seeded species have been protected by burying seeds in regenerating rainforest areas (Doust et al. 2006), by sowing seeds in large groups in regenerating pastures (Garcia-Orth and Martínez-Ramos 2008), and by using lethal granivore control (rodent trapping) in rainforests with invasive species (Pender et al. 2013). Seeds of all sizes can also be protected by constructing fence enclosures to prevent granivores from accessing seeds (Garcia-Orth and Martínez-Ramos 2008). Previous attempts to identify trends in seed predation using traditional meta-analyses were limited to assessments of a single type of human activity (Magrath et al. 2008) or pooled activities across ecosystems (Neuschulz et al. 2016). However, the results of these studies have limited use for designing granivore control methods because they did not estimate the probability of predation for different human activities or for specific seeds within ecosystems. Hierarchical Bayesian network meta-analyses (NMA) can estimate the probability that a particular type of seed is depredated in ecosystems that are modified by specific types of human activities. NMAs are extensions of traditional pair-wise meta-analyses that were designed to inform decision-making in medical drug research (Lu and Ades 2004, Dias et al. 2013b, 2013a). The analytic framework combines data across multiple studies and estimates the probability that each drug leads to a particular outcome, such as death, by comparing data among groups of patients (Sutton et al. 2008, Warren et al. 2014, Greco et al. 2016). For predicting post-deposition seed predation in human-modified

ecosystems, one can use the NMA framework to combine data across multiple ecosystems and estimate the probability that seeds are depredated for a specific set of human activities. Despite a recent call for conservation decision-making to be based on wide-scale evidence synthesis (Niu et al. 2014, Sutherland and Wordley 2018, Shackelford et al. 2019), NMAs have still, to my knowledge, not been used to inform forest restoration.

Previous work in human-modified ecosystems can be used to develop conceptual hypotheses for why certain seeds might be at higher risk of predation there than in undisturbed areas (see Table 3.1). Here, I used an NMA to predict the probability of post-deposition seed losses for different ecosystems that were modified by various human activities. My objectives were to (1) determine if seed predation probability was higher (or lower) than in undisturbed conditions across human-modified ecosystems, (2) test for within ecosystem differences in predation probability using an activity type \times seed size interaction, and (3) identify which seed types might benefit from granivore control in ecosystems that were modified by a particular human activity. I also extracted posterior estimates of seed predation probabilities for a subset of seed genera that can be used to inform future analyses. By accounting for variation in seed predation both within and between ecosystems, my results identified ecosystem-human activity combinations where granivore control may enhance the regeneration of sowed seeds.

3.3 METHODS

I used a three level NMA to predict the probability of post-dispersal seed loss due to mammal predation for seeds ($n = 25$ genera) in different tropical ecosystems ($n = 4$) that were modified by a combination of human activities ($n = 10$). On the first level, I estimated the effect

of each activity on increasing or decreasing the probability of seed predation compared to undisturbed conditions across all ecosystems. On the second and third levels, I estimated a fine-scale, within-ecosystem effect of each activity as an interaction with seed size (cm^3) while also accounting for additional random effects of phylogeny (genus), duration of seed exposure, and ecosystem defaunation status. Please see Appendix B Table B.3.1 for morphology data used to calculate seed size.

3.3.1 Dataset

I searched the ISI Web of Science for peer-reviewed studies (1990–2015) that experimentally quantified post-dispersal seed predation in undisturbed and human-modified ecosystems and requested the raw data from each lead author (additional studies included when offered). I stopped literature search in 2015 and then started the analysis. It took five years to organize the data, learn the methods, and code the model. No preference was given to plant taxa, life form, or human activity. Each experimental data set met the following criteria: (1) seed predation was estimated by following the fate of experimentally placed seed depots in natural conditions (i.e., no cafeteria-type feeding experiments, but manipulative exclosures were allowed), (2) seed predators were identified as mammal, bird, or invertebrate (with mammals and decapods identified at least to genus), (3) the total number seeds exposed and predated was provided for each depot, (4) study locations and all human activities at the locations were provided, and (5) the experimental duration was provided.

Altogether, I compiled post-dispersal seed predation observations from 49,587 depots across 103 experiments. These datasets were considered a random sample from over 200 requests. I grouped experiments into ‘ecosystems’ based on study site location using the FAO

and FRA (FAO and FRA 2001) ecological zone classification system. Overall, experiments were conducted in four boreal ecosystems, 12 temperate ecosystems, 11 subtropical ecosystems, and nine tropical ecosystems. The data set was therefore spatially structured by ecosystem with data pooled over studies. Within ecosystems, all experimental seed depots in areas modified by the same human activity were pooled and assigned a unique ‘depot group’ identity. I used this spatial structure because I was interested in identifying systematic differences in seed predation within and between ecosystems not studies. Therefore, depot group data were analyzed as cluster randomized experiments because (1) seeds were collected from the same ecosystem-disturbance combination in which they are exposed and (2) activities are applied at the depot group-, not depot-, level.

For this analysis, I included only tropical ecosystems and seeds from a random sample of families found on Buton Island, Southeast Sulawesi, Indonesia (list compiled during a seed predation experiment in 2015; see Chapter 4). These data were from 18 different studies in 35 different sites (Appendix B Table 3.2). For experiments using manipulative exclosures, I used observations from the open (control) treatment where predation observations were assigned to mammals. This data set ($n = 613$ depots) contained comparisons of seed predation from 17 depot groups exposed to one of 10 activities in four ecosystems (Table 3.2).

Across experiments, research groups identified seed predation as eaten *in situ*, removed and assumed eaten, and removed and confirmed eaten for seed caching rodents. Not all rodent seed predators cache seeds after removal (Corlett 2017), and for those that do, it is often difficult to quantify seed fate. Long-term studies (not included in this analysis) following seed fate have identified low survival for cached seeds. For example, Kitamura et al. (2008a) found that only 6.3% of removed and cached seeds survived. Xiao et al. (Cao et al. 2011) followed seeds from

removal to tertiary caches over one year and found that a maximum of 6% survived. After six weeks, Forget et al. (2000) found that only 8,3% of removed seeds survived. Therefore, I treated all predation and removal observations across studies as equal. I assumed that any seed caching would not affect overall trends in predation probability among ecosystems and activity types because the total number of seeds that survived these events was likely very low.

I began the analysis by creating a network showing the direct ('head-to-head') and indirect comparisons of seed predation that could be made using the data set (Figure 3.1 a). For each of the four ecosystems, I plotted a node for each experimental data set that was obtained under a specific human activity. I then added lines (or 'edges') between activities to indicate which seed predation data sets could be compared both within and across ecosystem. These comparisons were made from two activities in tropical dry forest, seven activities in tropical moist deciduous forest, two activities in tropical mountain system forests, and six activities in tropical rainforest. Direct comparisons were made within ecosystems. Indirect comparisons were made between ecosystems via activities that were common among ecosystems (see *Network meta-analyses: assumptions and pooled disturbance effects* for details). Human activities included: (1) undisturbed (not modified by any human activity), (2) hunting, (3) hunting + livestock grazing + non-timber forest product (NTFP) extraction + edge, (4) hunting + logging + edge, (5) hunting + NTFP extraction + edge, (6) hunting + edge, (7) livestock grazing + logging + edge, (8) edge, (9) logging, and (10) NTFP extraction. Edge indicates that observations were collected in edge habitats.

3.3.2 Predictions

I developed a set of predictions for the effect of human activities on the probability of seed predation based on conceptual hypotheses that have been proposed to explain why some seeds might be at a higher (or lower) risk of predation in human-modified versus undisturbed ecosystems (see Table 3.1 for conceptual hypotheses and predictions). I designed the NMA regression model in three-levels (ecosystem, depot group, and seed) with random effects and varying intercepts to investigate each of these predictions (see 3.3.3 *Modelling random effects and varying intercepts*).

At the ecosystem and depot group levels, I predicted that seeds in human-modified areas would have a higher, lower, or equal probability of predation compared to undisturbed conditions depending on the type of activity that modified the ecosystem. I also predicted that the level of defaunation for a given ecosystem would affect seed predation because some areas without large-bodied species have a higher abundance of small-bodied seed eating species (e.g., Dirzo et al. 2007). At the seed level, I predicted that seed size (volume in mm³) would interact with activity type to account for the foraging behaviour of seed eating species in modified vegetation (Perea et al. 2011) and for dietary preference (Brewer 2001, Cao et al. 2018).

3.3.3 Modelling random effects and varying intercepts

I added random effects and varying intercepts (i.e., random intercept random slope model; Gelman & Hill 2007, Schmidt-Catran et al. 2019) to each level (ecosystem, depot group, and seed) of the model to account for within-level variances and to address possible heteroscedasticity related to non-homogeneity in seed-level characteristics (McCarthy et al.

2008; Schmidt-Catran et al. 2019). These observation-level random effects also account for any overdispersion in the data by capturing additional parametric variation (Harrison 2015).

Level 1: ecosystem-level

A random effect was added to the ecosystem level to account for variation related to the amount of defaunation that had occurred within the mammal community at a given site. The amount of defaunation was either experimentally assessed by each research group or based on published literature within a given study areas. The defaunation random effect accounted for differences related to mammal communities that were intact or had light or moderate defaunation. Ideally defaunation status would be based on relative abundance for each granivore, but this information was not available for any study included in the NMA.

Level 2: depot-group level

The depot-group level was nested within the ecosystem level. Within ecosystems, all depots of seeds that were placed in areas modified by the same human activity were grouped into depot groups. A random effect was added to the depot-group level to account for variation related to the amount of time seeds were exposed to predators across studies (2–365 days). Differences in experimental duration might explain variation in the total number of seed predated at each experimental depot (Chapman and Chapman 2003). Experimental duration was divided into six categories: 0–7 days, 7–30 days, 30–90 days, 90–180 days, 180–270 days, or 270–365 days.

Level 3: seed-level

The seed level was nested within the depot-group level. A varying intercept was added to the seed-level to account for dependencies related to observations taken from the same genus (phylogenetic effects) or the same study following the methods of McCarthy et al. (2008) method and Gelman and Hill (2007).

3.3.4 Network meta-analysis: the basics

The NMA calculated an effect size (log scale) for each human activity that represented a comparison of the probability of seed predation in human-modified compared to undisturbed conditions. Effects sizes were calculated as follows (modified from Saramago et al. 2012): consider the network of pairwise activities 6, 8, and 10 (Figure 3.1 b) created from direct evidence obtained in tropical dry forests and moist deciduous forests. Direct comparisons are available for 6 vs. 10 (dry forests) and 6 vs. 8 (moist deciduous forests) but not for 8 vs. 10. However, activities 8 and 10 are linked indirectly through the ‘common comparator’ activity 6 (*sensu* Lu and Ades 2004, Saramago et al. 2012). The indirect effect size (log scale) is estimated for 8 vs. 10 using direct evidence from 6 vs. 10 and 6 vs. 8 (i.e., $d_{8,10} = d_{10,6} - d_{8,6}$). Extending this example to include activity 1 (Figure 3.1 c), we now have direct comparisons of 6 vs. 10, 6 vs. 8, 1 vs. 6, and 1 vs. 8 and can use the same approach to estimate indirect effect sizes for 1 vs. 10 and 8 vs. 10.

The assumptions of NMA are (Higgins et al. 2012, Saramago et al. 2012, Dias et al. 2013b, Warren et al. 2014): (1) all activities were connected to at least one other activity within the network (Figure 3.1 a), (2) activity effects were assumed exchangeable across a common distribution of potential outcomes at the seed- and ecosystem-level (see *Statistical model*), and

(3) there was no systematic difference in experimental data that influenced disturbance effects (i.e., consistency between direct and indirect evidence; see *Statistical model*).

3.3.5 Statistical model

I used a random effects NMA model (Lu and Ades 2004, Dias et al. 2013a, 2013b) extended to include individual-level covariates (Sutton et al. 2008, Riley and Steyerberg 2010, Saramago et al. 2012) and varying intercepts (Gelman & Hill 2007, McCarthy et al. 2008). The likelihood of post-deposition seed predation at the depot level was modelled with a binomial distribution where the outcome was total number seeds predated out of total number exposed. The binomial distribution was appropriate because the data set did not contain an excess of zero predation events (not zero inflated) at any of the depots (i.e., most depots had at least one out of n seeds depredated).

I chose to model the likelihood with a Binomial distribution because I assumed that the probability of predation for any one seed within a given depot was independent of the probability that the other seeds were also depredated. Almost all studies included in the NMA reported that rodents were responsible for predation events. At the microhabitat level, rodent foraging depends on the abundance of different food types (Brown & Morgan 1995), the amount of vegetation cover (Perea et al. 2011), and the number of conspecific and heterospecific seed predators (Bouskila 1995). In addition, the theory of optimal foraging (MacArthur & Pianka 1966) and give-up densities (Brown 1988, Bedoya-Perez et al. 2013) suggest that rodents make decisions on whether to remain in a patch and continue to eat or leave the patch in search of other patches with more abundant resources. These decisions are thought to be trade-offs between time spent handling food, predation risk for the rodents, and the energy required to search for a new patch

of resources vs. the energy gained from eating food in current patch (McArthur & Pianka 1966, Brown 1988, Bedoya-Perez et al. 2013). All of these factors are likely to vary at the depot-level for all experiments included in the NMA, which suggests that the probability that one seed is depredated from a depot is independent of the probability that the other seeds will also be depredated. However, this independence assumption might not hold if seeds were presented to a single granivore under controlled conditions (e.g., a laboratory cafeteria experiment) where the probability that seeds are depredated would be similar to removing coloured balls from a bag without replacement. Under such controlled conditions, a Beta-binomial distribution would be more appropriate to account for non-independence of consumption probabilities.

Hierarchical models with many parameters and complex datasets often take very long to converge and suffer from high dependencies and correlations between posterior point estimates (Papaspiliopoulos et al. 2003, 2007). Therefore, I used a non-centered parameterization (Papaspiliopoulos et al. 2007, Monnahan et al. 2017, Gorinova et al. 2018) to speed up convergence, improve mixing of the Markov Chain Monte Carlo (MCMC) algorithm, increase effective sample size, and lower posterior correlations.

The basic model structure is (Saramago et al. 2012):

$$Y_{imjk} = \text{Binomial}(p_{imjk}, n_{imjk})$$

where:

Y_{imjk} is the number of seeds predated out of n_{imjk} seeds exposed at the i^{th} depot in the m^{th} depot group of the j^{th} ecosystem exposed to the k^{th} human activity

p_{imjk} is the logit probability (hereafter ‘probability’) of seed predation for each depot

b is the ecosystem-specific control activity (undisturbed in tropical moist deciduous, mountain system, and rainforests; hunting + edge in tropical dry forests)

$$\text{logit}(p_{imjk}) = \begin{cases} \mu_{mjb} + \beta_{0j} \times x_{imj} & b = 1, 2, 3, \dots \text{ if } k = b, \\ \mu_{mjb} + \delta_{jbk} + \beta_{0j} \times x_{imj} + & \text{if } k \text{ numerically after } b \\ \beta_{bk}^B \times \bar{x}_j + \beta_{bk}^W \times (x_{imj} - \bar{x}_j) & . \end{cases}$$

$$\mu_{mjb} \sim N(\theta_j, \tau_j^2)$$

$$\delta_{jbk} \sim N(d_{bk}, \sigma^2) \sim N(d_{1k} - d_{1b}, \sigma^2)$$

$$\beta_{0j} \sim N(0, 10^6)$$

$$\beta_{bk}^W \sim N(\beta_b k^W, \sigma_{B^W}^2) \sim N(b_{1k}^W - b_{1b}^W, \sigma_{B^W}^2)$$

$$\beta_{bk}^B \sim N(\beta_b k^B, \sigma_{B^B}^2) \sim N(b_{1k}^B - b_{1b}^B, \sigma_{B^B}^2)$$

for:

$i = 1, 2, \dots, n$ depots in the m^{th} depot group of the j^{th} ecosystem

$m = 1, 2, \dots, n$ depot groups in the j^{th} ecosystem

$j = 1, 2, \dots, n$ total ecosystems

$k = 1, 2, \dots, n$ total activities applied to depots across ecosystems

where:

μ_{mjb} is an unconstrained control group odds for each depot group on the logit scale within ecosystems calculated as the log-odds of predation for activity b in depot group m of ecosystem j

δ_{jbk} is the log odds ratio for activity k relative to the control activity b within ecosystem j

d_{bk} is the log odds ratio for activity k relative to the ecosystem-specific control activity b ($d_{11} = 0$)

β_{0j} is the ecosystem-specific, seed size (mm^3) effect on probability of seed predation

x_{imj} is the size (mm^3) of one seed in depot i in depot group m of ecosystem j

\bar{x}_j is the mean seed size (mm^3) across all depot groups in ecosystem j

β_{bk}^W is the within-ecosystem interaction between activity and seed size indicating variation in probability of predation at depot i for a change in seed size x_{imj} ($\beta_{11}^W = 0$)

β_{bk}^B is the between-ecosystem interaction of activity and seed size indicating variation in mean probability of predation ($\beta_{11}^B = 0$)

b_{bk}^W is the log odds ratio for the within-ecosystem interaction between activity k relative to the control activity b and seed size (mm^3)

b_{bk}^B is the log odds ratio for the between-ecosystem interaction between activity k relative to the control activity b and seed size (mm^3)

and:

$\beta_{bk}^B \times \bar{x}_j$ models the between-ecosystem activity \times seed size (mm^3) effect k relative to the ecosystem-specific control activity b by multiplying by mean seed size in ecosystem j

$\beta_{bk}^W \times (x_{imj} - \bar{x}_j)$ models the within-ecosystem activity \times seed size (mm^3) effect k relative to the ecosystem-specific control activity b by mean centering the value of each depot i in depot group m of ecosystem j

with:

μ_{mjb} assumed exchangeable within ecosystems with mean zero and variance τ_j^2 where depot group-level effects were assumed independent between ecosystems (Saramago et al. 2012)

δ_{jbk} assumed exchangeable (random effect) across all activity effects with mean d_{bk} and variance σ^2

b_{bk}^W assumed exchangeable for all activities across ecosystems but varying for each disturbance vs. control comparator

b_{bk}^B assumed exchangeable for all activities across ecosystems but varying for each disturbance vs. control comparator

and non-centered priors and hyperpriors with standard deviation specified as half-Cauchy distribution with scale 2.5 (Gelman 2006, Monnahan et al. 2017) as:

μ_{mjb} mean 0; variance $\theta_j \sim Cauchy(0,0.16)$

δ_{jbk} mean $d \sim Normal(0,1)$; variance $\sigma \sim Cauchy(0,0.04)$

β_{bk}^W mean $b^W \sim Normal(0,1)$; variance $\sigma_{B^W} \sim Cauchy(0,0.16)$

β_{bk}^B mean $b^B \sim Normal(0,1)$; variance $\sigma_{B^B} \sim Cauchy(0,0.16)$

I extended the basic model by adding the meta-regression parameters for ecosystem defaunation level, experimental duration, study, and genus. Meta-regression parameters were assumed exchangeable across seeds and ecosystems as follows:

$\alpha_{defaunation}$	for $d = 1, \dots, n$ total defaunation statuses for the random effect of defaunation status within ecosystems
$\alpha_{ecosystem \times duration}$	a nested interaction for $e = 1, \dots, n$ total ecosystems and $t = 1, \dots, n$ total experimental duration categories for the random effect of time seeds were exposed within ecosystems
α_{genus}	for $g = 1, \dots, n$ total genera for the random effect of genera
α_{study}	for $s = 1, \dots, n$ total studies providing experimental data for the random effect of study

I assumed all meta-regression α -parameters were drawn from normal distributions with mean 0 and estimated standard deviation with half-Cauchy scale 5 (Gelman 2006, Monnahan et al. 2017) hyperpriors assigned as follows:

parameter:

$\alpha_{genus} \sim Cauchy(0,0.04)$

$\alpha_{study} \sim Cauchy(0,0.04)$

$\alpha_{defaunation} \sim Cauchy(0,0.04)$

$\alpha_{ecosystem \times duration} \sim Cauchy(0,0.04)$

I used broad, uninformative priors following the methods set out by Lu and Ades 2004, Saramago et al. 2012, Dias et al. 2013b and others. In certain cases, using informative priors (narrower than broad) can reduce the chances of counterintuitive results. Informative priors are assigned to parameters either subjectively (e.g., by expert opinion) or through data synthesis meta-analyses (e.g., McCarthy et al. 2008, Porteus et al. 2018). I am not aware of any study before mine that has synthesized data to produce results that can be used to assign informative priors to any activity effects on seed predation probability or on the random intercept terms. Therefore, I used broad priors but also show how the posterior distribution of certain parameters in my model (i.e., genus varying intercepts) can be used to construct informative priors for use in future analyses.

Medical NMAs include an adjustment to reduce bias in effect sizes that are related to correlations between observations taken from the same study (Lu and Ades 2004, Saramago et al. 2012, Dias et al. 2013b). In contrast, I had several observations taken from the same ecosystems where data within ecosystems were grouped by activity type at the depot-group level and were collected in different study locations (Table 3.1 and Appendix B Table B.3.2). Therefore, I ran several models with an adjustment at the depot-group level to account for correlations taken from seeds exposed in ecosystems that were modified by the same human activity. However, the adjustment did not produce sensible results. As an alternative, I included a random effect for α_{study} following McCarthy et al. (2008) and Schmidt-Catran et al. 2019 to account for correlations between observations taken from depot groups nested within ecosystems.

3.3.6 Model implementation and fit

I first ran a fully parameterized model with all random effects and β^W and β^B covariates and checked for convergence and fit. The model was slow to converge and had poor fit (i.e., low effective size) for the β^B , $\alpha_{defaunation}$, $\alpha_{ecosystem \times duration}$ parameters. Poor fit indicated that I did not have enough data to estimate these parameters. Therefore, I removed all badly behaved parameters and included only the following covariates in the final model: β^W activity \times seed size effect, α_{genus} , and α_{study} . Removing the β^B , $\alpha_{defaunation}$, $\alpha_{ecosystem \times duration}$ parameters did not affect my ability to investigate the effects of different types of human activities on seed predation across ecosystems, although I could not account for random variation in the data related to defaunation status or experimental duration on this level. These across ecosystem effects were estimated by the d_{bk} parameter, which was included in the final model. However, removing the β^B parameter affected my ability to test between ecosystem effect of the interaction between human activity and seed size. I was still able to test the within ecosystem effect of this interaction because the β^W parameter was estimated in the final model.

All models were coded in BUGS (Lunn et al. 2003) and run in JAGS (Plummer 2003) called from R (R Core Team 2018) using the “jagsUI” (Kellner 2018) package. I ran two chains per model for 200,000 iterations after discarding 600,000 burn-in and 5,000 adaptive phase iterations with a 10-iteration thinning rate (inferences based on maximum 20,000 iterations). I based convergence on: trace plots (complete mixing of chains), density plots of the posterior distributions for each parameter (for approximate normality), parameter \hat{R} values < 1.09 (Gelman and Shirley 2016, Kellner 2018), and Gelman-Rubin multi-variate psrf value of 1 (Plummer 2003). I inspected model fit by calculating posterior cross-correlations between all model

parameters using the R package “CODA” (Plummer et al. 2006) and by creating bivariate plots for all parameter combinations.

3.3.7 Genus-specific priors for future analyses

The posterior point estimates for the genus varying intercept can be used to inform future analyses of seed predation data collected from human-modified ecosystems. Specifically, the posterior mean and standard deviation of each genus intercept can be used to construct an informative prior (Lunn et al. 2003, McCarthy et al. 2008) for probability of predation in a tropical forest ecosystem. Here, I confirmed the shape of the posterior distribution (using posterior density plots) and then extracted posterior estimates for four genera (*Aglaia*, *Calamus*, *Litsea*, *Syzygium*) calculated as the mean and standard deviation of their α_{genus} MCMC simulation values (Gelman and Hill 2007) but defer prior construction to a concurrent analysis (Chapter 4). Please see Chapter 4 for steps on how to use these values to construct informative priors for a logistic regression of genus-specific seed predation in a tropical rainforest reserve and the mixed-farmland area outside the reserve boundary.

3.4 RESULTS

3.4.1 Model fit

The model containing the β^W seed size \times disturbance effect, α_{genus} varying intercept, and α_{study} random effect fit the data best with adequate effective sample size and no non-identifiable parameters (bivariate plots not shown). All parameters converged (complete mixing of chains, \hat{R} values < 1.09 , and Gelman-Rubin multi-variate psrf value = 1; results not shown),

although there were considerable updates ($\tau_{posterior}:\tau_{prior} > 2$) for only a few parameters (results not shown).

Although the non-centered parameterization improved convergence and fit, posterior correlations remained high (maximum correlation of 0.85) between some (1) $\alpha_{genus}-\alpha_{genus}$ ($n = 1$) and (2) $b^W-\beta^W$ pairs ($n = 7$). However, I expected high correlations between these parameters because (1) both genera were from the same family and (2) the parameters were estimated for the same activity type. For $b^W-\beta^W$, I also expect high posterior correlations for the same activity type in different ecosystems because of the dependency imposed by hierarchical levels (i.e., β^W calculated from b^W).

3.4.2 Across ecosystem seed predation

There was almost no variation in the log odds of seed predation across ecosystems between disturbed and undisturbed conditions for any human activity (Figure 3.2 a). Similarly, there was little variation in the log odds of predation across genera (Figure 3.2 b) when the effects of human activity type and seed size were ignored. *Actinodaphne*, *Chisocheton*, and *Phoebe* were at a greater risk of predation compared to the average risk of predation across genera. Likewise, there was no apparent variation in log odds of predation across studies except for data from one (McConkey 2005) where the log odds of predation were slightly higher than in other studies (results not shown).

3.4.3 Within ecosystem seed predation

There was more variation in the effect size of the activity \times seed size interaction across activities (Figure 3.2 c) compared to the across ecosystem activity effect size (Figure 3.2 a).

Depending on the ecosystem, the log odds of predation increased with increasing size for seeds exposed to (1) hunting + logging + edge activities and (2) hunting + edge activities compared to undisturbed conditions. On the other hand, the log odds of predation also decreased with increasing size for seeds exposed to (1) hunting + non-logging product extraction + edge activities and (2) edge activities compared to undisturbed conditions.

Activity \times seed size interactions were identified only in moist deciduous forests, mountain system forests, and rainforests (Figure 3.3). In moist deciduous forests edges that were modified by hunting + logging (Figure 3.3 a), there was a rapid acceleration in predation probability with increasing seed size that only begun to slow for the largest seeds for which the predation probability reached 100%. Seeds below average size had essentially no risk of predation. The same pattern was observed for edges where hunting occurred, albeit with more uncertainty (Figure 3.3 b). On the other hand, smaller seeds were at higher risk of predation than larger seeds in edge areas that were not modified by any human activity (Figure 3.3 c).

In tropical mountain system forest edge habitats, there was an almost linear decrease in seed predation probability with increasing seed size (Figure 3.3 d). However, the relative differences were much less extreme than in moist deciduous forests (Figure 3.3 c) and tropical rainforests (Figure 3.3 d).

In tropical rainforest edges (Figure 3.3 e), there was a rapid deceleration in predation probability with increasing seed size starting around average size and only beginning to slow for the largest seeds that were almost never predated. The same patterns were found in edges with hunting + non-logging product extraction albeit with less uncertainty (Figure 3.3 c).

3.4.4 Genus predation probability in tropical forest ecosystems

There was minimal variation in posterior mean seed predation estimates for *Aglaiia*, *Calamus*, *Litsea*, or *Syzygium* (Figure 3.4). The posterior distribution of the varying intercept for each genus was approximately Normal (results not shown). Please see Chapter 4 for an application of these values as informative priors in another seed predation experiment.

3.5 DISCUSSION

Much time, effort, and money has been spent implementing seed sowing regeneration projects for tropical ecosystems that have been modified by human activities. Here, I used an NMA to identify where seed sowing projects might use granivore control methods by calculating the probability of post-sowing predation of particular seeds in human-modified tropical forest ecosystems. Although there was no across-ecosystem trend in increased or decreased seed predation for any human activity compared to undisturbed conditions, there were several seed size \times activity interactions that indicated where and for what seeds predator-control methods might reduce seed losses. In general, high rates of seed predation suggested that granivore control methods might increase survival of management-planted seeds in the edge areas of tropical forests, but the seeds that would likely benefit most from protection varied among ecosystems and human activities.

Across the tropics, post-dispersal mammal seed predators have been reported to destroy between 20–100% of experimentally-dispersed seeds (Holl and Lulow 1997, Lambert 2002, Chapman and Chapman 2003) with the exact percentages varying among ecosystem, plant species, and whether the ecosystem was modified by human activities. This variation might explain why I did not find an across-ecosystem trend in the probability of seeds being predated in

human-modified versus undisturbed conditions. Previous frequentist meta-analyses have also not found general effects of human-activities on post-dispersal seed predation across ecosystems (Magrath et al. 2008, Markl et al. 2012, Neuschulz et al. 2016).

3.5.1 Ecosystem- and seed-specific granivore control

In tropical moist deciduous forests, my results suggest that large seeds ($> 2.5 \text{ cm}^3$) might benefit from granivore control tactics in edge habitats where hunting and logging also occur. Larger seeds are almost always predated in these areas, whereas smaller seeds ($< 0.63 \text{ cm}^3$) are almost never predated. Smaller seeds could therefore be sown without the need for additional granivore control. On the other hand, smaller seeds might benefit from protection from granivores in the edges of unlogged, unlogged tropical moist deciduous forests where larger seeds could be sown without additional protection.

In mountain system forests, my results suggest that smaller seeds require, and larger seeds might also benefit from, protection from granivores in edge areas that are otherwise undisturbed. In rainforests, my results suggest that small seeds ($< 0.93 \text{ cm}^3$) might benefit from granivore control in undisturbed edge habitats and in edge habitats where hunting and NTFP extraction also occur. Large seeds ($> 9.5 \text{ cm}^3$) have negligible risk of predation in these rainforest edges and so likely would not benefit from additional protection from granivores.

The magnitude of the seed size \times activity interaction was greater in moist deciduous forest edge areas with hunting and logging and in rainforest edge areas with and without hunting and NTFP extraction. The magnitude of the interaction was much weaker in moist deciduous and mountain system forest edge areas that are otherwise undisturbed. From a management perspective, this suggests that the benefits of protecting seeds in areas where the magnitude of

the interaction was greater would outweigh the costs more than protecting seeds in undisturbed edges.

3.5.2 **How could seed predators be driving these trends?**

I found that the probability of seed predation increased with increasing seed size in moist deciduous forest edges that were also hunted and logged. In contrast, larger seeds were at considerably lower risk of predation in rainforest edges that were both hunted and not hunted. This variation was most likely associated with granivore abundance and foraging behavior, which are also habitat and species dependent within human-modified ecosystems (Feuntes-Montemayor et al. 2009, Gutiérrez-Granados et al. 2011, Püttker et al. 2013).

Human activities can affect granivore abundance. For example, edge habitats of hunted tropical forests often have fewer large- and more small-bodied species compared to undisturbed areas (Laurance et al. 2008). Logging can also exacerbate the negative effects of hunting on mammal communities by increasing access to hunters (Ochoa and Soriano 2001, Peres 2001) and facilitating rodent invasion (Loveridge et al. 2016). Given that small-bodied species are usually granivores (Fleury et al. 2014), differences in predation risk for seeds of increasing size could be associated with a higher abundance of granivores in edge areas.

Human activities that affect plant community structure can also affect granivore foraging patterns. For example, Perea et al. (2011) found that rodents spend less time feeding in open microhabitats compared to sheltered areas where the risk of rodents being attacked by their predators was low. These rodents also removed heavier seeds from sheltered habitats. NTFP extraction can change vegetation density (Widayati and Carlisle 2012), and edge areas created after habitat fragmentation often have high abundance of vines and lianas (Laurance 1994).

Therefore, the low probability of seed predation for larger seeds in edge areas with NTFP extraction uncovered here might be related to reduced understory vegetation cover and increased risk of predation for granivores. Finally, granivore diets can range from generalist to specialist (Cao et al. 2018), so contrasting predation probabilities between ecosystems could also be driven by which granivore species are present.

3.5.3 Limitations

I did not investigate the effect of granivore abundance, species, or dietary preference on the probability of post-deposition seed predation. Each of these factors are likely to vary among study sites and so could contribute to observed differences in the activity \times seed size effect within ecosystems. However, estimating the effects of granivore abundance, species, and dietary preference were not possible in this analysis due to limited sample size (granivore species identity) and missing information (granivore abundance and dietary preference). In addition, hierarchical models with many parameters often suffer from high posterior correlations between point estimates, parameter non-identifiability, and convergence issues (Papaspiliopoulos et al. 2003, 2007). I could not fit a model that included between ecosystem activity \times seed size effects nor the $\alpha_{defaunation}$ and $\alpha_{ecosystem \times duration}$ random effects. Adding additional parameters for granivore abundance and identity would likely have exacerbated convergence and fit issues. These issues could potentially be solved using sensitivity analysis in which the priors of badly behaved parameters are tightened by excluding values that do not make biological sense. However, in terms of decision-making, a manager can still use my results to determine where and for which seeds granivore control methods might reduce the number of seeds lost post-planting without knowing the effect of granivore species or dietary preference.

I limited the scope of this analysis to 25 trees from genera that were also observed on Buton Island, Southeast Sulawesi, Indonesia. My objective was to compare disturbance effects across tropical ecosystems and to use the results to inform an analysis of seed predation at my site where almost no experimental research has been conducted to date (see Chapter 4). Although my results meet this objective for tropical dry, moist deciduous-, mountain system-, and rain-forests, seed predation is also important for all life forms in other ecosystems (Lindquist et al. 2009, Orrock et al. 2015, Larios et al. 2017). Therefore, I recommend completing additional NMAs for all life forms using data from my original data set including experiments from boreal ($n = 4$), temperate ($n = 12$), subtropical ($n = 11$), and tropical ($n = 9$) ecosystems. One might begin with ecosystem-specific analyses to potentially avoid convergence and fit issues discussed above.

3.5.4 Which granivore control method is best?

I identified which seeds (by size) might have increased survival if protected from post-deposition mammal granivores for ecosystems that were modified by a specific human activity. However, I did not test the effectiveness of different methods that could be used to protect seeds. Numerous studies have investigated the efficacy of non-lethal (e.g., Doust et al. 2006, Garcia-Orth and Martínez-Ramos 2008, Castro et al. 2015) and lethal (Pender et al. 2013) granivore control, and managers could consider using any of these methods as discussed below. Alternatively, in cases where seeds are lost at excessively high rates, managers might consider planting seedlings germinated in nurseries (Mangueira et al. 2019).

Non-lethal granivore control can reduce mortality of sown seeds by providing a physical barrier between seeds and granivores. For example, Doust et al. (2006) found that seeds buried in

soil, under soil and mulch, and in soil mounds had ten times higher establishment than unburied seeds. Protective devices can also reduce post-deposition predation. For example, Leverkus et al. (2015) found that acorns (*Quercus spp.*) buried in a protective polypropylene device experienced zero rodent predation compared to 17% predation for unprotected seeds. Sowing seeds in large piles, rather than singly, and fencing exclosures can also decrease the number of sown seeds lost to predators (Garcia-Orth and Martínez-Ramos 2008). Additional costs would arise to implement protective measures including protective devices (Castro et al. 2015) and to purchase more seeds for sowing in piles (Mangueira et al. 2019). Lethal granivore control, such as rodent trapping (Pender et al. 2013), would likely only be realistic at small spatial scales if concentrated in the area where seeds are planted.

Post-deposition seed predation can be avoided by planting seedlings of species at high risk of seed predation. However, this option comes with additional costs associated with growing seedlings in nurseries. Mangueira et al. (2019) compared the cost of direct seeding and planting seedlings of four different species. The cost per hectare of planting large seedlings was 34–42% more than the cost of planting small seedlings and almost 10 times more than direct seed sowing. However, after accounting for seed mortality, Mangueira et al. (2019) concluded that direct sowing was less expensive for only the one species that did not have 100% mortality of seeds.

A manager has several options to control for seed losses related to rodent granivory. Here I identified which seeds are at high risk of post-deposition predation for a given human-modified ecosystem. For each ecosystem-activity combination, I suggest that a manager assess several options to determine the most efficient and economical method. Furthermore, additional steps will need to be taken to reduce mortality of seedlings that germinate from sowed and protected seeds.

Chapter 4: Will post-deposition seed predation affect the regeneration of mixed-farmland at a tropical rainforest reserve boundary?

4.1 SUMMARY

Small-scale ‘forest-gardens’ are common at many rainforest margins where local farmers plant cash crop trees (e.g., cacao, cloves, nutmeg) alongside native vegetation. Conservationists have emphasized the need for sustainable management of these mixed-farmland areas for both biodiversity conservation and human livelihoods. Many management projects assume that enhanced animal-mediated seed rain from forest areas will assist natural regeneration of the mixed-farmland areas, but the fate of those forest seeds is rarely considered. Here, I investigated the potential for enhancing forest regeneration in mixed-farmland via facilitating use of those areas by seed-dispersing primates. I did this by designing an experiment that quantified post-dispersal seed predation in forest and mixed-farmland sites that were used and avoided by the only non-human seed-dispersing primate, the Buton macaque (*Macaca orchreata*), on Buton Island, Southeast Sulawesi, Indonesia. Macaques were previously observed in both the forest and the mixed-farmland outside a reserve boundary, but they appeared to select areas that were less accessible to humans. Seeds from eight woody plants and one herb were collected from within the reserve and experimentally placed to mimic *M. orchreata* deposition patterns in low and high access forest and mixed-farmland sites. Rodents were the only vertebrates that removed and predated seeds. There was no evidence that native pigs (*Sus celebensis*), introduced civets (*Viverra zibetha*), or junglefowl (*Gallus gallus*) removed seeds. The probability of seed predation in mixed-farmland was significantly lower than in forest regardless of area accessibility for seven (*Aglaonema*, *Calamus*, *Licuala*, *Litsea*, *Magnolia*, *Pterocarpus*, *Syzygium*) of nine (excluding *Atuna* and *Entada*) genera. Low probability of seed loss in mixed-

farmland, as compared to forest, indicated that post-dispersal seed predation is not a significant factor affecting the potential for regeneration in mixed-farmland. Rodents did not significantly reduce the survival of seeds in areas either avoided or selected by macaques. These results suggest that conservation tactics designed to increase macaque distribution in mixed-farmland landscape could enhance natural forest regeneration because primate-dispersed seeds appear to be at low risk of predation everywhere. Understanding the dynamics of post-dispersal seed predation is a necessary first step before assuming that regeneration of disturbed habitats will necessarily follow from the protection of particular seed-dispersing animals.

4.2 INTRODUCTION

Human activities have modified almost every ecosystem on earth. Many animal species persist in modified areas by changing their diet (Riley 2007), activity patterns (Riley 2008), or habitat selection (Remis and Kpanou 2010) in response to the distribution of human activities across the landscape. However, these behavioural changes can affect plant-animal interactions when, for example, a mutualistic animal partner no longer occurs in a once occupied habitat (McConkey and Drake 2006) or when an antagonistic partner increases in abundance (Dirzo et al. 2007, Beck et al. 2013). The subsequent risk of co-extinction to interacting plants (Chapman and Chapman 1995, Eklöf and Ebenman 2006) has underscored the need to manage highly connected species (Soulé et al. 2003) and important functional guilds (Brodie et al. 2018b) to maintain natural regeneration patterns (Koné et al. 2008, Chapman and Dunham 2018) in human-modified ecosystems.

Tropical Southeast Asia has among the highest rates of human intrusion, exploitation, and destruction of ecosystems worldwide (Hughes 2017). Many degraded habitats just outside

protected areas are used as forest-gardens (Sorensen 1996, Pangau-Adam et al. 2006) where cash-crop trees (e.g., cacao *Theobroma cacao*, cloves *Syzygium aromaticum.*, coffee *Coffea* spp., nutmeg *Myristica* spp.) are planted among naturally occurring vegetation. These areas have considerable economic (Abdulkadir-Sunito and Sitorus 2007) and conservation (Dietz et al. 2007) value because they are also used by animals from within protected area boundaries (Albert et al. 2014, Hardwick et al. 2017). One way to maintain natural regeneration of forest-farmland areas, and thus to support sustainable use by humans and wildlife, is to facilitate the dispersal of seeds by animals from within the reserve into the adjacent farmland (Wunderle 1997, Shono et al. 2007).

Non-human primates play an important role in seed dispersal throughout the tropics (Corlett and Lucas 1990, Corlett 2017, Chapman and Dunham 2018). Evidence that some species move between protected and degraded areas (Koné et al. 2008, Estrada et al. 2012, Albert et al. 2014) suggests that strategies designed to protect primates might also indirectly enhance natural regeneration of degraded habitats (Vulinec et al. 2006, Andresen et al. 2018). Studies have investigated the contribution of primates to seed rain into degraded habitats (Estrada et al. 2012, Albert et al. 2014); however, much less research has quantified post-dispersal predation rates of these primate-dispersed seeds in degraded habitats (Lambert 2002). Understanding the dynamics of seed predation is critical because it can dramatically alter the initial pattern of seed deposition even in undisturbed areas (Andresen and Levey 2004, Razafindratsima 2017). For example, post-dispersal seed predation by rodents has destroyed up to 90% of primate-dispersed seeds (Estrada and Coates-Estrada 1991) and between 20–100% of experimentally-dispersed seeds (Holl and Lulow 1997, Lambert 2002, Chapman and Chapman 2003) in human-modified areas. Therefore, identifying how primates use habitat in relation to human activities (Lambert and Chapman

2005, Vulinec et al. 2006), and quantifying post-dispersal seed predation (Lambert 2002, Chapman and Dunham 2018) in areas slated for primate recovery, are critical first steps in predicting the potential for restoration of degraded areas via seed dispersal.

Not all dispersed seeds will contribute to regeneration of degraded habitats. Seeds must be deposited into areas that allow germination (Wenny and Levey 1998), escape post-dispersal seed predation (Clark and Clark 1984), and then survive past the seedling and sapling stages before recruiting as reproductive adults. Here, I experimentally quantified the effect of post-dispersal vertebrate seed predation on the natural regeneration potential of degraded mixed-farmland areas surrounding a tropical rainforest reserve on Buton Island, Southeast Sulawesi, Indonesia. Given that post-dispersal seed predation also occurs within the forest, I assumed that vertebrate granivores did not interfere with regeneration potential if there was equal or significantly lower probability of seed loss in mixed-farmland than in forested areas (similar to Chapman and Chapman 1999 and Blackham and Corlett 2015).

Many management projects assume that enhanced animal-mediated seed rain from forest areas will assist natural regeneration of disturbed areas. Therefore, I asked if a conservation strategy designed to increase the distribution of primates across the mixed-farmland landscape would indirectly enhance regeneration of mixed-farmland by increasing seed deposition into areas that are not currently used by non-human primates. Building on previous observations of primates in areas that were less accessible to humans (Chapter 2), I compared the probability of vertebrate seed predation in mixed-farmland areas that were easy or difficult for humans to access. This comparison allowed me to determine the expected percent of newly dispersed seeds that would escape predation with potentially expanding primate distributions. Identifying small-scale differences in seed predation across a gradient of non-human primate habitat use provides

an evidence-based assessment of the potential to enhance forest regeneration via facilitating natural zoochorous seed dispersal. The method outlined here is a simple step that all conservation planning could take before assuming that assisted regeneration of disturbed habitats will necessarily follow from the protection of a particular species or functional guild.

4.3 METHODS

A conservation strategy designed to enhance regeneration of degraded areas by promoting seed dispersal from contiguous forest must first confirm that animal seed dispersers use degraded habitats, second determine if post-dispersal seed predation causes considerable losses of dispersed seeds in those areas, and third follow the fate of non-predated seeds through germination. I previously confirmed that the seed-dispersing macaque uses the forested area contiguous to the degraded mixed-farmland at my site but also preferred areas that were more difficult for human to access compared to easy access areas (Chapter 2). Here, I quantify post-dispersal seed losses to mammal granivores in easy and difficult to access mixed-farmland areas. My objectives were to (1) estimate the current regeneration potential of mixed-farmland sites compared to contiguous forest areas based on post-deposition seed predation losses and (2) compare the probability of vertebrate post-dispersal seed predation in mixed-farmland areas in terms of current primate habitat use (easy vs. difficult to access areas). I did this by experimentally quantifying the probability of predation of seeds dispersed to mimic primate seed deposition patterns within forest and mixed-farmland considering the accessibility of areas to humans.

4.3.1 Study system

I completed a one-month seed addition experiment in the forest within and mixed-farmland just outside the boundaries of Suaka Margasatwa Buton Utara (SMBU; 4°57'S, 123°14'E), a wildlife reserve (WDPA ID 8877; IUCN and UNEP-WCMC 2017) on Buton Island, Southeast Sulawesi, Indonesia (Figure 4.1a). SMBU was established in 1979 and is federally governed and managed by the Balai Konservasi Sumber Daya Alam Sulawesi Tenggara. Hunting and non-timber forest product (NTFP) extraction are not permitted but still occur within the reserve. Logging is illegal and appears very rare (*personal observation*). The climate is equatorial and changes with elevation from Köppen-Geiger climate zone Aw (equatorial savanna with dry winter) outside the reserve boundaries to Am (equatorial monsoon) in the interior (Kottek et al. 2006, ORNL DAAC 2017). Rainfall (1,500–2,000 mm annual average) is greatest from April–June with a dry season from June–September (Jennings et al. 2006).

My forest sites were within SMBU boundaries. The forest is lowland tropical evergreen rainforest on karst limestone (Whitten et al. 1987). There is a high diversity of tree species (Powling 2006, Powling et al. 2015), but the forests are not dominated by the Dipterocarpaceae family as on Borneo or Sumatra. Powling et al. (2015) inventoried 89 plant families on Buton. The most speciose were from Poaceae, Arecaceae (mostly through *Calamus* spp.), Asteraceae, Fabaceae, Malvaceae (mostly *Pterocymbium* spp.), Moraceae (mostly *Ficus* spp.), Rubiceae, and Sapindaceae (see Powling et al. 2015 Table 2 for full list). The forest within SMBU has not been logged, but NTFP (mostly rattan, *Calamus* spp.) occurs throughout (Widayati and Carlisle 2012; *personal observation*). Rattan extraction has not affected tree species richness or diversity in the Lambusango Forest Reserve in southern Buton; however, it has affected understory vegetation

density including tree seedlings and saplings (Widayati and Carlisle 2012). Similar effects of rattan harvest likely occur in SMBU in northern Buton.

My mixed-farmland sites were in degraded forest just outside SMBU boundary contiguous with the forest. These areas are owned by local farmers who plant small-scale tree cash crops (e.g., cacao, cloves, nutmeg) interspersed with native vegetation. Mixed-farmland or ‘forest-gardens’ (Pangau-Adam et al. 2006) are common farming systems in many forest margin areas throughout Indonesia (Sorensen 1996). These areas are distinct from more rural-farmland on Buton Island where farmers plant agricultural crops (e.g. sweet potato *Ipomoea batatas*, maize *Zea mays*, cassava *Manihot esculenta*, papaya *Caricapapaya*) (Priston et al. 2012, Hardwick et al. 2017) within individual fenced plots that are fully deforested and separated from reserves (Priston et al. 2012). Natural regeneration of rural-farmland via primate seed dispersal becomes more difficult with increasing separation from forested areas (White et al. 2004), especially when primate species do not move from forested areas into crop fields (Chapman and Dunham 2018). However, seed limitation should not be an issue in my mixed-farmland sites because the areas are contiguous to the forest and because primates were observed using the area (Chapter 2).

I previously identified small-scale occurrence patterns for all terrestrial animal species at my sites in SMUB and the mixed-farmland (Figure 4.2; see also Chapter 2). The macaque, the only semi-frugivorous primate in SMBU, selected forest and mixed-farmland areas that were more difficult for humans to access and avoided easy to access areas. To protect macaque, I recommended that patrolling efforts focus on reducing retaliation killing (Hardwick et al. 2017), hunting, and habitat destruction in mixed-farmland and forest areas. The goal of the conservation strategy was to increase macaque use of mixed-farmland and forest across all areas including

those easy and difficult to access. Macaques (Cercopithecidae) are important components of Indonesian seed dispersal networks (Kaplin and Lambert 2002, Albert et al. 2013a) along with hornbills (Bucerotidae), bulbuls (Pycnonotidae), pigeons (Columbidae), and deer (Cervidae). Macaques eat many different fruits (Albert et al. 2013a, 2013b) and spit, drop, or defecate seeds (Corlett 1998, Tsuji and Su 2018). They use both intact and degraded forest (Albert et al. 2014) as well as agricultural fields (Hardwick et al. 2017). Therefore, it is possible that increasing the distribution of macaques across the mixed-farmland could also enhance regeneration of those areas by increasing seed deposition into areas not currently used by macaques.

4.3.2 Seed predation experimental design

Experimental blocks

I ran seed predation experiments (26 June–28 July 2015) during an ongoing camera trap survey of terrestrial animals within the forest and mixed-farmland. Please see Chapter 2 for details of the camera trap survey. Seed removal can vary over the year (Chapman and Chapman 2003, Rosin and Poulsen 2016), so I completed the experiments within one month to avoid any seasonal variation that might affect removal rates. Experimental blocks (Figure 4.1 a) were set up at $n = 12$ randomly selected camera trap stations. Initially, I planned to use eight stations in the forest and four in the mixed-farmland. However, I could only place two blocks in the mixed-farmland ('mixed-farmland blocks') because of logistical and permission issues. I stopped experiments at two of the 10 forest blocks: one that was destroyed and another due to an equipment error. Overall, I ran experiments at $n = 10$ blocks including two mixed-farmland blocks and eight forest blocks.

At each experimental block, I assigned a human accessibility value based on how quickly the area could be accessed on foot (km/hr) from all villages within a 15 km radius of my study site. I obtained these values from the camera trap survey (see Chapter 2 methods for details) which assigned all stations to one of two categories that indicated if the area was more ('high access') or less ('low access') accessible to farmers, hunters, and gatherers. Stations assigned high access were assumed to have higher amounts of farming, hunting, and/or NTFP extraction (e.g., rattan and other timber harvest; Widayati and Carlisle 2012) than low access stations.

Forest vegetation tends to be most disturbed in edge areas. Differences in understory vegetation can affect small mammal granivore community structure (Laurance 1994) and foraging activity (Kollmann and Buschor 2002, Orrock and Danielson 2005) between 200 and 500 m from forest boundaries. The mixed-farmland area at my study site is within degraded forest that is contiguous with the forest reserve. Therefore, I assumed that the effects of vegetation disturbance and human activities within edge areas (Laurance 1994, Fleury and Galetti 2004) would be evident within the mixed-farmland blocks and placed all forest blocks within the reserve boundaries separated by greater than 250 m. Within the forest, differences in block accessibility lead to unequal sampling among high ($n = 3$) and low ($n = 5$) access forest areas. Therefore, to ensure that results matched macaque habitat use patterns (high vs. low access mixed-farmland and forest), I included only data from the two high access mixed-farmland blocks, two high access forest blocks, and three low access forest blocks.

Seeds

I collected fallen fruits and seeds in the forest. Seeds were not collected from mixed-farmland areas. I could not access the forest canopy to harvest fruit, nor were fruits of any

species available in large amounts on the ground. Therefore, I collected fallen fruits and seeds from fifteen different species to maximize the total number of seeds used in the analysis. I brought fruits back to the field camp laboratory in separate plastic bags (I did not wear gloves during the experiment) for each species and extracted the seeds using a knife. I inspected all seeds for invertebrate and pathogen damage and disposed of all apparently unviable seeds. I then photographed, weighed, and measured the seeds and super glued a 50 cm long piece of fishing twine with flagging tape (with unique seed ID) to one end. A trained botanist identified seeds to genera from photographs. I assigned seed size (cm^3) to each genus as the average across all seeds included in the experiment.

I added the flagging tape and unique seed ID for two reasons. First, I intended to investigate the effects of individual seed mass on predation probability. However, I did not pursue this analysis due to correlation issues when modelling average seed size in my statistical analyses (see Step 2 of *Assessing regeneration potential of mixed-farmland: a three-step process*). Second, I intended to relocate removed seeds by searching for the flagging tape within a 20 m radius of the experimental site (following Kitamura et al. 2008b and Xiao et al. 2013). However, the topography at different sites suggested that heavy rains might move some of the seeds. Therefore, I instead fixed the piece of flagging tape into the ground using a piece of wire to prevent seeds from being washed away by excessive rains that might have occurred during the experiment. Other seed predation experiments (Chapman and Chapman 2003) have also adjusted experimental design to prevent losing seeds to heavy rains.

Experiments

At each block, I set up two replicate exclosure treatments to quantify seed predation. Each replicate included $n = 5$ seeds from two randomly selected genera placed 5 cm apart in each of two treatments (Figure 4.1 b and c): an open treatment and a closed treatment. The closed treatment was a *ca.* 0.5 m³ bottomless box constructed with 1 cm × 1 cm chicken wire with the sides placed just at ground level. The open treatment was placed directly in front of the closed treatment. I assumed that using two species per experiment would mimic the macaque natural seed deposition pattern given that I did not encounter clumps of dispersed seeds (free of fruity flesh) in the forest. Other macaque species – such as *M. leonina* in Thailand (Albert et al. 2013a) and *M. fascicularis* in Singapore (Corlett and Lucas 1990) – drop and spit seeds in a non-clumped pattern when seeds are not ingested and then defecated.

After placing the seeds, I checked each station twice during the experiment and noted seed fate in open treatments as vertebrate predation (i.e., gnaw marks or complete removal) or no vertebrate predation (i.e., alive, germinated, pathogen damage, or insect predation). After 5–7 days, I removed all remaining seeds and reran the experiments with two different genera.

Rodents are the main seed predators in Indonesian forests (Corlett 1998). Scatterhoarding has not been reported for any murid rodents (Corlett 1998) or squirrels (Corlett 2017) on Sulawesi. However, junglefowl (Arshad et al. 2000), warty pigs (Curran and Webb 2000), and Malay civets (Corlett 2017) might also eat seeds. (Figure 4.2; animal species within with red polygon). Therefore, I established several protocols to determine which species was responsible for predation or removal events at each block. The closed treatment was meant to exclude all mammals and birds but allow access by insects. However, there was at least one instance at each block where a rodent dug under the wire to access the seeds. It was extremely unlikely that a

warty pig removed these seeds as the hole was not large and the box was not disturbed. Likewise, a junglefowl could not have accessed the seeds based on the size of the hole. I also attempted to identify seed predators by placing the blocks in front of camera traps. This method was unreliable because of equipment and placement. Some cameras did not take photographs at night (when rodents are active) and others malfunctioned during the experiment. I also placed some treatments too close to or out of view of the camera (seeds not visible in photographs). I did not use photographs to identify seed predators because of these issues. However, of the photographs that were taken, several showed that warty pigs avoided the boxes when present and no photographs were taken of junglefowl.

Based on the above, I assumed that all removal and predation events were caused by rodents. This assumption was confirmed by the following observations: (1) gnaw marks on destroyed seeds that were left in place (following Holl and Lulow 1997), (2) seeds were also accessed and removed from the closed treatment by a hole dug under the wire, (3) the closed treatment boxes were never destroyed (eliminating warty pig), and (4) warty pigs appeared to avoid closed treatments in limited photographs and open treatments placed directly in front of closed treatments. Therefore, I did not test for the effect of different granivore species on predation/removal rates in the analysis.

4.3.3 Seed predation in the mixed-farmland: predictions

There is limited information on post-dispersal seed predation in mixed-farmland areas contiguous to forest reserves. However, some studies have quantified post-dispersal seed predation rates in cleared agricultural lands separated from forest reserves. For cleared agricultural lands, seed predation tends to be higher in pastures than within tropical forests

(Notman and Gorchov 2001, Myster 2018). For regenerating agricultural lands contiguous to forests, a higher abundance of seed-eating rodents in regenerating areas caused more seed loss than in the forest (Chapman and Chapman 1999). For degraded edge areas contiguous to forest reserves, a network meta-analysis (NMA) investigating the effects of human activities on the probability of seed predation in four tropical ecosystems (Chapter 3) found an interaction between seed size and activity type in edge areas, but agriculture appeared to have no effect on overall predation rates. I used these patterns to develop several predictions for seed predation in the mixed-farmland surrounding SMBU and for the subsequent influence on natural forest regeneration.

I collected seed removal data for nine different species with varying seed size, and although I did not place experiments in fully cleared agricultural areas, I expected that farming in general would lead to increased predation in mixed-farmland. Therefore, I predicted that there would be differences in seed predation between species in forest and mixed-farmland sites [*Seed predation prediction 1a*] and that all species would be at higher risk of seed predation in the mixed-farmland compared to the forest [*Seed predation prediction 1b*]. In terms of regeneration, I predicted that high rates of seed predation would reduce the regeneration potential of mixed-farmland [*Regeneration prediction 1*]. A conservation strategy that increases the distribution of primates across the mixed-farmland might also indirectly enhance natural regeneration by increasing seed deposition into areas that are not currently used by macaques. Rodent occurrence in the forest and mixed-farmland at my site was not affected by area accessibility (Figure 4.2). Therefore, I predicted that there would be no difference in seed predation of experimentally placed seeds in high versus low access sites [*Seed predation prediction 2*].

4.3.4 Assessing regeneration potential of mixed-farmland

After a pre-analysis data processing (*Step 1*), I determined if post-dispersal seed predation would affect regeneration of mixed-farmland by fitting a Bayesian varying-intercept logistic regression model to data collected in mixed-farmland and forest sites that were in high and low access areas (*Step 2*). I estimated coefficient values for the effect of area accessibility (low or high access) and habitat location (mixed-farmland or forest) and included a varying intercept to account for variation in seed predation among genera. I then used the linear predictor model (Gelman and Hill 2007) to calculate genus-specific probability of seed predation in forest and mixed-farmland sites across accessibility (*Step 3*). *Seed predation predictions 1a–b* were investigated using the genera-specific varying intercept and location regression coefficient values. *Seed predation prediction 2* and *Regeneration prediction 1* were investigated by the comparing 95% CIs for estimated seed predation in high and low access forest and mixed-farmland sites calculated from the linear predictor.

Step 1: Pre-analysis data processing and experimental data matrix

Although I ran experiments with 15 different plant genera, I limit analyses to the nine genera (Table 4.1) with at least one observation in both mixed-farmland and forest. Overall, the experimental data matrix included seed-level observations ($n = 180$) from two high access mixed-farmland blocks ($n = 45$), two high access forest blocks ($n = 50$), and three low access forest blocks ($n = 85$ total experiments) (Figure 4.1 a). I did not include observations from the closed treatment in analyses.

Step 2: Bayesian varying-intercept logistic regression

I estimated the probability that a seed was depredated or removed by a rodent using a Bayesian varying-intercept logistic regression with coefficients for habitat location and accessibility and a varying intercept for plant genus. I used a varying-intercept model to address unequal sample sizes among genera in mixed-farmland and forest stations (Millar and Anderson 2004, Gelman and Hill 2007). For the analysis, I only considered additive effects of habitat location (mixed-farmland vs. forest) and access (low vs. high) on the probability of seed removal. I did not consider nested or synergistic effects of accessibility within mixed-farmland and forest because none of the mixed-farmland sites were low access and because I did not collect enough observations to fit this hierarchical parameter.

Before fitting the model, I collapsed the data matrix of sampling observations for each seed into sampling observations for each genus at each station. Each sampling observation i was therefore the total number of seeds depredated y_i out of total number exposed n_i for each genus j in each open treatment at each experimental block, where experimental block was defined by its location in mixed-farmland/forest and high/low access area. This data structure allowed me to use a binomial likelihood function $y_i = \text{Binomial}(p_i, n_i)$ for the data observations. I assumed that the probability of predation for a given seed from each depot was independent of the other seeds in that depot following the justification outlined in Chapter 3 Methods 3.3.5 Statistical model.

The fully parameterized regression model was $\text{logit}(p_i) = \alpha_{\text{genus}_{j[i]}} + \beta_{\text{location}} \times \text{location}_i + \beta_{\text{accessibility}} \times \text{accessibility}_i$. I also considered an interaction effect between habitat location and accessibility $\beta_{\text{location} \times \text{accessibility}}$ and between seed size (cm^3) and habitat

location $\beta_{location \times seedsize}$. However, these parameters were not accurately estimated (high posterior correlations among point estimates), so I did not include either effect in the final model. I assigned informative prior probability distributions to the varying intercepts for three of the genera (*Calamus*, *Litsea*, and *Syzygium*) whose prior mean and standard deviation were obtained from a NMA (Chapter 3). The NMA (also a logistic regression) estimated a varying intercept coefficient for 25 different genera in disturbed tropical forests. Therefore, I coded location and access as binary variables with mixed-farmland = 1 and forest = 0 and low access = 1 and high access = 0, respectively, so that the genus intercept in my model would represent the probability of seed predation for each genus j in forest areas that were easiest for humans to access (where access is assumed proportional to human activity; see Chapter 2 Methods).

In the NMA, I showed that the posterior distribution of the varying intercept for *Calamus*, *Litsea*, and *Syzygium* were approximately Normal (see Chapter 3). Therefore, I assigned Normal priors to the genus varying intercept in this analysis. For the informative *Normal* priors, assigned prior mean and standard deviations to the regression coefficients using the posterior estimates from the NMA as follows (Lunn et al. 2003): $\alpha_{Calamus} \sim N(0.4818, 0.4396^2)$, $\alpha_{Litsea} \sim N(0.1635, 0.3608^2)$ and $\alpha_{Syzygium} \sim N(0.3776, 0.7832^2)$. I assigned uninformative *Normal* priors to all other genera with a mean zero and estimated standard deviation as $\alpha_j \sim N(0, \sigma_{alpha}^2)$ with a uniform prior on the standard deviation as $\sigma \sim Uniform(0, 100)$. I followed the Gelman and Hill (2007) method for assigning *Normal* priors to varying intercepts. I assigned uninformative normal priors for the location and access covariates as $\beta_{location} \sim Normal(0, 100^2)$ and $\beta_{access} \sim Normal(0, 100^2)$.

I coded each candidate model in BUGS (Lunn et al. 2003) and ran them in JAGS (Plummer 2003) called from R (R Core Team 2018) using the “jagsUI” (Kellner 2018) package.

I ran two chains per model for 300,000 iterations after 200,000 burn-in iteration with a 5-iteration thinning rate. I based convergence on the following diagnostics: trace plots (complete mixing of chains), density plots of the posterior distribution (inspected for Normality), parameter \hat{R} values < 1.09 (Gelman and Shirley 2016, Kellner 2018), and Gelman-Rubin multi-variate psrf (Plummer et al. 2006) value of 1. I inspected model fit by calculating posterior cross-correlations between all model parameters using the R package “CODA” (Plummer et al. 2006) and inspecting bivariate plots for banana shaped curves indicating non-identifiability (Gabry et al. 2019). I also confirmed updates to the prior using the ratio of posterior to prior precision ($\tau_{posterior} : \tau_{prior}$), where larger values (≥ 1.25) indicate estimates are driven by the data and smaller values (< 1.25) indicate estimates are driven by the prior.

Step 3: Calculating the probability of seed predation in forest and mixed-farmland at high and low access sites

I calculated the probability of post-dispersal seed predation for each genera in forest and mixed-farmland at high and low access sites using the linear predictor model (Gelman and Hill 2007). I created the model by combining the regression coefficients as $linpred_i = \alpha_{genus_{j[i]}} + \beta_{location} \times location_i + \beta_{accessibility} \times accessibility_i$ and used the model to predict the probability of seed predation in high vs. low access mixed-farmland and forest sites for each genera j . For each combination of habitat location and access for each genus, the linear predictor was calculated as the average of the MCMC simulations from the fitted model (Gelman and Hill 2007).

4.4 RESULTS

4.4.1 Model convergence and fit

The model fit the data well with low posterior correlations (absolute value < 0.602) and no non-identifiable parameters (bivariate plots not shown). All parameters converged (complete mixing of chains, \hat{R} values ≤ 1.001 , and Gelman-Rubin multi-variate psrf value = 1; results not shown). There were considerable updates ($\tau_{posterior}:\tau_{prior} > 2$) to the α_{genus} priors for *Aglaonema*, *Atuna*, *Entada*, *Licuala*, *Magnolia*, *Petrocarpus*, and *Syzygium* suggesting that the parameter values for these genera were driven by information within the experimental data.

4.4.2 Overall post-deposition seed predation

Rodents were responsible for a much larger proportion of seed predation/removal from experimental stations than invertebrates. Invertebrate damage was observed on 3.7% of seeds in the forest (2.2% *Syzygium* and 1.5% *Entada*). No invertebrate predation was observed in mixed-farmland.

The total number of seeds predated or removed by rodents from mixed-farmland was much less than in forest sites. Overall, 17.8% of seeds were predated/removed in mixed-farmland, whereas 63.0% of seeds were predated/removed from forest areas. However, when considering area accessibility, there was almost no difference in the overall number of seeds removed (50.5% removed from high access areas vs. 52.9% removed from low access areas).

There was an effect of location (forest vs. mixed-farmland) on probability of seed removal/predation. The coefficient for mixed-farmland (-3.645; Table 4.2) confirmed that seeds in high access mixed-farmland areas were less likely to be predated than seeds in high access

forest areas after controlling for genus effects. There was no apparent effect of accessibility on seed predation (95% credible interval crosses zero; Table 4.2) in forest areas.

4.4.3 Habitat-specific post-deposition predation

There was very little variation in seed predation or removal probability among genera in forest and mixed-farmland sites (providing little support for *Seed predation prediction 1a*). In the forest, *Atuna* and *Magnolia* were the only genera that were at a greater risk of predation compared to the average risk across genera (Table 4.2; Figure 4.3). *Atuna* was also more likely to be predated from mixed-farmland than the average risk across genera except *Magnolia*.

All genera were at lower risk of post-dispersal seed predation in mixed-farmland than in forest in both high and low access areas (Figure 4.3; white vs grey panels) except for *Atuna* and *Entada* (contrary to *Seed predation prediction 1b*). Post-dispersal seed predation for *Atuna* was high but quite variable in mixed-farmland sites, whereas predation of *Entada* was more variable in forest.

4.4.4 Regeneration potential of mixed-farmland

Aglaonema, *Calamus*, *Licuala*, *Litsea*, *Magnolia*, *Pterocarpus*, or *Syzygium* were at lower risk of seeds loss in mixed-farmland compared to forest areas suggesting high regeneration potential in the mixed-farmland (contrary to *Regeneration prediction 1*). There was little variation in predation risk for any genera in low compared to high access mixed-farmland (Figure 4.3; orange vs brown points). Rodent predation did not appear to reduce the survival of seeds experimentally dispersed into high access areas.

4.5 DISCUSSION

Small-scale subsistence agriculture is common at reserve boundaries across the tropics (Myster 2004, Pangau-Adam et al. 2006). These areas have considerable conservation value because they can both support human livelihoods and animals from within the reserve if managed sustainably (Dietz et al. 2007). Conservation strategies designed to protect primates might contribute to natural regeneration if seeds are dispersed from reserves into mixed-farmland areas (Vulinec et al. 2006, Koné et al. 2008) and if some portion of those dispersed seeds also escape predation.

Here I assessed the effects of post-dispersal rodent seed predation on forest regeneration potential in mixed-farmland at a reserve boundary via enhanced seed dispersal. Extremely low rates of post-dispersal seed removal in seven of nine plant genera confirmed that seed predators do not appear to reduce the regeneration potential in the mixed-farmland. These results suggested that regeneration of the mixed-farmland areas at the SMBU boundaries could be enhanced by increasing macaque distribution or abundance in the area because there was no difference in predation probability for any genus in areas that were used versus avoided by macaques.

4.5.1 Low post-deposition seed predation in mixed-farmland areas

Area accessibility did not appear to affect within genera seed predation across forest and mixed-farmland sites. Previous studies have provided some empirical evidence that seed predation is higher in areas where human activities have indirectly increased the proportion of granivores in the community (Dirzo et al. 2007, Rosin and Poulsen 2016). However, occurrence of granivorous rodents in my system was not affected by area accessibility (Chapter 2), so it is not surprising that seed predation was not different in low versus high access areas. Several

meta-analyses have also shown that seed predation is not significantly different in undisturbed versus disturbed areas (Muller-Landau 2007, Magrath et al. 2008) (also see Chapter 3).

Post-dispersal seed predation was extremely low in mixed-farmland areas. This is somewhat contrary to other studies that have found no difference (Holl and Lulow 1997) or significantly higher (Notman and Gorchov 2001, Myster 2018) rates of seed predation in agricultural pastures than in tropical forests. However, my mixed-farmland sites were within degraded forests rather than areas that had been completely cleared for agricultural plots. High rates of seed predation in cleared agricultural fields could be related to other factors such as rodents being attracted to food crops. Low predation and removal rates in mixed-farmland habitat more are consistent with the results of a forest regeneration study in peatland forests of Central Kalimantan, Indonesia (Blackham and Corlett 2015). There, seeds from four species were removed significantly more often in forest than in non-forest areas. Likewise, seed-eating rodents did not interfere with experimental test of regeneration potential for abandoned agricultural lands beside unlogged forests in Uganda (Chapman and Chapman 1999).

Small-scale changes to habitat structure in human-modified areas can also affect granivore foraging patterns. In temperate regions, rodents remove more seeds under complex vegetation cover than in open areas where the risk of predation is higher (Kollmann and Buschor 2002, Orrock and Danielson 2005, Perea et al. 2011). At my mixed-farmland sites, the canopy was visibly more open (unmeasured) than it was in the forest sites. In addition, I placed experimental seeds into open areas away from understory vegetation. Therefore, it is possible that low rates of rodent seed predation in mixed-farmland are related to higher risk of predation if predatory birds (e.g., *Accipiter* spp., *Ninox* spp. Martin et al. 2015, 2018) use the mixed-

farmland. Mixed-rural habitat and plantations in Central Sulawesi support a high diversity of bird species (Sodhi et al. 2005).

Rodents have species-specific dietary preference for seeds of different nutritional value and size (Brewer 2001, Cao et al. 2018). The seed species that is eaten can also vary under different disturbances such as fragmentation (Chen et al. 2017a) or vegetation removal (Perea et al. 2011). In temperate agricultural fields, Fischer and Türke (2016) found that rodents modified vegetation by disproportionately reducing the number of exotic plant seeds relative to native species. Other studies have found that rodent predation affects regeneration by either limiting or promoting the success of exotic seeds compared to natives (Maron et al. 2012, Connolly et al. 2014). I did not identify which rodent species were responsible for seed predation or removal in forest or mixed-farmland sites, but it is possible that the rodent communities in the mixed-farmland are made of different species than in the forested reserve as observed in other edge vs. interior areas (Laurance 1994). Therefore, differences in rodent community structure and dietary preference could explain low rates of seed predation in mixed-farmland as seeds were harvested from forest interior.

4.5.2 Limitations and improvements

I was interested in determining if a macaque-focused conservation strategy would indirectly assist in forest regeneration of mixed-farmland via increased seed rain. Therefore, I quantified the probability that seeds experimentally placed to mimic macaque seed dispersal from the reserve would escape predation in the mixed-farmland area. Sulawesi dwarf hornbill (*Penelopides exarhatus*) and Malay civet likely also disperse seeds from the forest into the mixed-farmland. However, I did not collect fine-scale habitat use patterns in mixed-farmland for

these species and so could not assess the habitat-specific predation probability of their deposited seeds. To gain a complete understanding of the amount of seed rain entering the farmland via zoochorous dispersal, I suggest completing habitat selection studies for hornbills and Malay civets within the mixed-farmland and then quantifying the probability of seed predation for seeds deposited into areas that are used and avoided by these species.

My study suffers from low experimental replication because I obtained removal rates from only two mixed-farmland sites. Low sample size likely affected my ability to quantify seed predation in mixed-farmland sites. Future studies should both increase the number of experimental blocks within mixed-farmland and consider placing seeds singly within depots, rather than in piles, to increase replication.

I attempted to control for seasonal variation in post-deposition seed predation by completing the experiments within one month. Although this design avoided contamination of my results with seasonal variation, I cannot generalize the results presented here for predation rates in different seasons. Additional experiments quantifying seed predation in different seasons are required to determine, first, if there is true variation in post-deposition seed predation among seasons and, second, if the results of this study are generalizable across seasons.

Post-dispersal seed predation is one of many environmental filters that seeds must pass to reach reproductive life history stages (Clark and Clark 1984, Wenny and Levey 1998, Maron et al. 2017). Seeds must also germinate and survive through seedling and sapling stages before recruiting to adults and contributing to population maintenance or growth. I did not follow seed fate past one week. Although some seeds began to germinate by the end of the experiment, I cannot confirm if any experimental seeds would contribute to future population growth rates.

4.5.3 Conservation implications

I provided experimental evidence that increasing primate distribution across a mixed-farmland area would contribute to natural forest regeneration of rainforest margin areas. Mixed-farmland has considerable value for both local farmers and wildlife within reserves, and sustainable management could therefore benefit both human livelihoods (Abdulkadir-Sunito and Sitorus 2007) and biodiversity conservation (Chapman and Chapman 1999). Therefore, managers could consider increasing patrolling and other community-based conservation strategies to reduce human-macaque conflict (e.g., crop raiding; Hardwick et al. 2017) in mixed-farmland areas.

Identifying how primates use habitat in relation to human activities (Lambert and Chapman 2005, Vulinec et al. 2006) and quantifying post-dispersal seed predation (Lambert 2002, Chapman and Dunham 2018) are important first steps in predicting the potential for restoration of degraded areas via seed dispersal. I developed a method to identify small-scale differences in seed predation in relation to non-human primate habitat use and provide an evidence-based assessment of the potential to enhance forest regeneration via natural seed dispersal. Managers might consider incorporating these steps into conservation planning before assuming that indirect regeneration of disturbed habitats will occur simply by protecting a species or functional guild.

Chapter 5: Conclusion

Human activities are driving the loss of species from tropical ecosystems. Protected reserves can shield animals and plants from human-related threats, but even well designed areas are often subject to human encroachment and livelihood generating activities on both sides of the reserve boundaries (Laurance et al. 2012, Hughes 2017). It is therefore crucial that we find ways to manage areas at the boundary of reserves for maximal biodiversity conservation and continued use by humans.

Small-scale agriculture is common at reserve boundaries across the tropics (Myster 2004, Pangau-Adam et al. 2006) where farmers plant cash-crop trees interspersed with natural vegetation (Dietz et al. 2007). In this thesis, I provided evidence that these mixed-farmland areas can be managed for use by animals, regeneration of plants, and income-generating activities of local farmers. Identifying strategies to address the effects of human activities on animals while also accounting for changes to plant-animal interactions that might enhance (seed dispersal) or reduce (seed predation) plant regeneration can assist in the economic allocation of limited time and funds for conservation.

I began by investigating how human activities have shaped the habitat selection and distribution of animals within a rainforest reserve and the surrounding mixed-farmland on Buton Island, Southeast Sulawesi, Indonesia. After modelling co-occurrences of animals in relation to local habitat and human activities, I assessed whether protecting a single species (i.e., an umbrella species conservation strategy; Wilcox 1984) would indirectly benefit the remaining animals by virtue of overlapping habitat selection. The umbrella and other species focused strategies are attractive to managers who cannot protect all animal species within a community due to time (Fleishman et al. 2001) and funding (Roberge and Angelstam 2004) constraints.

Next, I used a pantropical, evidence-synthesis approach to investigate the long-standing hypothesis that human activities affect the regeneration of plants by changing plant-animal interactions (Muller-Landau 2007, Magrach et al. 2008, Markl et al. 2012, Kurten 2013, Neuschulz et al. 2016). There is good evidence that human activities suppress animal-mediated pollination (Quesada et al. 2003) and seed dispersal (Brodie et al. 2009), but less is known about the effects on post-deposition seed predation. Understanding trends in post-deposition seed predation can help design granivore control methods targeted at decreasing the probability of seed loss in assisted regeneration projects (Doust et al. 2006, Garcia-Orth and Martínez-Ramos 2008). After accounting for variation in post-deposition seed predation both within and between human-modified ecosystems and accounting for the effect of seed size, I identified where, and for which seeds, granivore control might be required across four different tropical forest types.

Finally, I used the evidence-synthesis results to guide an assessment of the potential effect of post-deposition seed predation in the mixed-farmland surrounding the reserve at my site. There is evidence that non-human primates increase natural seed rain into human-modified habitats (Vulinec et al. 2006, Andresen et al. 2018), but the effect of post-deposition seed predation on the survival of those seeds is rarely quantified (Lambert 2002). At my site, seed-dispersing macaques were observed in the reserve and in the mixed-farmland, but they tended to use areas that were more difficult for humans to access. Therefore, I investigated if efforts to increase macaque use of mixed-farmland sites might also indirectly enhance natural forest regeneration of those areas via increased seed rain.

I completed these steps in three separate analysis chapters and found the following:

Chapter 2: Umbrella species conservation: what can we learn from modelling small-scale co-occurrence patterns? A case study from the rainforests of Buton Island, Indonesia

In Chapter 2, I answered the question: ‘could protecting one animal species and its habitat also protect other co-occurring animals from human activities’? I found that human activities affected the co-occurrence of only a subset of animal species within the community. Macaques and warty pigs were more likely to co-occur in mixed-farmland and forest with low hunting and little NTFP extraction than in areas with high levels of these activities.

The anoa is a flagship species for Sulawesi, and the Indonesian government has imposed a Strategy and Action Plan for Conservation of Anoa 2013–2022 (Mustari et al. 2015). There was no evidence that this strategy would serve as an effective umbrella strategy to mitigate the effects of human activities on the distribution of macaques at my site. The anoa did not appear to be an effective umbrella species for macaques because the two species did not have overlap in their habitat use. Although, the anoa might serve as an effective umbrella species for red junglefowl, Malay civet, and Murid rodents. Additional conservation measures will be required to increase in the distribution of macaque in forest and mixed-farmland.

Chapter 3: Assisted regeneration of human-modified tropical forest ecosystems: where might seed predator control improve the survival of sown seeds? A hierarchical network meta-analysis

In Chapter 3, I answered the question: ‘where and for what seeds might granivore control mitigate seed losses in assisted regeneration projects’? Post-deposition seed predation of management sowed seeds varied among human-modified ecosystems depending on seed size. Granivore control might help to reduce seed mortality for those at higher probability of predation.

In tropical moist deciduous forests, granivore control could help to reduce loss of large seeds in edge areas where hunting and logging activities occur. However, smaller seeds would benefit more from granivore-control than large seeds in moist deciduous forest, mountain system forest, and rainforest edges that are not otherwise modified by human activities. Granivore control efforts could also protect small seeds sowed in rainforest edges where hunting and non-logging product extraction occur.

Chapter 4: Will post-deposition seed predation affect the regeneration of mixed-farmland at a tropical rainforest reserve boundary?

In Chapter 4, I answered the question: ‘in addition to human-sowing, could increasing the distribution of a seed-dispersing animal contribute to the regeneration of human-modified habitats’? In Chapter 2, I identified that additional conservation measures might increase in the distribution of macaque in forest and mixed-farmland. Given that macaques are also seed dispersing primates, the resultant changes might also increase seed rain to mixed-farmland. Therefore, I experimentally quantified the probability of post deposition seed predation in areas used and avoided by macaques.

There was no evidence that post-deposition mammal granivores reduced seed survival in the mixed-farmland. All seeds were at lower probability of predation in those areas compared to within the forest reserve. The low risk of seed predation suggested that increasing the distribution of seed dispersing macaques into the mixed-use area might also assist in forest regeneration via increased natural seed rain.

Significance

There is an increasing need for modelling approaches that investigate the possible connection of animal and plant conservation strategies for multi-use areas throughout the tropics. The negative effects of human activities on animal habitat use and on plant regeneration are particularly concerning in Southeast Asia where many endemic species are threatened by deforestation, conversion of land to agriculture, and hunting (Hughes 2017). Here I provided recommendations to assist in developing a plan to mitigate the effects of human activities on a relatively unknown animal and plant community in a rainforest reserve and the surrounding mixed-farmland on Buton Island, Southeast Sulawesi, Indonesia.

My assessment of the umbrella species conservation strategy uncovered concerns that have been echoed by others regarding species-specific discrepancies in habitat selection and avoidance of areas used by humans. By using Bayesian Network inference, I highlighted the importance of modelling small-scale co-occurrence patterns for conservation decision-making. Ignoring these patterns could lead to the failure of umbrella species conservation strategies. In addition to measures directed at protecting animals, I provided recommendations on where and for which seeds granivore control might assist the natural regeneration of human-modified ecosystems. Identifying how management-induced changes in animal distribution might affect concurrent projects to assist plant regeneration can help to reduce seed losses and contribute to the success of these expensive and laborious projects.

Overall, I showed how many conservation projects might benefit from considering wide-scale evidence synthesis using network meta-analyses when designing tactics to combat the effects of human activities on plants. I recommend that conservation managers conduct similar assessments of species co-occurrence and post-dispersal seed predation before assuming that

protection of entire animal communities and regeneration of disturbed habitats will necessarily follow from the management of particular animals or guilds.

Tables

Table 2.1 Bird and mammal species captured on camera traps in SMBU, Buton Island, Southeast Sulawesi, Indonesia (Jun–Aug 2013, May–Aug 2014, and Jun–Aug 2015). Species grouped by class, diet, and body size (body length and mass). Anoa identified to genus and rodents identified to family because species were indistinguishable in photographs.

body size	diet	animal	Morphology	
			length (cm)	mass (kg)
Aves				
medium	omnivore	red junglefowl (<i>Gallus gallus</i>)	57.5	0.9
Mammalia				
small	omnivore	rodent (Muridae)	16.3	–
medium	omnivore	Malay civet (<i>Viverra zibetha</i>)	58.2	3.8
		Buton macaque (<i>Macaca ochreata</i>)	48.4	8.3
large	herbivore	anoa (<i>Bubalus</i> sp.)	165.9	225
	omnivore	Sulawesi warty pig (<i>Sus celebensis</i>)	105	55

Table 2.2 Conditional probability (mean, standard deviation SD, and 95% confidence intervals) of macaque-warty pig co-occurrence along an elevation gradient within forest and mixed-farmland at the boundary of SMBU, Buton Island, Southeast Sulawesi, Indonesia (2013–2015). Co-occurrence was affected by the accessibility of each area for human where high access areas were easier to reach on foot from village than low access areas. Human activities in forest included hunting and non-timber forest product extraction. Human activities in mixed-farmland included agriculture (small-scale cash crop trees planted within native vegetation[†]), hunting, and non-timber forest product extraction. Conditional probabilities calculated using logic sampling queries ($n = 5,000$) of the Bayesian Network of co-occurrences.

Conditional probability of co-occurrence	mean	SD	Lower CI	Upper CI
low elevation				
low access farmland	0.769	0.081	0.607	0.917
high access farmland	0.485	0.012	0.462	0.509
low access forest	0.715	0.134	0.429	1.000
high access forest	0.452	0.018	0.418	0.486
mid elevation				
low access forest	0.717	0.009	0.700	0.734
high access forest	0.452	0.010	0.432	0.472
high elevation				
low access forest	0.717	0.009	0.699	0.735
high access forest	0.450	0.080	0.294	0.610

[†]Sorensen 1996, Pangau-Adam et al. 2006

Table 2.3 Conditional probability (mean with standard deviation SD and 95% confidence intervals) of anoa, junglefowl, rodent, and Malay civet co-occurrence along an elevation gradient within forest and mixed-farmland at the boundary of SMBU, Buton Island, Southeast Sulawesi, Indonesia (2013–2015). Co-occurrence among species pairs was affected by canopy height (m) and distance from river or ephemeral stream (‘close to’ or ‘far from’ water). Conditional probabilities calculated using logic sampling queries ($n = 5,000$) of the Bayesian Network of co-occurrences.

Conditional probability of co-occurrence	mean	SD	Lower CI	Upper CI
anoa and junglefowl				
low elevation				
low canopy	0.550	0.016	0.519	0.583
high canopy	0.131	0.009	0.114	0.147
mid elevation				
low canopy	0.156	0.009	0.139	0.173
high canopy	0.602	0.008	0.585	0.619
high elevation				
low canopy	0.120	0.004	0.005	0.020
high canopy	0.372	0.013	0.347	0.397
junglefowl and rodent				
low elevation				
low canopy, close to water	0.596	0.027	0.543	0.649
low canopy, far from water	0.329	0.020	0.290	0.369
high canopy, close to water	0.297	0.018	0.261	0.334
high canopy, far from water	0.164	0.012	0.142	0.187
mid elevation				
low canopy, close to water	0.315	0.018	0.281	0.349
low canopy, far from water	0.174	0.011	0.153	0.196
high canopy, close to water	0.632	0.013	0.606	0.659
high canopy, far from water	0.349	0.011	0.329	0.370

Conditional probability of co-occurrence	mean	SD	Lower CI	Upper CI
high elevation				
low canopy, close to water	0.213	0.023	0.168	0.260
low canopy, far from water	0.118	0.015	0.089	0.147
high canopy, close to water	0.469	0.021	0.428	0.511
high canopy, far from water	0.259	0.014	0.232	0.288
rodent and Malay civet				
low elevation				
low canopy, close to water	0.483	0.028	0.428	0.536
low canopy, far from water	0.285	0.019	0.249	0.323
high canopy, close to water	0.310	0.019	0.274	0.347
high canopy, far from water	0.205	0.013	0.180	0.230
mid elevation				
low canopy, close to water	0.310	0.018	0.276	0.345
low canopy, far from water	0.203	0.012	0.179	0.226
high canopy, close to water	0.525	0.014	0.497	0.552
high canopy, far from water	0.308	0.010	0.287	0.328
high elevation				
low canopy, close to water	0.246	0.025	0.199	0.295
low canopy, far from water	0.173	0.017	0.141	0.207
high canopy, close to water	0.420	0.021	0.377	0.460
high canopy, far from water	0.253	0.014	0.229	0.287
anoa, junglefowl, rodent, and Malay civet				
low elevation				
low canopy, close to water	0.399	0.026	0.347	0.450
low canopy, far from water	0.220	0.018	0.185	0.254
high canopy, close to water	0.098	0.012	0.075	0.122
high canopy, far from water	0.054	0.007	0.041	0.069
mid elevation				
low canopy, close to water	0.113	0.012	0.089	0.137
low canopy, far from water	0.063	0.007	0.049	0.077
high canopy, close to water	0.453	0.014	0.425	0.481
high canopy, far from water	0.251	0.009	0.232	0.269

Conditional probability of co-occurrence	mean	SD	Lower CI	Upper CI
high elevation				
low canopy, close to water	0.009	0.005	0	0.020
low canopy, far from water	0.005	0.003	0	0.012
high canopy, close to water	0.281	0.019	0.245	0.318
high canopy, far from water	0.154	0.012	0.131	0.178

Table 3.1 Predictions for the across- and within-ecosystem effects of human activities on the probability of post-planting seed predation. Human activities are grouped by the component of the ecosystem that is affected (animals, plants, or animals + plants). Outcome indicates whether the probability of predation is predicted to be higher, lower, or no different compared to undisturbed conditions. Justification based on observations from published literature not included in the NMA. NTFP is non-timber forest product extraction.

activity	target	predicted outcome	justifications
across ecosystems			
hunting	animals	no difference in probability of predation	hunting can decrease (e.g., <i>Tayassu pecari</i> ; Silman et al. 2003), indirectly increase (e.g., rodents; Dirzo et al. 2007, Rosin and Poulsen 2016), or have no effect (e.g., <i>Sus scrofa</i> , Gamelon et al. 2011; rodents, Effiom et al. 2013b) on the abundance of granivores
hunting + edge			effects likely to be ecosystem, seed, and granivore specific and difficult to identify without data on granivore abundance
logging	plants	higher probability of seed predation	logging facilitates invasion by small-bodied granivores (Loveridge et al. 2016) fragmentation creates edge areas with high abundance of vines and lianas that provide rodent granivores with foraging substrates (Laurance 1994)
hunting + livestock grazing + NTFP + edge	plants	lower probability of seed predation	rodent granivores forage for less time and remove fewer seeds from area with sparse understory vegetation because of reduced risk of predation for granivores in those areas (Gutiérrez-Granads 2011, Perea et al. 2011)

activity	target	predicted outcome	justifications
livestock grazing + logging + edge		lower probability of seed predation	NTFP reduces understory vegetation cover in tropical rainforests (Widayati and Carlisle 2012)
NTFP		lower probability of seed predation	livestock grazing reduces vegetation ground cover and increases predation risk for small mammals (Legge et al. 2019)
hunting + logging + edge	animals + plants	no difference in probability of predation	unpredictable effects of hunting on granivore abundance
hunting + NTFP + edge			possible interactions between changing granivore abundance and foraging behavior might make it difficult to detect a trend
edge			
within ecosystems			
all	animals	higher or lower probability of predation with	small seeds were at 30-times higher risk of predation in a defaunated tropical rainforest in Mexico (Dirzo et al. 2007)
	plants	magnitude of effect varying within ecosystems for	Lighter wind-dispersed seeds were removed less often than animal dispersed seeds in a tropical peat land forest and other deforested areas on Kalimantan, Indonesia (Blackham and Corlett 2015)
	animals + plants	different activities	Rodent preference for seeds of a certain size can change in different ecosystems (Brewer 2001, Cao et al. 2018) and when exposed to different human activities (e.g. fragmentation Chen et al. 2017a; vegetation removal, Perea et al. 2011)

Table 3.2 Ecosystem-, depot group-, and depot-level data used in the NMA. Seed predation was quantified by different research groups (study) by placing seed depots within an ecosystem (black) that was modified by a human activity. Within ecosystems, all depots were grouped into ‘depot groups’ (grey). At the depot-level, seeds are described by size (cm³), life form, and dispersal mode. Human activities are coloured by the ecosystem component that was modified: undisturbed (ivory); animals (brown); animals & plants (red), or plants (green).

Ecosystem & depot group-level data		Depot-level data			
human activity (experimental study)	family	genus	volume (cm ³)	life form	dispersal mode [†]
tropical dry forest					
depot group 1					
hunting + edge					
Kitamura et al. (2004)	Meliaceae	<i>Aglaia</i>	7.735	tree	animal
depot group 2					
non-timber forest product extraction					
Lopez-Toledo et al. (2013)	Arecaceae	<i>Brahea</i>	2.928	palm	animal
tropical moist deciduous forest					
depot group 1					
undisturbed					
Fleury and Galetti (2006)	Arecaceae	<i>Syagrus</i>	2.477	palm	animal
Fleury and Galetti (2004)	Arecaceae	<i>Euterpe</i>	1.425	palm	bird
		<i>Syagrus</i>	2.477	palm	animal
Vieira et al. (n.d.)	Fabaceae	<i>Sawrtzia</i>	6.283	tree	animal
	Meliaceae	<i>Cedrela</i>	0.130	tree	abiotic
Adler and Kestell (1998)	Arecaceae	<i>Attalea</i>	1.513	tree	mammal
depot group 2					
hunting					
Fleury and Galetti (2006)	Arecaceae	<i>Syagrus</i>	2.477	palm	animal
depot group 3					
hunting + livestock grazing + non-timber forest product extraction + edge					
Dutton et al. (2014)	Myrtaceae	<i>Syzygium</i>	0.628	tree	mammal
depot group 4					
hunting + logging + edge					
Fleury and Galetti (2006)	Arecaceae	<i>Syagrus</i>	2.477	palm	animal
Fleury and Galetti (2004)	Arecaceae	<i>Euterpe</i>	1.425	palm	bird

Ecosystem & depot group-level data		Depot-level data			
human activity (experimental study)	family	genus	volume (cm ³)	life form	dispersal mode [†]
depot group 5					
hunting + edge					
Fleury and Galetti (2006)	Arecaceae	<i>Syagrus</i>	2.477	palm	animal
Fleury and Galetti (2004)	Arecaceae	<i>Euterpe</i>	1.425	palm	bird
depot group 6					
livestock grazing + logging + edge					
Vieira et al. (n.d.)	Fabaceae	<i>Swartzia</i>	6.283	tree	animal
	Meliaceae	<i>Cadrela</i>	0.130	tree	abiotic
depot group 7					
edge					
Fleury and Galetti (2006)	Aracaceae	<i>Syagrus</i>	2.477	palm	animal
tropical mountain system forest					
depot group 1					
undisturbed					
Holl and Lulow (1997)	Arecaceae	<i>Chamaedorea</i>	0.239	shrub	animal
	Lauraceae	<i>Ocotea</i>	0.933	tree	animal
		<i>Phoebe</i>	0.681	tree	bird
depot group 2					
edge					
Holl and Lulow (1997)	Arecaceae	<i>Chamaedorea</i>	0.239	shrub	animal
	Lauraceae	<i>Ocotea</i>	0.933	tree	animal
		<i>Phoebe</i>	0.681	tree	bird
tropical rainforest					
depot group 1					
undisturbed					
Andresen and Levey (2004)	Lauraceae	<i>Ocotea</i>	0.933	tree	animal
Whittaker and Turner (1994)	Meliaceae	<i>Dysoxylum</i>	0.424	tree	bird
Young et al. (2013)	Arecaceae	<i>Cocos</i>	27.667	palm	abiotic
depot group 2					
hunting					
Norghauer et al. (2006)	Meliaceae	<i>Swietenia</i>	0.500	tree	abiotic
depot group 3					
hunting + livestock grazing + non-timber forest product extraction + edge					
Montaño et al. (n.d.)	Arecaceae	<i>Astrocaryum</i>	1.339	palm	mammal
	Arecaceae	<i>Socratea</i>	5.089	palm	mammal
depot group 4					
hunting + non-timber forest product extraction + edge					
Sidhu and Datta (2015)	Lauraceae	<i>Actinodaphne</i>	0.890	tree	bird
		<i>Beilschmiedia</i>	3.700	tree	bird

Ecosystem & depot group-level data		Depot-level data			
human activity (experimental study)	family	genus	volume (cm ³)	life form	dispersal mode [†]
		<i>Litsea</i>	2.572	tree	animal
	Magnoliaceae	<i>Talauma</i>	0.005	tree	animal
	Meliaceae	<i>Chisocheton</i>	9.481	tree	bird
depot group 5					
edge					
Fadini et al. (2009)	Arecaceae	<i>Euterpe</i>	1.425	palm	bird
Fleury et al. (2014)	Arecaceae	<i>Euterpe</i>	1.425	palm	bird
		<i>Syagrus</i>	2.477	palm	animal
depot group 6					
logging					
McConkey (2005a)	Arecaceae	<i>Calamus</i>	0.729	liana	animal
	Lauraceae	<i>Beilschmiedia</i>	3.267	tree	animal
	Meliaceae	<i>Aglaia</i>	1.639	tree	animal
McConkey (2005b)	Apocynaceae	<i>Leuconotis</i>	0.549	tree	animal
		<i>Willughbeia</i>	3.688	liana	animal
	Arecaceae	<i>Calamus</i>	0.729	liana	animal
	Lauraceae	<i>Beilschiedia</i>	3.267	tree	animal
		<i>Cryptocarya</i>	2.697	tree	animal
		<i>Litsea</i>	0.882	tree	animal
	Meliaceae	<i>Aglaia</i>	1.639	tree	animal

[†] vertebrate animals including birds and mammals

Table 4.1 Seed genera collected in SMBU, Buton Island, Southeast Sulawesi, Indonesia (Jun–July 2015). Seed volume (cm³) calculated as mean of all seeds collected using equation for ellipse or sphere (*Calamus* and *Syzygium*) following Chen and Moles (2015). All genera (except *Pterocarpus*) assumed to be dispersed by macaques eaten by rodents based on observations of other species eating fruits and seeds of the same genus[†]. Rodent examples provided as location of observation. All local seed names provided by local experts.

Family	Genus (local name)	volume (cm ³)	dispersal mode	life form	macaque species (reference)	rodent observation (reference)
Arecaceae	<i>Aglaonema</i> (unknown)	0.722	animal	herb	<i>M. fascicularis</i> Ilham et al. (2017)	Indo-Pacific [†] Meyer and Butaud (2009)
	<i>Calamus</i> (rotan)	4.084	animal	liana	<i>M. fascicularis</i> Lucas and Corlett (1998) <i>M. tonkeana</i> Riley et al. (2013) <i>M. leonina</i> Albert et al. (2013)	Indonesia McConkey (2005)
						
	<i>Licuala</i> (unknown)	0.356	animal	tree	<i>M. leonina</i> Albert et al. (2013) <i>M. fascicularis</i> Ilham et al. (2017)	Indo-Pacific [†] Meyer and Butaud (2009)
						

Family	Genus (local name)	volume (cm ³)	dispersal mode	life form	macaque species (reference)	rodent observation (reference)
Chrysobalanaceae	<i>Atuna</i> (unknown) 	42.970	animal	tree	<i>M. fascicularis</i> [†] Ilham et al. (2017) Ruslin et al. (2019)	Brazil Galetti et al. (2015) Indo-Pacific Meyer and Butaud (2009)
Fabaceae	<i>Entada</i> (kolondue) 	64.432	abiotic	liana	<i>M. fascicularis</i> [†] Yeager (1996) Ilham et al. (2017)	Mexico Dirzo et al. (2007) Venezuela Lopez and Terborgh (2007)
	<i>Pterocarpus</i> (cendana) 	5.506	abiotic	tree		Venezuela Lopez and Terborgh (2007)
Lauraceae	<i>Litsea</i> (unknown) 	0.588	animal	tree	<i>M. leonina</i> Albert et al. (2013) <i>M. fascicularis</i> Sha and Hanya (2013)	India Sidhu and Datta (2015)

Family	Genus (local name)	volume (cm ³)	dispersal mode	life form	macaque species (reference)	rodent observation (reference)
Magnoliaceae	<i>Magnolia</i> (unknown)	0.314	animal	tree	<i>M. fascicularis</i> Lucas and Corlett (1998)	Mexico Vásquez-Morales and Sánchez-Velásquez (2011)
						
Myrtaceae	<i>Syzygium</i> (dongkalano wita)	16.344	animal	tree	<i>M. fascicularis</i> Hadi et al. (2007) <i>M. fascicularis</i> Sha and Hanya (2013) <i>M. leonina</i> Albert et al. (2013)	Indonesia Blate et al. (1998)
						

† observed eating fruit or seed from same family

Table 4.2 Logistic regression coefficients (posterior mean, standard deviation SD, and 95% credible intervals) for genus varying intercepts and habitat effects used to estimate probability of post-dispersal seed predation by rodents. Experimental data collected in SMBU, Buton Island, Southeast Sulawesi, Indonesia (Jun–July 2015). Credible intervals that do not include zero indicated in **bold**.

	mean	SD	lower CI	upper CI
genus intercepts				
<i>Aglaonema</i>	0.642	0.738	-0.805	2.094
<i>Atuna</i>	5.126	1.209	3.057	7.825
<i>Calamus</i>	-0.366	0.373	-1.103	0.361
Entada	0.094	0.979	-1.910	1.951
<i>Licuala</i>	0.551	0.504	-0.426	1.522
<i>Litsea</i>	0.444	0.318	-0.180	1.067
<i>Magnolia</i>	3.718	0.915	2.110	5.685
<i>Pterocarpus</i>	0.586	0.593	-0.565	1.770
<i>Syzygium</i>	-0.895	0.503	-1.901	0.069
habitat effects				
farmland	-3.645	0.808	-5.401	-2.228
low access	-0.812	0.432	-1.678	0.017

Figures

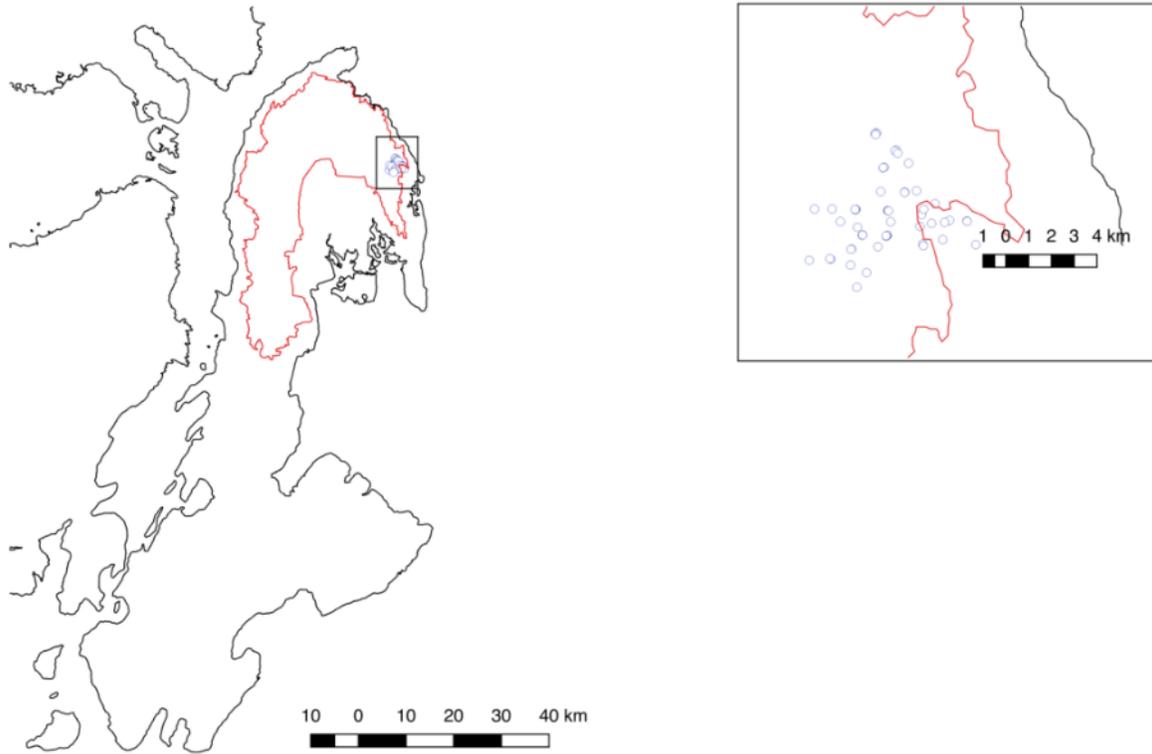


Figure 2.1 Buton Island, Southeast Sulawesi, Indonesia with boundaries (red) of SMBU. Inset shows grid of camera traps ($n = 40$) deployed within the forest and mixed-farmland at the reserve boundaries (Jun–Aug 2013, May–Aug 2014, Jun–Aug 2015). Overlapping camera stations indicate areas that were resampled over field seasons.

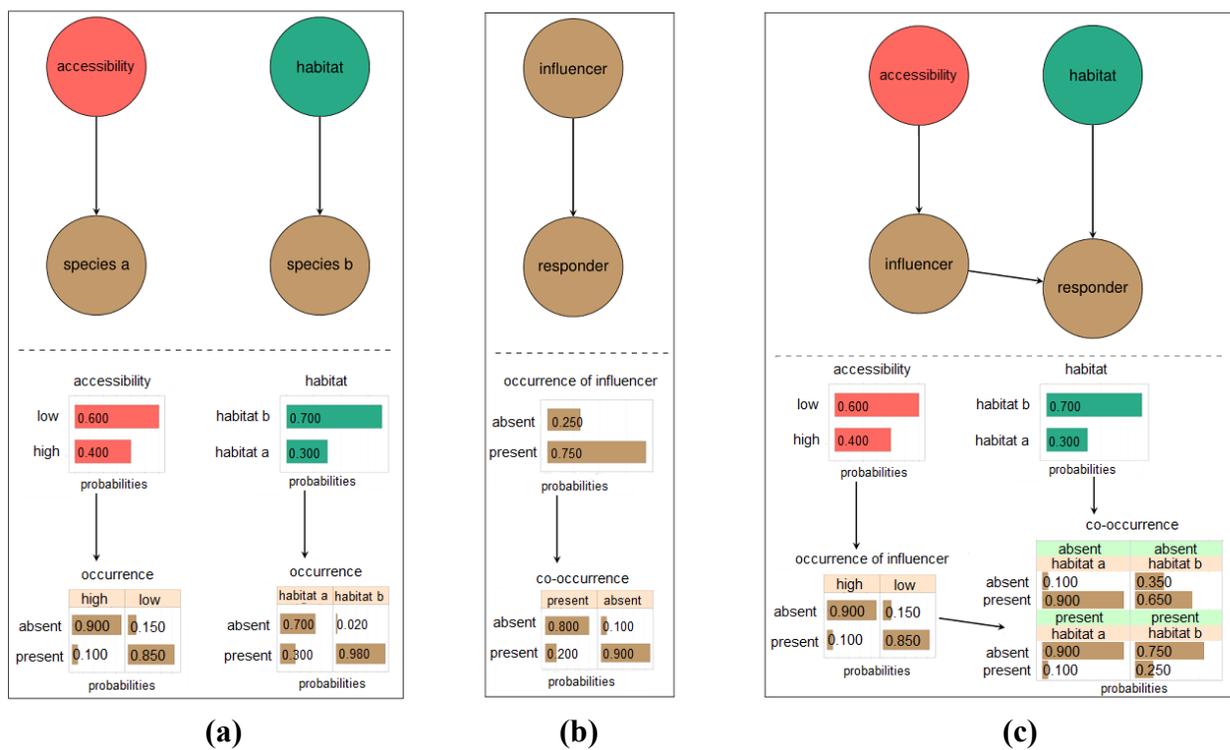


Figure 2. 2 Conventional Bayesian Network influence diagram showing simplified network of predicted relationships between (a) habitat and/or area accessibility and species occurrence and (b) species co-occurrence for influencer and responder species. Networks shown in (a) and (b) were combined in (c) to create a full network showing species co-occurrence within habitat based on area accessibility. Upper panels show variables as nodes. Arrows start at ‘parent’ nodes and end at ‘child’ nodes. Lower panels show conditional probability distributions (within conditional probability tables) of child states given different states of its parent.

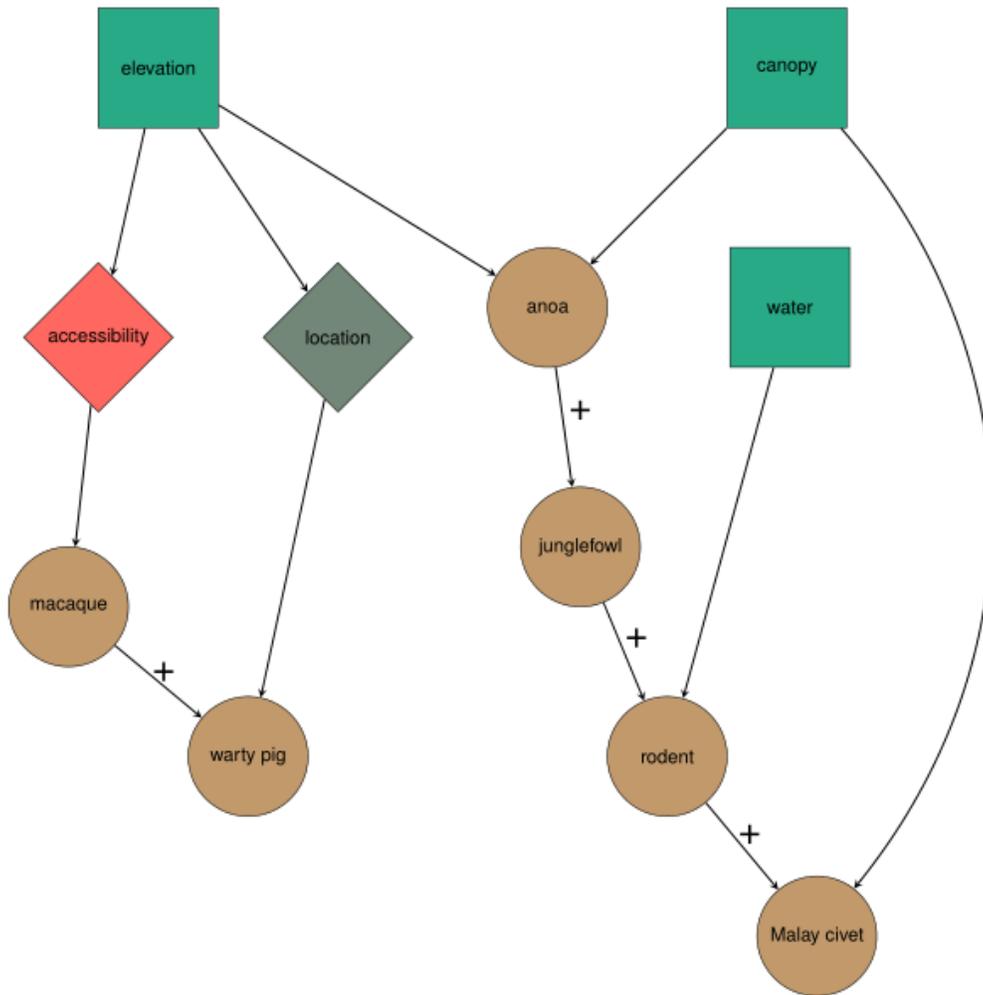


Figure 2.3 Empirical Bayesian Network of co-occurrences in forest and mixed-farmland just outside boundaries of SMBU, Buton Island, Indonesia (2013–2015). Arrows between species (brown circles) indicate positive co-occurrences. Arrows between species and habitat (green squares) indicate preference or avoidance of habitat features. Arrows between species and area accessibility (red and grey diamonds) indicate preference or avoidance of areas that were easy (high access) or difficult (low access) for humans to access within forest and mixed-farmland areas. See Methods for variable values and Figure A.2.4 for preference and avoidance scenarios.

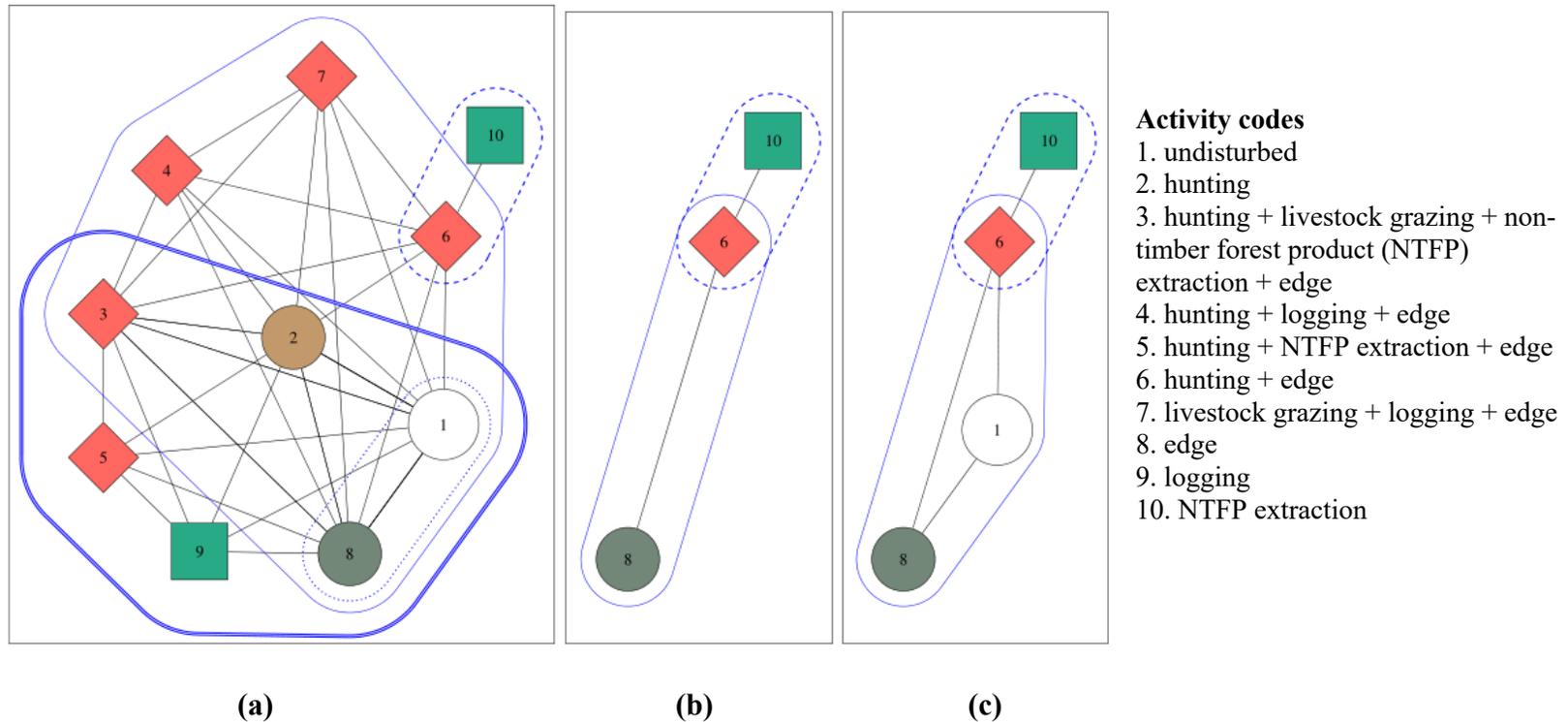


Figure 3.1 Network of human activity comparisons included in the Network meta-analysis (a) and simplified networks showing how direct (b only) and indirect (b and c) evidence is used to calculate activity effects. Direct comparisons are made within and between ecosystems using nodes connected by lines. Indirect comparisons are made between nodes connected by another node. Ecosystems are connected by overlapping activities. Blue lines group activities within tropical forest ecosystems (dashed: dry, solid: moist deciduous, dotted: mountain system, and double: rainforest). Activities coloured by component of ecosystem targeted (white circle: none; brown circle: animals; red diamond: animals and plants; green square: plants; drab green: edge location).

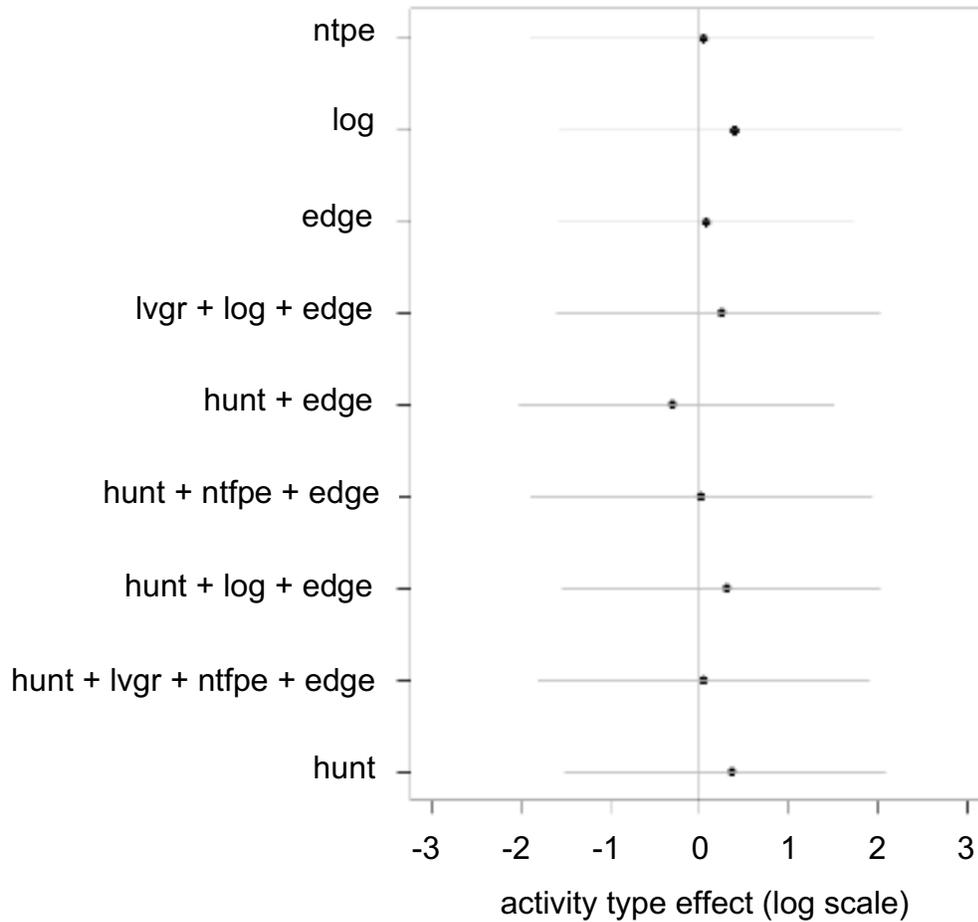


Figure 3.2 (a) Across ecosystem comparisons of the effect size (log scale) for each human activity type on probability of post-deposition seed predation relative to undisturbed conditions (indicated by zero). Values are given as posterior mean and 95% credible intervals (CIs). CIs that do not overlap zero indicate that the probability of seed predation is lower (negative values) or higher (positive values) in an area modified by a given human activity than in undisturbed conditions. Human activity codes: agr: agriculture; hunt: hunting; lvgr: livestock grazing; log: logging; ntfpe: non-timber forest product extraction. Edge indicates observations were taken in edge habitat.

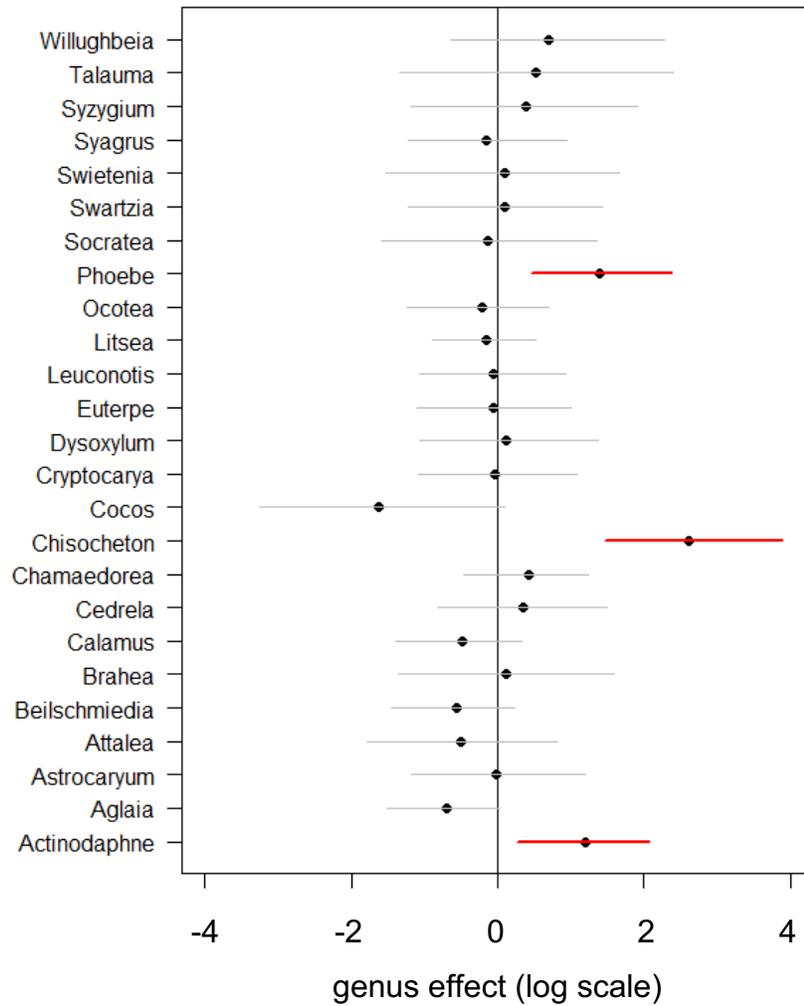


Figure 3.3 (b) The individual log odds of post-deposition seed predation of all genera compared to the log odds of post-deposition seed predation for the average genus (indicated by zero). Values are given as posterior mean and 95% credible intervals (CIs). CIs that do not overlap zero indicate that the probability of seed predation is lower (negative values) or higher (positive values) than the average risk of predation across genera. *Continued.*

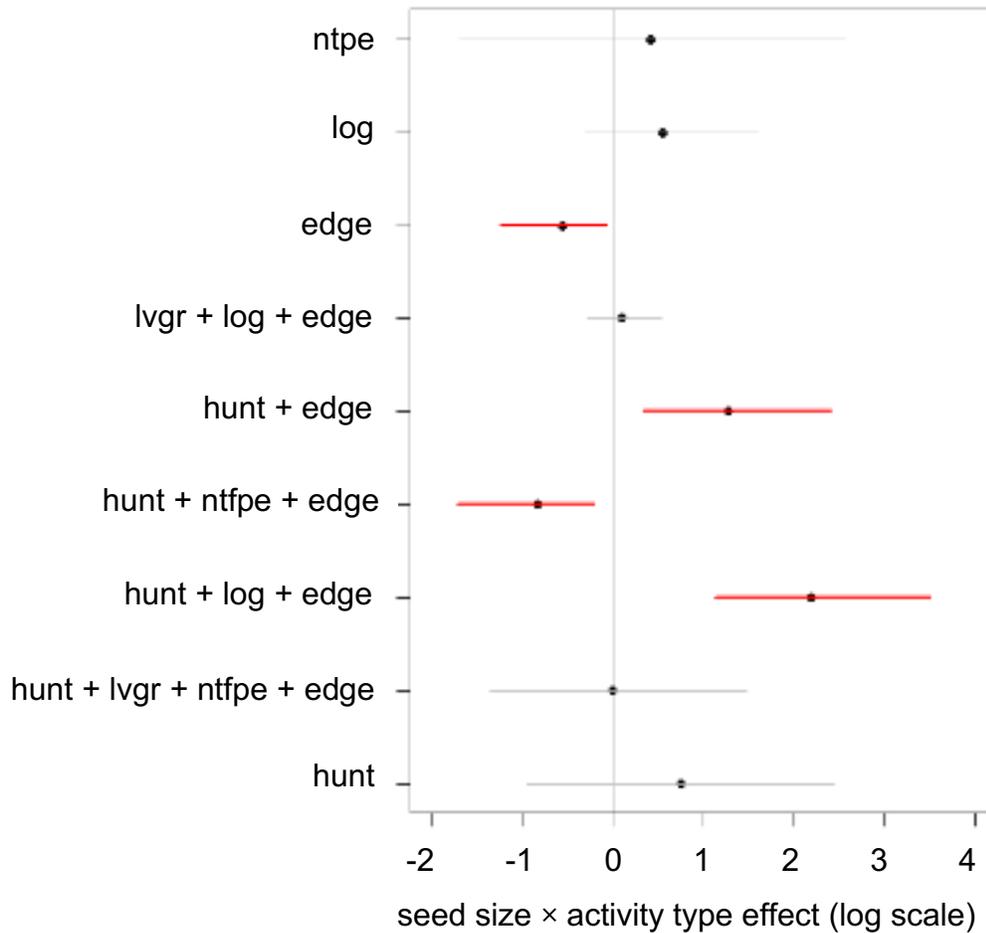
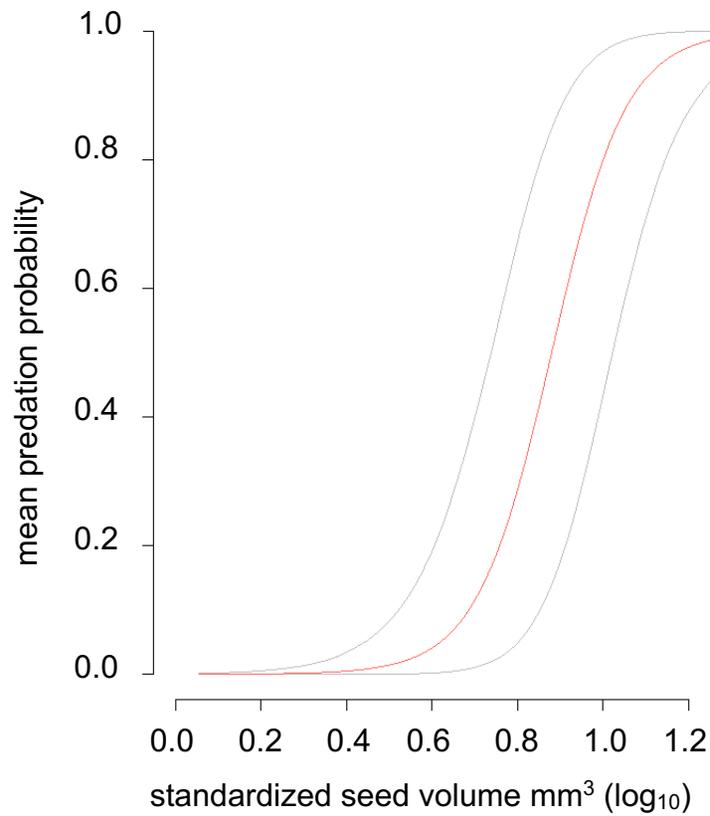
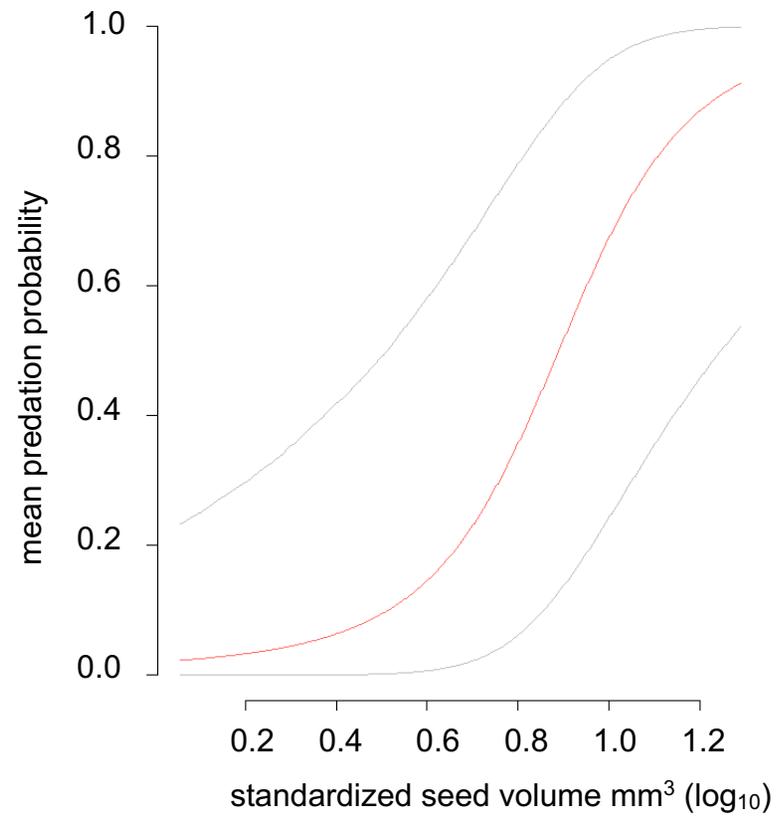


Figure 3.4 (c) The effect size (log scale) for each seed size (mm^3) \times human activity type on probability of post-deposition seed predation relative to undisturbed condition (indicated by zero). Values are given as posterior mean and 95% credible intervals (CIs). CIs that do not overlap zero indicate that the probability of seed predation is lower (negative values) or higher (positive values) with increasing seed size in an area modified by a given human activity compared to undisturbed conditions. Human activity codes: agr: agriculture; hunt: hunting; lvgr: livestock grazing; log: logging; ntfpe: non-timber forest product extraction. Edge indicates observations were taken in edge habitat. *Continued.*

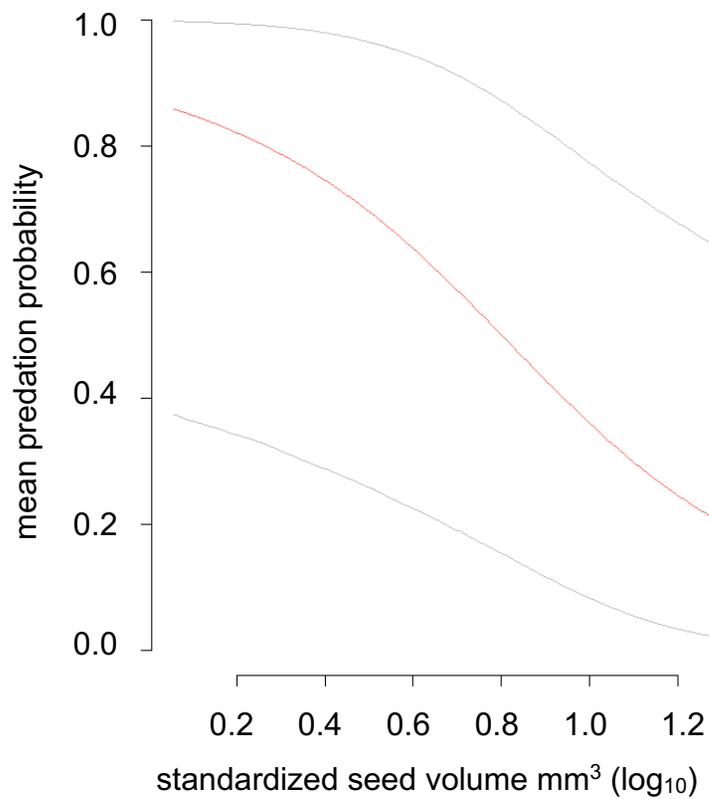


(a) moist deciduous forest edge with hunt + log

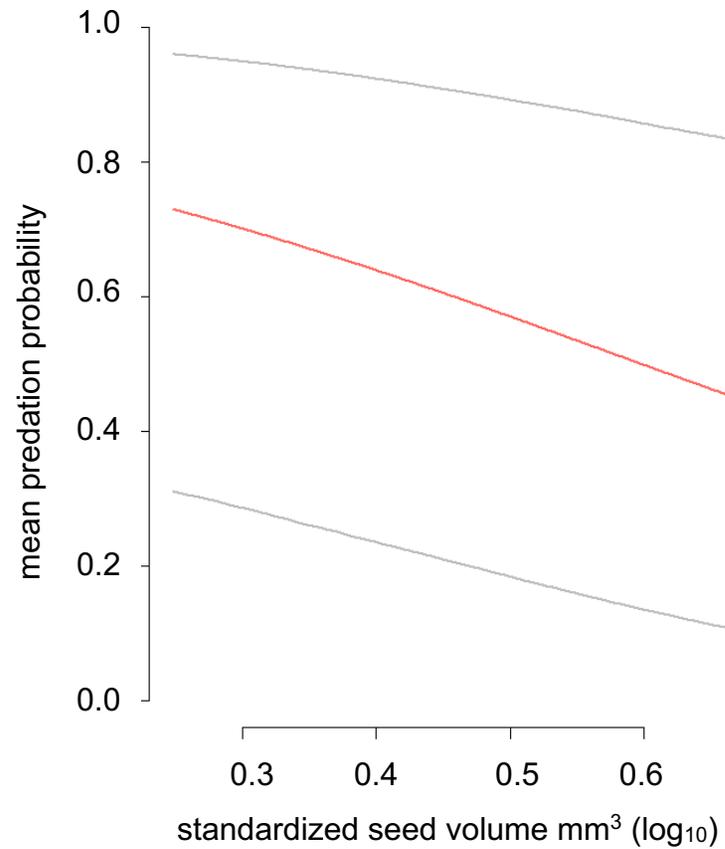


(b) moist deciduous forest edge with hunt

Figure 3.5 Predicted relationships (with 95% credible intervals) between post-deposition seed predation probability and increasing seed size (mm^3) for the average seed exposed to different human activities within an ecosystem. Predictions shown only for significant seed size \times human activity type interactions within ecosystems. Seed volume standardized across ecosystems. Edge indicates observations were taken in edge habitat.

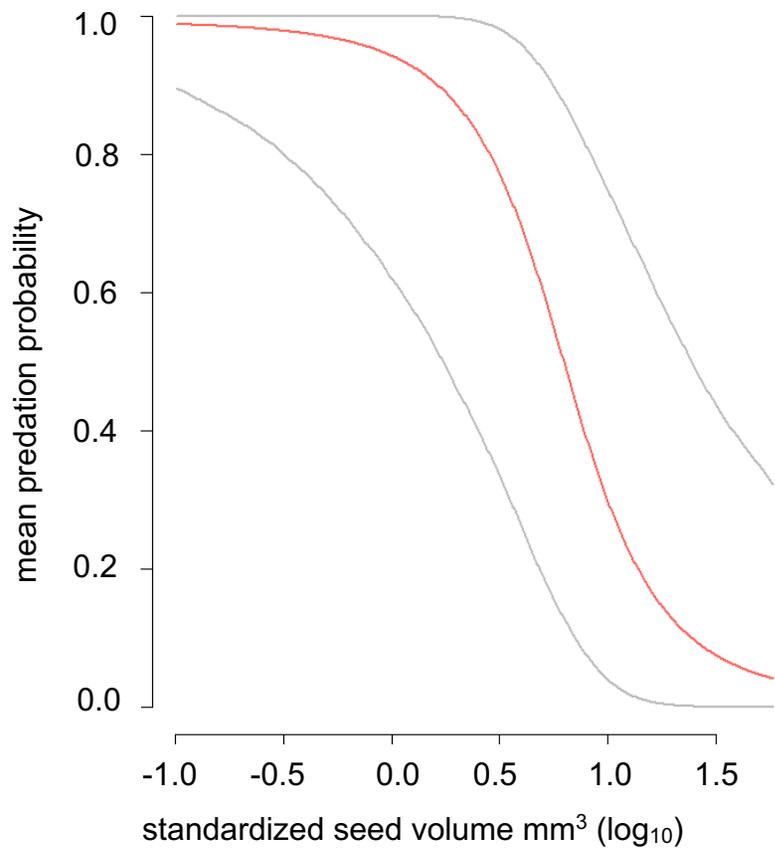


(c) moist deciduous forest edge

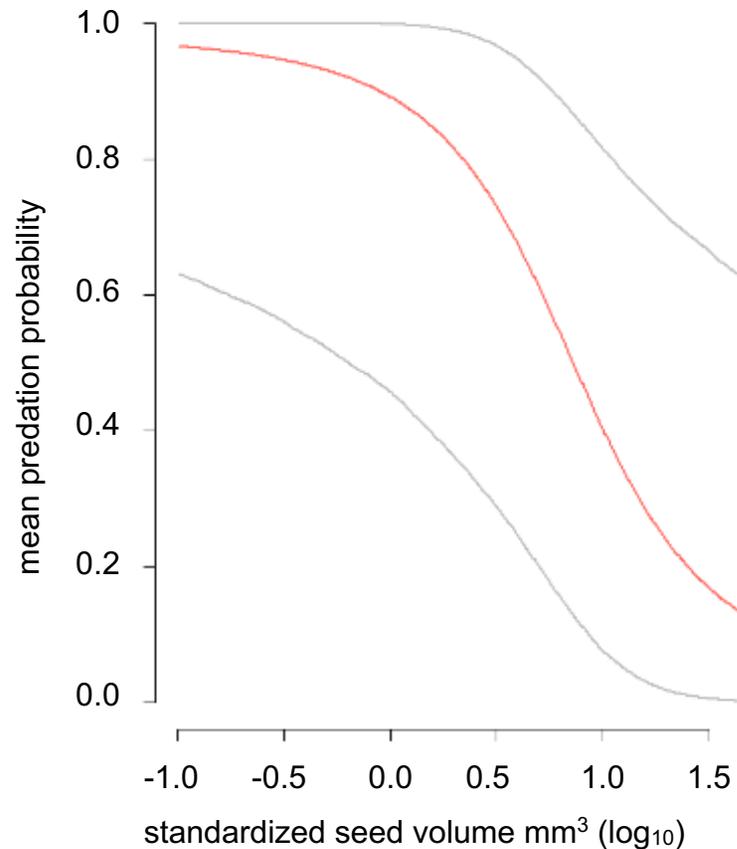


(d) mountain system forest edge

Figure 3.3. Predicted relationships (with 95% credible intervals) between post-deposition seed predation probability and increasing seed size (mm³) for the average seed exposed to different human activities within an ecosystem. Edge indicates observations were taken in edge habitat. *Continued*



(e) rainforest edge



(f) rainforest edge with hunt + ntfpe

Figure 3.3. Predicted relationships (with 95% credible intervals) between post-deposition seed predation probability and increasing seed size (mm^3) for the average seed exposed to different human activities within an ecosystem. Edge indicates observations were taken in edge habitat. *Continued*

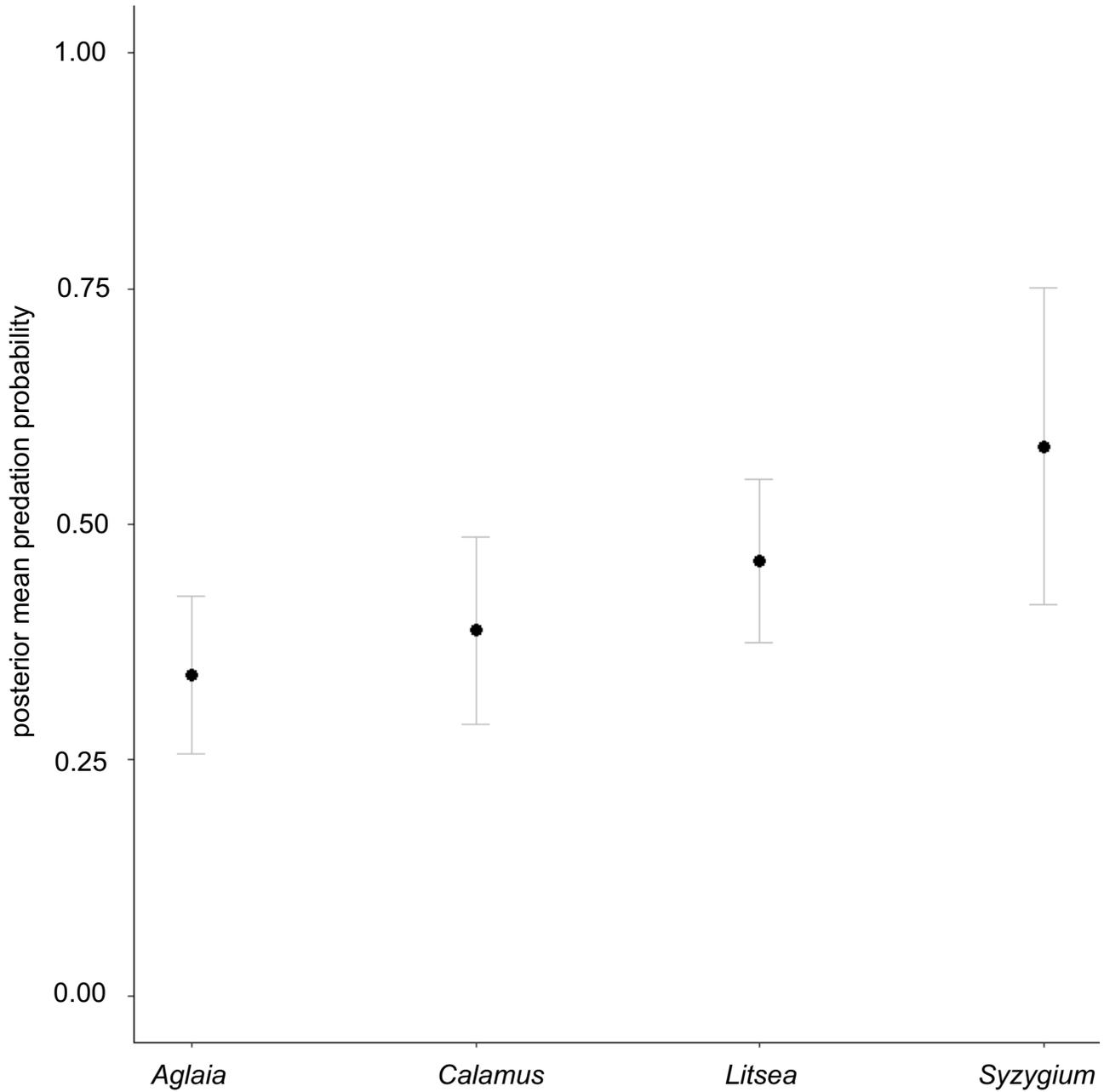


Figure 3.6 Genus posterior mean (points) and standard deviation (bars) for post-deposition seed predation probability in the average tropical forest ecosystem. Estimates calculated from 20,000 posterior samples.

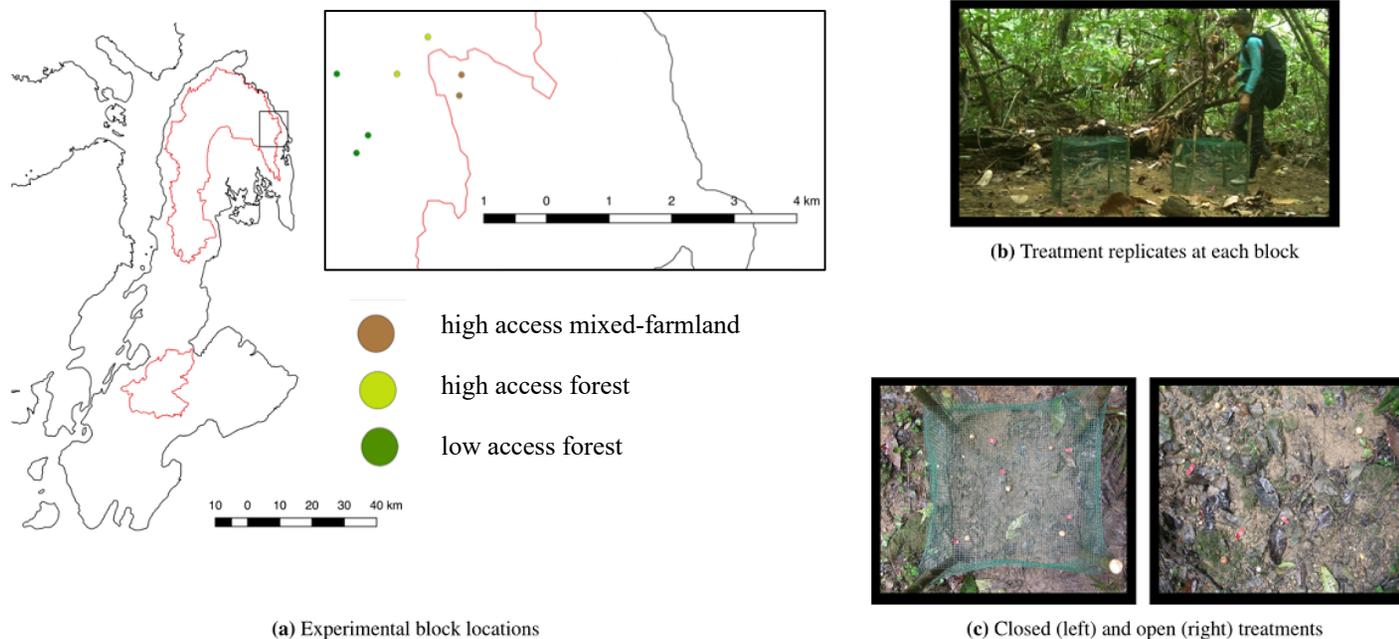


Figure 4.1 Buton Island, Southeast Sulawesi, Indonesia with boundaries (red) of SMBU (north) reserve (a) and post-dispersal seed predation experimental blocks (inset) in the forest and mixed- farmland. Forest blocks are coloured by area accessibility for humans (on foot from villages). Each experimental block contained two replicates of two treatments (b): a bottomless fenced enclosure treatment (*ca.* 0.5 m³ bottomless box constructed with 1 cm × 1 cm chicken wire) and an open treatment. Closed treatments excluded warty pigs, birds, and Malay civets but not digging rodents. For each experimental replicate, five seeds of one genus were placed into each treatment (c). Seeds in open treatment were placed directly in front of closed treatment.

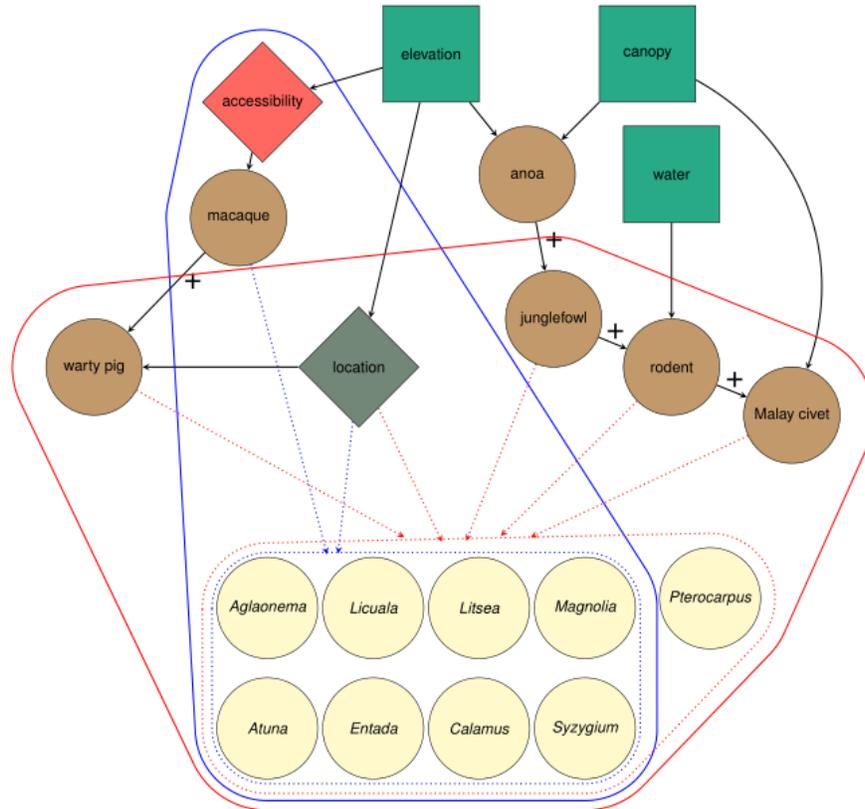


Figure 4. 2 Bird and mammal co-occurrences in SMBU, Buton Island, Southeast Sulawesi, Indonesia (2013–2015) showing the macaque seed dispersal (solid blue polygon) and post-dispersal seed predation (solid red polygon) networks for nine seed genera (yellow circles). Dotted blue line and arrows indicate which seeds are dispersed by macaques (based on observations of other *Macaca* sp.). Dotted red line and arrows indicate seeds eaten by granivores. Black arrows between species nodes (brown circles) indicate positive co-occurrences among species. Black arrows between species nodes and habitat nodes (green squares) indicate preference or avoidance of habitat features. Black arrows between species nodes and human activity nodes (red and grey diamonds) indicate preference or avoidance of areas with high or low amount of human activity within forest and mixed-farmland areas. See Methods for variable values and Figure A.2.4 for preference and avoidance scenarios.

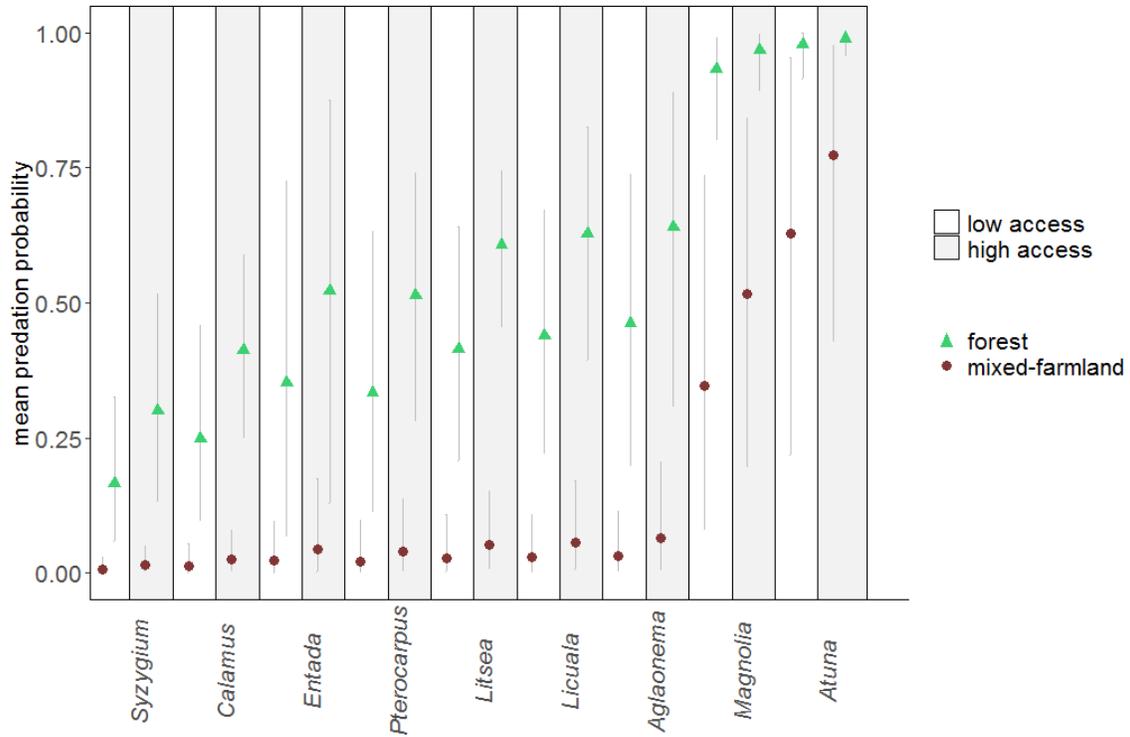


Figure 4.3 Genus-specific probability of post-dispersal seed predation in low and high access mixed-farmland and forest in SMBU, Buton Island, Southeast Sulawesi, Indonesia. Posterior means and 95% credible intervals calculated from Bayesian logistic regression model, which was parametrized using experimental data collected in mixed-farmland and forest (June–July 2015).

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Appendices

Appendix A

Appendix A contains supporting Tables and Figures for Chapter 2.

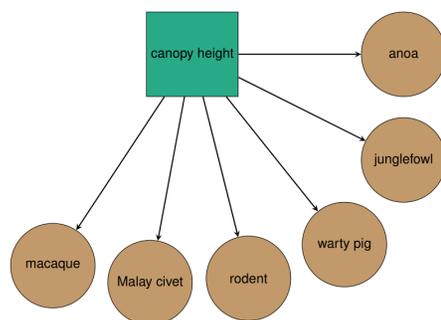
A.1 Chapter 2 supporting Tables

Table A.2.1 Diet and activity patterns for focal species in SMBU, Buton Island, Southeast Sulawesi, Indonesia. Information used to set “influencer” and responder species in hypothesized co-occurring pairs.

Animal	Diet and activity patterns		citation
Diet			
Aves			
red junglefowl	omnivore	fallen fruits, leaves, shoots, invertebrates	1
Mammalia			
murid rodent	omnivore	fallen fruits, seeds, invertebrates	2, 3
Malay civet	omnivore	fallen fruits, invertebrates, small vertebrates	4
Buton macaque	frugivore	fruit, crops	5, 6
anoa	herbivore	grasses, ferns, shoots, leaves, fallen fruits	7, 8
Sulawesi warty pig	omnivore	grasses, ferns, shoots, leaves, roots, fallen fruits, invertebrates, small vertebrates	9, 10
Activity patterns			
Aves			
red junglefowl	terrestrial, group living	diurnal; most activity during the morning	11
Mammalia			
murid rodent	terrestrial, solitary	observed during night only	
Malay civet	terrestrial, solitary	mostly nocturnal; most active between dusk and dawn	12
Buton macaque	half arboreal, group living	diurnal; active from dawn to dusk	5
anoa	terrestrial, solitary	observed during day and night	
Sulawesi warty pig	terrestrial, group living	cathemeral; forage at dawn and dusk	13

1. (Arshad et al. 2000); 2. (Ratanweera and Wijesinghe 2009); 3. (Galetti et al. 2015); 4. (Colon and Sugau 2012); 5. (Frondeius 2010); 6. (Hardwick et al. 2017); 7. (Burton et al. 2005); 8. (Flores-Miyamoto et al. 2005); 9. (Burton and Macdonald 2008b); 10. (Ballari and Barrios-García 2013); 11. (Arshad and Zakaria 2011); 12. (Colon 2002); 13. (Burton et al. 2017)

A.2 Chapter 2 supporting Figures



Prediction HO1: animals select habitat based on canopy height or select vegetation characteristics associated with changing canopy height

Trends

1. understory of high canopy forests rarely have high light events (Messier et al. 2009)
2. plant and mammal species richness increases with canopy height in lowland rainforests on Sumatra, Indonesia (Gillison et al. 2013)
3. dense understory vegetation in young Neotropical secondary forests; sparse understory vegetation in old-growth forests (DeWalt et al. 2003)
4. more understory fleshy fruit in young vs. older stand and old-growth forests in the Neotropics (DeWalt et al. 2003)
5. low resource availability for ungulates at high canopy cover where biomass is mostly tree trunks and inedible leaves protected by secondary compounds (Robinson and Bennett 2004)

Responder anoa
example forest-dependent species (Mustari et al. 2015); *Syncerus caffer nanus* select open forest with open canopy in Central African Republic (Melletti et al. 2007)

Responder junglefowl

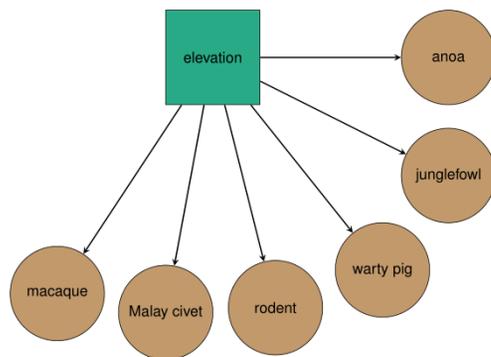
Responder Warty pig

Responder rodent
example Negative relationship between small mammal abundance and tree size in Xingú Basin, Brazil (Lambert et al. 2006)

Responder Malay civet

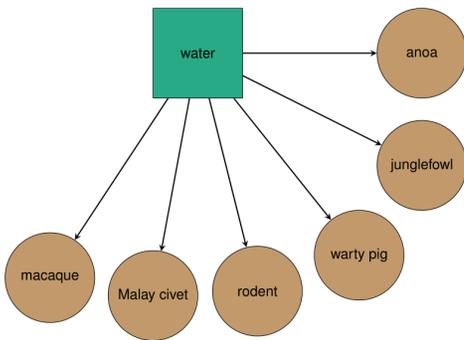
Responder macaque
example *Ateles geoffroyi* and *Cebus capuchins* prefer higher canopy on Barro Colorado Island, Panama (McLean et al. 2016)

Figure A.2.1 Habitat-occurrence (HO) predictions included in the conceptual BN. Habitat variables (green squares and grey diamond) predicted to affect species-specific occurrence (brown circles) in SMBU, Buton Island, Southeast Sulawesi, Indonesia.



Prediction HO2:	animals select habitat based on elevation or based on vegetation characteristics associated with changing elevation
Trends	1. tree species richness and diversity increase along an elevation gradient in Lambusango Forest Reserve, Buton Island, Indonesia (Widayati and Carlisle 2012)
Responder example	anoa anoa signs more abundant at high elevations in Central Sulawesi (Burton and Macdonald 2008a)
Responder example	junglefowl <i>Gallus gallus murghi</i> select high elevations in a Pakistan National Park (Subhani et al. 2010)
Responder example	warty pig Preferred fruit <i>Pangium edule</i> found between 50 and 200 masl (Burton et al. 2017); signs more abundant at low elevation in Central Sulawesi (Burton and Macdonald 2008a)
Responder example	rodent rodents distribute by functional guild along an elevation productivity gradient in Mexico (Ramírez-Bautista and Williams 2019)
Responder example	Malay civet <i>Hemigalus derbyanus</i> and <i>Diplogale hosei</i> select habitat based on elevation in Borneo (Brodie et al. 2018a)
Responder example	macaque <i>Macaca fascicularis</i> and <i>M. nemestrina</i> select habitat based on elevation in Borneo (Brodie et al. 2018a); <i>M. tonkeana</i> signs more abundant at low elevation in Central Sulawesi (Burton and Macdonald 2008a)

Figure A.2.1 Habitat-occurrence (HO) predictions included in the conceptual BN. *Continued*



Prediction HO3: animals select habitat based on water availability or vegetation characteristics associated with riparian vs. *terra firme* habitats

Trends 1. notable differences in riparian vs. in-land vegetation in tropical rainforests (Caley 1997)
2. movement patterns of large-bodied species tied to water when in short supply (Kay et al. 2017)

Responder anoa
example *Syncerus caffer nanus* show seasonal reference for marsh habitat in Gabon (Korte 2008)

Responder junglefowl

Responder warty pig

example *Sus scrofa* show seasonal preference for wetland habitat (O'Brien et al. 2019)

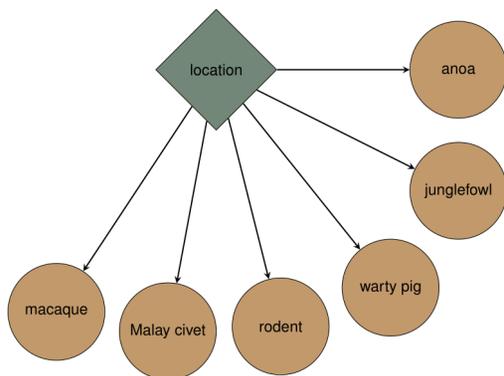
Responder rodent

example *Cuniculus paca* select habitat close to water in Brazil (Vilas Boas Goulart et al. 2009)

Responder Malay civet

Responder macaque

Figure A.2.1 Habitat-occurrence (HO) predictions included in the conceptual BN. *Continued*



Prediction HO4a: animals select mixed-farmland habitat

Trends 1. vegetation disturbances are linked to increased plant growth, high light levels, and abundant browse resources (Robinson and Bennett 2004)
 2. insect biomass resources were higher in disturbed edge forest in Xingú Basin, Brazil (Lambert et al. 2006)

Responder example warty pig
 signs observed in more disturbed forests at park boundaries in Central Sulawesi (Burton and Macdonald 2008a); crop raiding is common across Sulawesi (Burton et al. 2017)

Responder example rodent
Rattus rattus and *R. norvegicus* occupancy probability increased with intermediate land-use on Borneo (Wells et al. 2014)

Responder example macaque
Macaca orchreata crop raid farmland on Buton (Hardwick et al. 2017); *M. tonkeana* signs were more abundant at park boundaries in Central Sulawesi (Burton and Macdonald 2008a)

Prediction HO4b: animals avoid mixed-farmland habitat

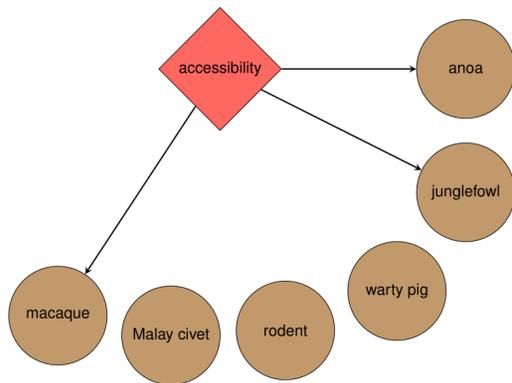
Trends 1. risk of hunting increases in agricultural plots vs. forested areas (Jorgenson 2000, Robinson and Bennett 2004)

Responder example anoa
 agriculture linked to population decline across Southeast Sulawesi (Burton et al. 2005)

Responder example junglefowl
 Male *Argusaianus argus* select undisturbed forest on Sumatra, Indonesia (Winarni et al. 2009)

Responder example Malay civet
 select undisturbed forests on Borneo (Colon 2002)

Figure A.2.1 Habitat-occurrence (HO) predictions included in the conceptual BN. *Continued*



Prediction AAO4a: animals avoid areas with high levels of human activities

Responder anoa

example Hunting linked to local extirpations across mainland Sulawesi (Burton et al. 2005)

Responder junglefowl

Responder macaque

example *Macaca nigra* observed at low density in a heavily hunted site at a park boundary in North Sulawesi (Rosenbaum et al. 1998)

Prediction AAO4b: animals neither select nor avoid areas with high levels of human activities

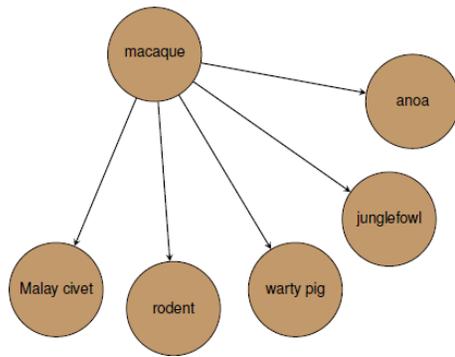
Responder warty pig

example *Sus scroa* observed near villages in Southwestern China (Guo et al. 2017); population size not affected by hunting in Italy (Servanty et al. 2011)

Responder rodent

Responder Malay civet

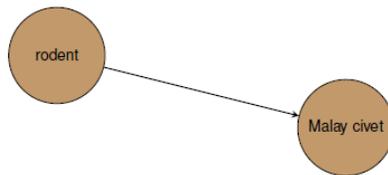
Figure A.2.2 Area accessibility-occurrence (AAO) predictions included in the conceptual BN. Human activity level is assumed proportional to area accessibility where high access areas have more human activities than low access areas. Area accessibility is calculated as average walking speed (km/hr) from surrounding villages. Human activities include subsistence agriculture, hunting, and non-timber forest product extraction.



Hypothesis COH1a: species have positive co-occurrence because of diet overlap

Influencer	macaque
Responder	anoa junglefowl warty pig rodent Malay civet

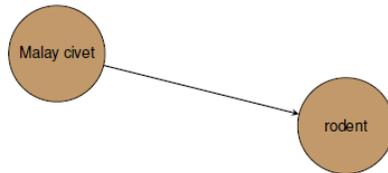
Justification	1. terrestrial species eat primate fruitfall in the Neotropics (Denis et al. 2019) 2. <i>Sus barbatus</i> track dipterocarp mast fruitfall in Borneo (Granados et al. 2019)
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Hypothesis COH1a: species have positive co-occurrence because of bottom-up predator-prey

Influencer	rodent
Responder	Malay civet

Justification	Malay civet eat rodent (Colon and Sugau 2012)
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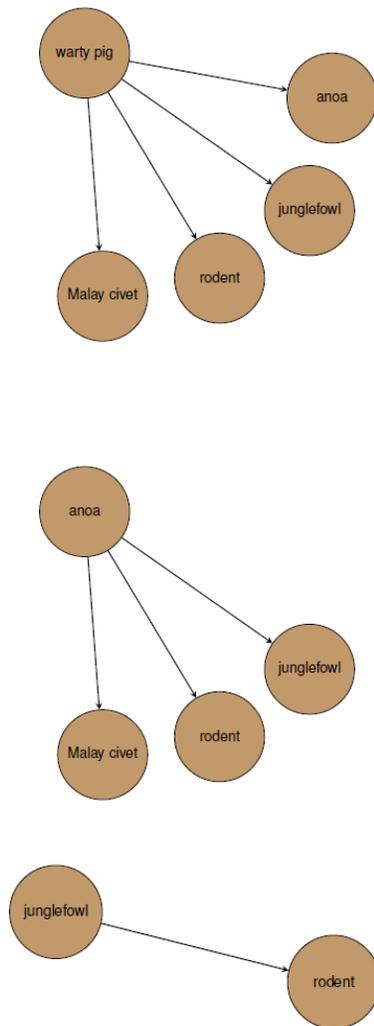


Hypothesis COH1a: species have positive co-occurrence because of top-down predator-prey

Influencer	Malay civet
Responder	rodent

Justification	Malay civet eat rodent (Colon and Sugau 2012)
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Figure A.2.3 Co-occurrence hypotheses (COH) included in the conceptual BN. Predicted species pairs with co-occurrence relationships in SMBU, Buton Island, Southeast Sulawesi, Indonesia. Hypotheses based on observations of similar species in different systems. These are conceptual and untested hypotheses.



Hypothesis COH1b: species have negative co-occurrence because of foraging activity

Influencer	warty pig
Responder	anoa
Justification	similar body size and diet overlap; warty pig more abundant than anoa
Responder	junglefowl
Justification	<i>S. scrofa</i> eat ground bird eggs (Giménez-Anaya et al. 2008) and junglefowl nest on ground (Yuan et al. 2009); negative co-occurrence between <i>Pecari tajacu</i> and <i>Odontophorus gujanensis</i> in French Guiana (Denis et al. 2019)
Responder	rodent
Justification	<i>S. scrofa</i> excavate small mammal burrows for cached seeds (Focardi et al. 2000)
Responder	Malay civet
Justification	Negative co-occurrence between small-bodied <i>Puma yagouaroundi</i> and <i>S. scrofa</i> in Brazil (Hegel et al. 2019)

Influencer	anoa
Responder	rodent
Justification	<i>Ovis aries</i> grazing reduce plant cover and population growth rate of <i>Microtus argestis</i> in Norway (Steen et al. 2005)
Responder	junglefowl
Justification	Negative co-occurrence between <i>Mazama nemorivaga</i> and <i>Tinamus major</i> in French Guiana (Denis et al. 2019)
Responder	Malay civet
	grazing changes vegetation structure (Gawel et al. 2018)

Influencer	junglefowl
Responder	rodent
Justification	diet overlap

Figure A.2.3 Co-occurrence hypotheses (COH) included in the conceptual BN. *Continued*



Figure A.2.4 Empirical Bayesian network of species co-occurrences with nodes plotted as (a) conditional and (b) marginal probability distributions. Conditional probability distributions indicate the probability that a species is either present or absent given the states of its parent nodes. Conditional probability distributions for habitat nodes (elevation, canopy height, water availability, location) indicate the proportion of habitat type available. Conditional probability tables for area accessibility indicate the proportion of habitat area that is high or low activity (based on area accessibility to humans). Marginal probability distributions have the same definition but are calculated for each node independent of all other nodes.

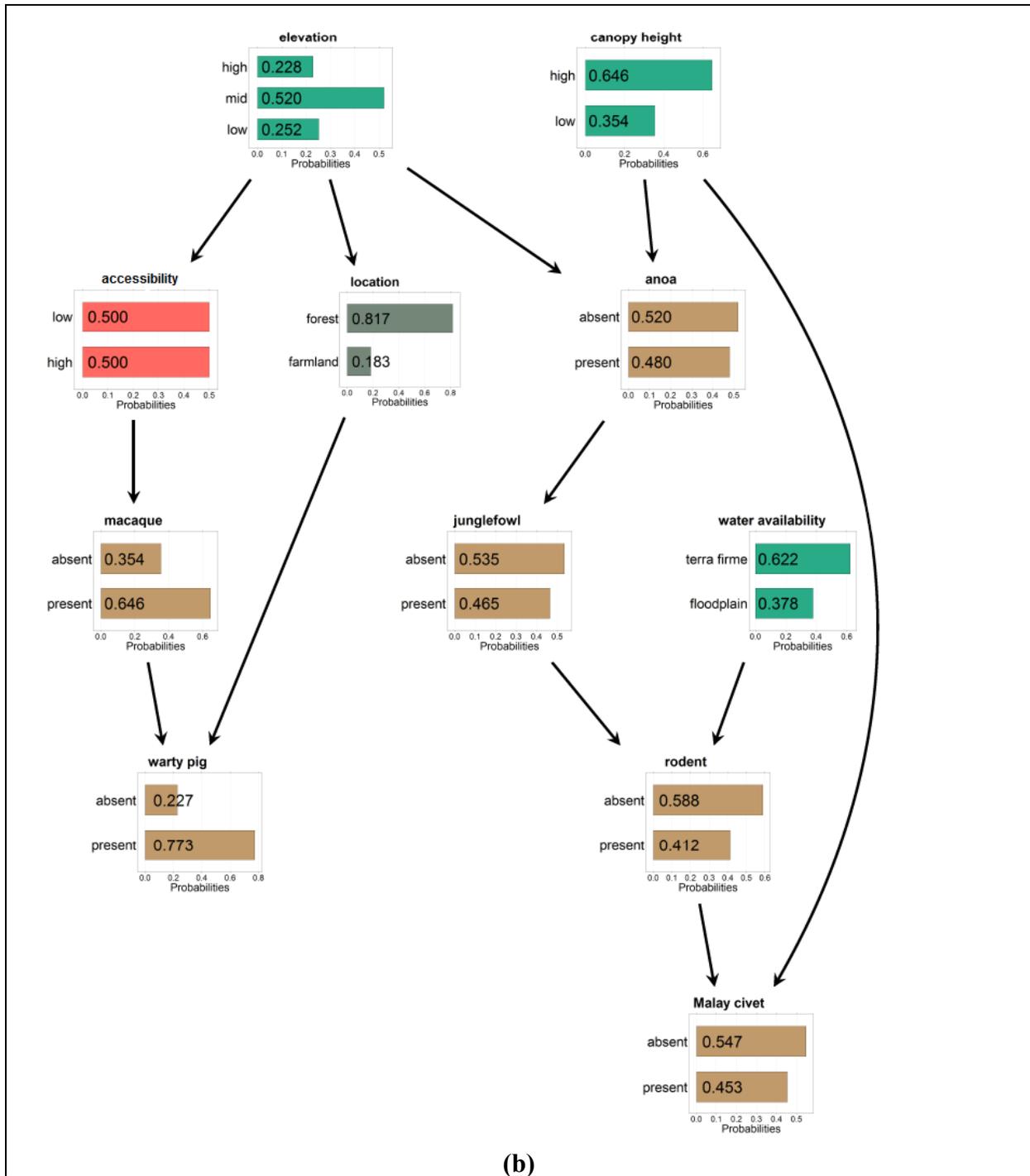


Figure A.2.4 Empirical Bayesian network of species co-occurrences with nodes plotted as (a) conditional and (b) marginal probability distributions. *Continued*

A.3 Hierarchical occupancy model

My camera trap occurrence data were subject to detection errors related to a species being present at a station but not captured (e.g., walked behind camera). I corrected for these detection errors before discretizing species-specific occurrence at each station by calculating a detection error-corrected true occurrence using a three-level hierarchical Bayesian Dorazio-Royle multispecies occupancy (hereafter “occurrence”) model (Dorazio and Royle 2005) with parameter expanded data augmentation (Dorazio et al. 2006, Royle et al. 2007, Royle and Dorazio 2012). On each of the three hierarchical levels, the model estimates metacommunity (level 1), community (level 2), and species (level 3) occurrence in relation to habitat or other variables such as human activities.

Data augmentation (DA) accounts for imperfect detection by adjusting the sampling occurrence matrix (Z ; see Chapter 2, Methods, *Camera trap surveys*) that contained detection-non-detection histories for each species at each of my stations. In the first step of the analysis, I assigned an informative prior to the total community size (N_{total}). Following Royle et al. (2007) and Kéry and Royle (2016), I set the informative prior by assuming my focal community (anoa, junglefowls, macaques, Malay civets, rodents, and warty pigs) was part of a larger metacommunity (M) of k additional, unobserved, species. As stated in Chapter 2, the only non-avian vertebrate species excluded from my analyses were the Sulawesi bear cuscus (*Ailurops ursinus*), the Sulawesi dwarf cuscus (*Strigocuscus celebensis*), the spectral tarsier (*Tarsius spectrum*), and squirrels (9 species). Therefore, I set M to 9 where the two cuscus species and nine squirrel species were grouped to match my grouping of species that could not be identified past order from camera traps. I then added zero detection histories to the Z matrix for each of these addition k species. N_{total} was modelled as $M \times \Omega$ (Ω = community occupancy parameter)

and was assigned a uniform prior with mean 0 and variance M ($N_{total} \sim Uniform(0, M)$ (Kéry and Royle 2016)).

After running the model, I obtained the occurrence probability of each species at each site from the adjusted Z matrix. I used the posterior point estimates to create the *Station-species occurrence matrix* (see Chapter 2 Methods) for the Bayesian Network inference calculations.

The basic model structure at each level (Kéry and Royle 2016) is:

Metacommunity process:

$$w_k \sim Bernoulli(\Omega)$$

where:

w_k indicates if species k is part of the studied metacommunity ($w = 1$ for all observed species)

Ω is the community occupancy parameter

State process for occurrence:

$$z_{ik}|w_k \sim Bernoulli(w_k\psi_k)$$

where:

z_{ik} is the true presence ($z = 1$)/absence ($z = 0$) of species k at station i taken from the species-specific occurrence matrix Z

ψ_k is the occupancy probability for species k

Observation process for detection:

$$y_{ijk}|z_{ijk} \sim Bernoulli(z_{ijk}p_{ijk})$$

where:

y_{ijk} is the detection ($y = 1$) non-detection ($y = 0$) observation for species k at station i during survey j

p_{ijk} is the detection probability for species k at station i during survey j

Model for species-specific occupancy (random effect):

$$\text{logit}(\psi_{ik}) = l\psi_k + \beta l\psi_k \times \text{covariate}_i + \dots$$

where:

$l\psi_k$ is the occupancy probability for species k at covariate value 0 at station i

$\beta l\psi_k$ is the response of occupancy probability for species k to the covariate value at station i

with normal priors on species-specific occupancy specified as:

$$l\psi_k \sim \text{Normal}(\mu_{l\psi}, \sigma_{l\psi}^2)$$

and normal priors (Tobler et al. 2015, Kéry and Royle 2016) on species-specific response to habitat specified as:

$$\beta l\psi_k \sim \text{Normal}(\mu_{\beta l\psi}, \sigma_{\beta l\psi}^2)$$

where:

$\mu_{l\psi}$ is the mean occupancy probability for the hunted community

$\sigma_{l\psi}^2$ is the interspecific variation in occupancy probability

$\mu_{\beta l\psi}$ is the mean aggregate response of the hunted community to a given habitat covariate

$\sigma_{\beta l\psi}^2$ is the interspecific variation in the aggregate response to given habitat covariate

Model for species-specific detection (random effect):

$$\text{logit}(p_{ijk}) = lp_k + \beta lp_k \times \text{covariate}_{ij} + \dots$$

where:

lp_k is the detection probability for species k at covariate value 0 at station i during survey j

βlp_k is the response of detection probability for species k to the covariate value at station i during survey j

with normal priors on species-specific detection specified as:

$$lp_k \sim \text{Normal}(\mu_{lp}, \sigma_{lp}^2)$$

and normal priors (Tobler et al. 2015, Kéry and Royle 2016) on species-specific response to detection covariates specified as:

$$\beta lp_k \sim \text{Normal}(\mu_{\beta lp}, \sigma_{\beta lp}^2)$$

where:

μ_{lp} is the mean detection probability for the hunted community

σ_{lp}^2 is the interspecific variation in detection probability

$\mu_{\beta lp}$ is the mean aggregate response of the hunted community to a given detection covariate

$\sigma_{\beta lp}^2$ is the interspecific variation in the aggregate response to a given detection covariate

with logistic (Lunn et al. 2003, Northrup and Gerber 2019) hyper-priors for mean occupancy parameters specified as:

$$\mu_{lp} \sim \text{Normal}(0,100)$$

and normal (Tobler et al. 2015, Kéry and Royle 2016) hyper-priors for mean habitat, detection, and detection covariate parameters specified as:

$$\mu_{\beta l \psi} \sim Normal(0,100)$$

$$\mu_{l p} \sim Normal(0,100)$$

$$\mu_{\beta l p} \sim Normal(0,100)$$

and half-Cauchy with one degree of freedom (Gelman 2006, Polson and Scott 2012, Outhwaite et al. 2018) hyper-priors for variance parameters specified as (truncated student-t):

$$\sigma_{lpsi}^2 \sim t(0,1,1)T(0,)$$

$$\sigma_{lp}^2 \sim t(0,1,1)T(0,)$$

$$\sigma_{\beta l \psi}^2 \sim t(0,1,1)T(0,)$$

$$\sigma_{\beta l p}^2 \sim t(0,1,1)T(0,)$$

I assumed exchangeability between species for all modelled parameters and set species-specific parameters as random effects following (Kéry and Royle 2016).

I *a priori* know that species-specific abundance responds to active human disturbance based on Froese et al. (2015), so I limited the analysis to the effect of habitat variables on occurrence. However, hierarchical models with many parameters are difficult to fit and often suffer from high posterior correlations between estimated parameters (Gelman and Hill 2007, Conn et al. 2018). Therefore, I adopted a simplistic approach and tested my candidate models including only one habitat variable in the occurrence model as follows: **Candidate 1**: canopy height, **Candidate 2**: elevation, **Candidate 3**: water availability, and **Candidate 4**: habitat location in mixed-farmland or forest. All candidate models included survey length (days camera active) and camera visibility (estimated camera view in meters) as covariates affecting detection.

I coded candidate models in BUGS (Lunn et al. 2009) and ran them in JAGS (version 4.2.0; Plummer 2003) called from R (R Core Team 2018) using the “jagsUI” package (Kellner 2018). I ran two parallel chains for 3 million iterations after a 3 million burn-in and initial 500,000 iteration adaptive phase with a 100-iteration thinning rate (inferences based 60,000 posterior samples). I based convergence on trace plots (complete mixing of chains), parameter \hat{R} values < 1.09 (Gelman and Shirley 2016, Kellner 2018), and Gelman-Rubin multi-variate psrf value of 1 (Plummer et al. 2006). I inspected model fit by calculating posterior cross-correlations between all model parameters and effective sample size using the R package “coda” (Plummer et al. 2006). I also inspected bivariate plots for banana-shaped distributions (Gabry et al. 2019), which indicate non-identifiable parameters (Hines et al. 2014), and updates to the prior by calculating the ratio of posterior to prior precision ($\tau_{posterior} : \tau_{prior}$), where larger values (≥ 1.25) indicate estimates are driven by the data and smaller values (< 1.25) indicate estimates are driven by the prior.

Kéry and Royle (2016) recommended running this model with three habitat covariates and data augmentation of $k = 150$ species in several steps to avoid maxing out a computer’s memory and having to wait several days for the model to fit. However, they only report running chains “much longer” and did not specify how many iterations were required to achieve convergence. Another application of this model including DA based inferences on 50,000 iterations (Cavada et al. 2019; 6 covariates, DA). However, the model was judged only on convergence diagnostics without reporting fit, specifically effective sample size for each parameter, which is common when using hierarchical models in ecology (Hooten and Hobbs 2015, Conn et al. 2018). Although my inferences were based on 60,000 posterior samples, I had

to run 3 million iterations with a 100-thinning rate to address correlations and achieve appropriate effective sample sizes.

Model convergence and fit

The community occurrence model including canopy height outperformed all other candidates. This model was the fastest to converge, had the lowest correlations between posterior point estimates ($r < 0.764$), the highest effective sample size for all estimated parameters, and no non-identifiable parameters (bivariate plots not shown).

Appendix B

Appendix B contains the research groups that provided experimental data for the seed predation Network Meta-Analysis (NMA) and supporting Tables for Chapter 3

B.1 Research groups who provided experimental data for the NMA

Group 1

Adler, G. H.¹ and D.W. Kestell¹. 1998. Fates of Neotropical tree seeds influenced by Spiny Rats (*Proechimys semispinosus*). *Biotropica*. 30(4):677–681.

Co-authors

Adler, Gregory H. and Kestell, Douglas W.

Institution

¹Department of Biology and Microbiology, University of Wisconsin (Oshkosh), Oshkosh, Wisconsin 54901, U.S.A.

Group 2

Andresen², E. and D. J. Levey³. 2004. Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. *Oecologia*. 139:45–54.

Co-authors

Andresen, Ellen and Levey, Douglas J.

Institution

²Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Apartado Postal 27 – 3, C.P. 58089 Morelia, Michoacán, Mexico; ³Department of Zoology, University of Florida, Gainesville, Florida 32611–8525, USA

Group 3

Dutton⁴, P. E., H. M. Chapman⁵ and E. Moltchanova⁴. 2014. Secondary removal of seeds dispersed by chimpanzees in a Nigerian montane forest. *African Journal of Ecology*. 52(4):438–447.

Co-authors

Dutton, Paul E. and Chapman, Hazel M. and Moltchanova, Elena

Institutions

⁴School of Biological Sciences, University of Canterbury, New Zealand; ⁵Department of Mathematics and Statistics, University of Canterbury, New Zealand

Group 4

Fadini^{6,7}, R. F., M. Fleury^{6,8}, C. I. Donatti⁹, and M. Galetti^{6,9}. 2009. Effects of frugivore impoverishment and seed predators on the recruitment of a keystone palm. *Acta Oecologica*. 35(2):188–196.

Co-authors

Fadini, Rodrigo F. and Fleury, Marina and Donatti, Camila I. and Galetti, Mauro

Institutions

⁶Laboratório de Biologia da Conservação, Departamento de Ecologia, Universidade Estadual Paulista; ⁷Coordenação de Pesquisas em Ecologia, Instituto Nacional de Pesquisas da Amazônia; ⁸Laboratório de Ecologia e Restauração Florestal, Departamento de Ciências Biológicas, Universidade de São Paulo; ⁹Department of Biology, Stanford University

Group 5 and 6

Fleury⁸, M., & Galetti, M.^{10,11} 2004. Effects of microhabitat on palm seed predation in two forest fragments in southeast Brazil. *Acta Oecologica*. 26(3):179–184.

Fleury^{9,10,11}, M. and M. Galetti.^{10,11} 2006. Forest fragment size and microhabitat effects on palm seed predation. *Biological Conservation*, 131(1), 1–13.

Co-authors

Fleury, Marina and Galetti, Mauro

Institutions

⁹Laboratório de Ecologia Animal, Escola Superior de Agricultura Luiz de Queiroz, Universidade de São Paulo; ¹⁰Grupo de Fenologia e Dispersão de Sementes, Departamento de Ecologia, I.B., Universidade Estadual Paulista; ¹¹Instituto de Biologia da Conservação

Group 7

Fleury^{10,12}, M., R.R. Rodrigues¹², H. T. Z. do Couto¹³, and M. Galetti¹⁰ 2014). Seasonal variation in the fate of seeds under contrasting logging regimes. *PLoS ONE*, 9(3), e90060.

Co-authors

Fleury, Marina and Rodrigues, Ricardo R and Do Couto, Hilton T. Z. and Galetti, Mauro

Institutions

¹⁰Departamento de Ecologia, Universidade Estadual Paulista; ¹²Laboratório de Ecologia e Restauração Florestal, Departamento de Ciências Biológicas, Universidade de São Paulo;

¹³Laboratório de Métodos Quantitativos, Departamento de Ciências Florestais, USP/ESALQ

Group 8

Holl¹⁴, K. D. and M. E. Lulow.¹⁵ 1997. Effects of species, habitat, and distance from edge on post- dispersal seed predation in a tropical rainforest. *Biotropica*. 29(4):459–468.

Co-authors

Holl, Karen and Lulow, Megan E.

Institutions

¹⁴Center for Conservation Biology, Stanford University; ¹⁵Environmental Studies Board, University of California, Santa Cruz

Group 9

Kitamura¹⁶, S., Suzuki¹⁷, S., T. Yumoto¹⁶, P. Poonswad¹⁸, P. Chuailua¹⁸, K. Plongmai¹⁸, K.

Plongmai¹⁸, N. Noma¹⁷, T. Maruhaski¹⁹, and C. Suckasam.²⁰ 2004. Dispersal of *Aglaia spectabilis*, a large-seeded tree species in a moist evergreen forest in Thailand. *Journal of Tropical Ecology*. 20(4):421–427.

Co-authors

Kitamura, Shumpei and Suzuki, Shunsuke and Yumoto, Takakazu and Poonswad, Oilai and Chuailua, Phitaya and Plongmai, Kamoi and Noma, Naohiko and Maruhashi, Tamaki and Suckasam, Chumphon

Institutions

¹⁶Center for Ecological Research, Kyoto University; ¹⁷School of Environmental Science, The University of Shiga Prefecture; ¹⁸Hornbill Project, Department of Microbiology, Mahidol University; ¹⁹Department of Human and Culture, Musashi University; ²⁰National Park, Wildlife and Plant Conservation Department

Group 10

López-Toledo^{21,22}, L., Y. Portillo-Cruz²³, M. T. Pulido²³, and B. A. Endress.²² 2013. Seed dynamics of an endemic palm in a Northwestern Mexican tropical dry forest: Implications for population spatial structure. *Plant Ecology*. 214(9):1115–1125.

Co-authors

Lopez-Toledo, Leonel and Portillo-Cruz, Yazmin and Pulido, María T. and Endress, Bryan A.

Institutions

²¹Instituto de Investigaciones sobre los Recursos Naturales-Universidad Michoacana de San Nicolás de Hidalgo; ²²Division of Applied Plant Ecology, Institute for Conservation Research, San Diego Zoo Global; ²³Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo

Group 11 and 12

McConkey^{24,25,26}, K. R. 2005a. Influence of faeces on seed removal from gibbon droppings in a dipterocarp forest in Central Borneo. *Journal of Tropical Ecology*. 21(1):117–120.

McConkey^{24,25,26}, K. R. 2005b. The influence of gibbon primary seed shadows on post-dispersal seed fate in a lowland dipterocarp forest in Central Borneo. *Journal of Tropical Ecology*. 21(1):117–120.

Co-author

McConkey, Kim R.

Institutions

²⁴Wildlife Research Group, Department of Anatomy, University of Cambridge; ²⁵School of Environmental and Geographical Sciences, The University of Nottingham Malaysia Campus

²⁶School of Natural Sciences and Engineering, National Institute of Advanced Studies

Group 13

Montaño²⁷, Roldán²⁷, & Pacheco^{28,29}. (unpublished)

Co-authors

Montaño and Pacheco, Luis F. and Roldán, Alejandra I.

Institutions

²⁷Departamento de Ecología, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile; ²⁸Centro de Postgrado en Ecología y Conservación, Instituto de Ecología, Casilla 10077, Universidad Mayor de San Andrés, La Paz, Bolivia; ²⁹Centro de Estudios en Biología Teórica y Aplicada-BIOTA, Casilla 9641, La Paz, Bolivia

Group 14

Norghauer³⁰, J. M., J. R. Malcolm³⁰, B. L. Zimmerman³¹, and J. M. Felfili.³² (2006). An Experimental Test of Density- and Distant-Dependent Recruitment of Mahogany (*Swietenia macrophylla*) in Southeastern Amazonia. *Oecologia*. 148(3):437–446.

Co-authors

Norghauer, Julian M. and Malcolm, Jay R. and Zimmerman, B. L. and Felfili, Jenine M.

Institutions

³⁰Faculty of Forestry, University of Toronto; ³¹Brazil Program, Conservation International; ³²Departamento de Engenharia Florestal, Universidade de Brasília

Group 15

Sidhu³³, S. and A. Datta.³³ 2015. Tracking seed fates of tropical tree species: Evidence for seed caching in a tropical forest in north-east India. *PLoS ONE*, 10(8), 1–21.

Co-authors

Sidhu, Swati and Datta, Aparajita

Institution

³³Eastern Himalaya Programme, Nature Conservation Foundation

Group 16

Vieira^{34,35}, D. L. M. unpublished experiment

Co-author

Viera, Daniel L. M.

Institution

³⁴Pós-Graduação em Ecologia, Universidade de Brasília, Brasília, DF, Brazil; ³⁵Laboratório de Ecologia e Conservação, Embrapa-Recursos Genéticos e Biotecnologia, Brasília, DF, Brazil

Group 17

Whittaker³⁶, R. J. and B. D. Turner.³⁷ 1994. Dispersal, Fruit Utilization and Seed Predation of *Dysoxylum gaudichaudianum* in Early Successional Rainforest, Krakatau, Indonesia. *Journal of Tropical Ecology*. 10(2):167–181.

Co-authors

Whittaker, Robert J. and Turner, Bryan D.

Institutions

³⁶School of Geography, University of Oxford; ³⁷Division of Life Sciences, King's College London

Group 18

Young^{38,39,40}, H. S., D. J. McCauley⁴¹, R. Guevara⁴² and R. Dirzo³⁸, R.¹ (2013). Consumer preference for seeds and seedlings of rare species impacts tree diversity at multiple scales. *Oecologia*, 172(3), 857–867.

Co-authors

Young, Hillary S. and McCauley, Douglas J. and Guevara, Roger and Dirzo Rodolfo

Institutions

³⁸Department of Biology, Stanford University; ³⁹Division of Vertebrate Zoology, Smithsonian Institution; ³⁹Center for the Environment, Harvard University; ⁴⁰Hopkins Marine Station, Stanford University; ⁴¹Red de Biología Evolutiva, Instituto de Ecología AC

B.2 Chapter 3 supporting Tables

Table B.3.1 Morphology data used to calculate seed volume for hierarchical Network Meta-Analysis. Data sources noted as numbers beside corresponding dimensions (see Table Notes for citations). Dimensions given as average from multiple data source, where applicable.

Model data species	Dimensions for volume calculation						
	volume (cm ³) ^a	mass (g) ^b	length (mm)		width (mm)	life form	dispersal mode ^c
Apocynaceae							
<i>Leuconotis</i>							
<i>eugenifolius</i>	0.549	–	14.500	²²	8.500	⁴⁰	tree animal ²⁷
<i>Willughbeia</i>							
spp.	3.688 ^d	–	23.000	²⁶	17.500	²⁶	liana animal ²⁷
Arecaceae							
<i>Astrocaryum</i>							
<i>murumuru</i>	13.387	7.488 ³⁰	43.300	³⁴	24.300	³³	palm mammal ³⁹
<i>Attalea</i>							
<i>butyracea</i>	1.513	49.063 ²⁹	40.000 ^c	³	8.500	³	tree mammal ^f ¹
<i>Brahea</i>							
<i>aculeata</i>	2.928	3.060 ²³	17.750	¹²	17.500	²³	palm animal ⁴⁰
<i>Calamus</i>							
spp.	0.729	1.700 ²⁷	11.500 ^h	⁴¹	11.000	²⁷	liana animal ²⁷
<i>Chamaedorea</i>							
<i>allenii</i>	0.239 ^g	0.059 ¹⁹	7.700	¹⁹	–		shrub animal ⁷
<i>Cocos</i>							
<i>nucifera</i>	27.667 ^d	1,638 ³⁸	262.000	³⁸	–		palm abiotic ³⁸
<i>Euterpe</i>							
<i>edulis</i>	1.425	0.826 ⁱ ¹³	14.200	¹¹	13.500	¹¹	palm bird ¹³
<i>Socratea</i>							
<i>exorrhiza</i>	5.089	3.440 ³⁰	30.000	¹⁶	18.000	¹⁶	palm mammal ⁴²

<i>Syagrus</i>								
<i>romanzoffiana</i>	2.477	1.626 ⁱ	¹⁴	19.820	¹⁷	15.450	⁵	palm animal ⁵

Model data	Dimensions for volume calculation								
species	volume (cm ³) ^a	mass (g) ^b		length (mm)		width (mm)		life form	dispersal mode ^c
Fabaceae									
<i>Swartzia</i>									
<i>multijuga</i>	6.823	–		30.000	³⁶	20.000	³⁶	tree	animal ³⁶
Lauraceae									
<i>Acinodaphne</i>									
<i>obovata</i>	0.890	–		17.000	³²	10.000	²	tree	animal ³²
<i>Beilschmiedia</i>									
<i>assamica</i>	3.700	–		31.000	³²	15.500	⁴³	tree	bird ³²
<i>dictyoneura</i>	3.267	2.000	²⁷	39.300 ^b	²¹	12.600	²⁸	tree	animal ²⁷
<i>Cryptocarya</i>									
<i>crassinervis</i>	2.697	–		24.500	⁹	14.500	⁹	tree	animal ²⁷
<i>Litsea</i>									
<i>ferruginea</i>	0.882	1.800	²⁶	11.700	²⁶	12.000	²⁸	tree	animal ²⁷
sp.	2.572	–		17.000	³²	–		tree	animal ³²
<i>Ocotea</i>									
<i>floribunda</i>	0.933	1.400	¹⁹	16.800	¹⁹	10.300	⁴³	tree	animal ⁴⁴
<i>Phoebe</i>									
<i>cinnamomifolia</i>	0.681	0.509	¹⁹	15.700	¹⁹	9.100	²⁵	tree	bird ⁴⁵
Magnoliaceae									
<i>Talauma</i>									
<i>hodgsonii</i>	0.005	–		4.000	³²	1.524	³¹	tree	animal ³²
Malvaceae									
<i>Aglaia</i>									
<i>ganggo</i>	1.639 ^g	4.400	⁶	37.800	²¹	9.100	²⁸	tree	animal ²⁸
<i>spectabilis</i>	7.735	4.350	⁴	26.750	²⁴	23.500	²⁰	tree	animal ²⁰
<i>Cedrela</i>									
<i>fissilis</i>	0.130	0.035 ^j	³⁶	10.000	⁴⁶	5.000	⁴⁶	tree	abiotic ³⁶
<i>Chisocheton</i>									
<i>cumingianus</i>	9.481	7.990	³⁵	31.700	³⁵	23.900	³⁵	tree	bird ³²
<i>Dysoxylum</i>									
<i>gaudichaudianum</i>	0.424	0.194	¹⁸	10.000	⁸	9.000 ^c	⁸	tree	bird ³⁷
Myrtaceae									
<i>Syzygium</i>									
<i>guineense</i>	0.628	0.360	¹⁰	12.000	¹⁰	10.000	¹⁰	tree	animal ¹⁹

^acalculated as ellipsoid shape unless otherwise stated

^bdry mass unless other stated

^cmammal includes all non-volant mammals unless otherwise stated; animal include mammals and bird

^dcalculated assuming spherical shape (formula from Chen and Moles 2015)

^emidpoint range

^fincludes bats

^gfrom Chen and Moles (2015)

^hfrom similar species

ⁱaverage across data sources

^jconverted from fresh mass (g) (formula from Moles and Westoby 2006)

1. (Adler and Kestell 1998); 2. (Allen 1938); 3. (Bernal et al. 2010); 4. (Bisht and Ahlawat 1999); 5. (Bufalo et al. 2016); 6. (Chen and Moles 2015); 7. (Cole et al. 2010); 8. (Conn and Damas 2006); 9. (de Kok 2015); 10. (Dutton et al. 2014); 11. (Fadini et al. 2009); 12. (Felger and Joyal 1999); 13. (Fleury and Galetti 2004); 14. (Fleury and Galetti 2006); 15. (Fleury et al. 2014); 16. (Ganade and Brown 2002); 17. (Goudel et al. 2013); 18. (Green and Juniper 2004); 19. (Holl and Lulow 1997); 20. (Kitamura et al. 2004); 21. (Kitamura et al. 2011); 22. (Leeuwenberg 2002); 23. (López-Toledo et al. 2013); 24. (Mabberley et al. 1995); 25. (Mazer and Wheelwright 1993); 26. (McConkey 2000); 27. (McConkey 2005); 28. (McConkey et al. 2002); 29. (Paine and Beck 2007); 30. (Paine et al. 2016); 31. (Prain 1890); 32. (Sidhu and Datta 2015); 33. (Suazo et al. 2013); 34. (Tobler et al. 2010); 35. (Velho et al. 2009); 36. (Vieira et al. n.d.); 37. (Whittaker and Turner 1994); 38. (Young et al. 2013); 39. (Beck and Terborgh 2002); 40. (Wehncke et al. 2010); 41. (Lucas and Corlett 1998); 42. (Link and Di Fiore 2006); 43. (Ara et al. 2007); (Guzmán and Stevenson 2011); 44. (Zamora and Montagnini 2007); 45. (Bosque et al. 1995); 46. (Vieira et al. 2008)

Table B.3.2 Site details for studies that contributed experimental data to post-deposition seed predation Network Meta-Analysis. Different research groups provided depot-level data indicating total number seed predation out of total exposed in each ecosystem. Experiments run by different research groups listed as citations.

Ecosystem Site	longitude	latitude	country
tropical dry forest			
Kitamura et al. (2004)			
Khao Yai National Park	101.083	14.083	Thailand
Lopez-Toledo et al. (2013)			
Sierra de Álamos-Río Cuchujaqui Reserve	-108.650	26.983	Mexico
tropical moist deciduous forest			
Adler and Kestell (1998)			
Gatun Lake (island 48)	-79.856	9.137	Panama
Gatun Lake (island 61)	-79.845	9.127	
Gatun Lake (island 69)	-79.840	9.128	
Gatun Lake (island 49)	-79.839	9.134	
Gatun Lake (island 59)	-79.838	9.130	
Gatun Lake (island 70)	-79.836	9.128	
Dutton et al. (2014)			
Ngel Nyaki Forest Reserve	6.503	11.000	Nigeria
Fleury and Galetti (2004)			
Mata São José	-47.467	-22.417	Brazil
Estação Ecológica dos Catetus	-49.667	-22.367	
Fleury and Galetti (2006)			
Parque Estadual Morro do Diabo	-52.283	-22.450	Brazil
Estação Ecológica dos Caetetus	-49.700	-22.400	
Mata do Viveiro Tabating Áera	-48.133	-22.683	
Mata do Monal	-48.183	-22.667	
Mata São José	-47.467	-22.417	
Mata do Ribeirão Cacheira	-46.917	-22.833	
Mata Pedreira	-47.817	-22.783	
Mata do Pomar	-47.617	-22.700	
Vieira et al. (n.d.)			
Zé Pereira	-46.758	-13.654	Brazil
Carlão	-46.766	-13.659	
Pimenta	-46.770	-13.611	
tropical mountain system forest			
Holl and Lulow (1997)			
Las Alturas Biological Research Station	-82.833	8.950	Costa Rica

Ecosystem Site	longitude	latitude	country
tropical rainforest			
Andresen and Levey (2004)			
Biological Dynamics of Forest Fragments Project	-60.000	-2.500	Brazil
McConkey (2005a)			
Barito Ulu Research Area	114.100	0.200	Indonesia
McConkey (2005b)			
Barito Ulu Research Area	114.100	0.200	Indonesia
Montaño et al. (n.d.)			
Beni Biosphere Reserve	-66.333	-14.667	Bolivia
Norghauer et al. (2006)			
Kayapó Centre for Ecological Studies	-51.962	-7.771	Brazil
Sidhu and Datta (2015)			
Pakke Tiger Reserve	92.875	27.083	India
Whittaker and Turner (1994)			
Krakatoa	105.417	-6.100	Indonesia
Young et al. (2013)			
Palmyra Atoll National Wildlife Refuge	-162.083	5.883	USA*

* Unorganized Incorporated Territory of the USA

Appendix C

Appendix C contains supporting tables for Chapter 4

C.1 Chapter 4 supporting Tables

Table C.4.1 Rodent species of Sulawesi, Indonesia

Genus	Species	English name	citation
Muridae			
<i>Bunomys</i>	<i>andrewsi</i>	Andrew's bunomys	1
	<i>chrysocomus</i>	common bunomys	
	<i>coelestis</i>	Lompobatang bunomys	
	<i>fratrorum</i>	Northeastern peninsula bunomys	
	<i>karokophilus</i>	Karoko hill rat	
	<i>penitus</i>	inland hill rat	
	<i>prolatus</i>	long-headed hill rat	
	<i>torajae</i>	–	
<i>Crunomys</i>	<i>celebensis</i>	Sulawesi shrew mouse	
<i>Echiothrix</i>	<i>centrosa</i>	Central Sulawesi echiothrix	2
	<i>leucura</i>	Northern Sulawesi echiothrix	
<i>Graciliumys</i>	<i>radix</i>	slender root rat	3
<i>Haeromys</i>	<i>minahassae</i>	lowland Sulawesi haeromys	4
<i>Hyorhinomys</i>	<i>stuempkei</i>	hog-nosed shrew rat	2
<i>Margaretamys</i>	<i>beccarii</i>	Beccari's margareta rat	5
	<i>christiane</i>	Christine's margareta rat	
	<i>elegans</i>	elegant margareta rat	
	<i>parvus</i>	little margareta rat	
<i>Maxomys</i>	<i>musschenbroekii</i>	Musschenbroek's spiny rat	6
	<i>wattsi</i>	Watts' spiny rat	
<i>Melasmothrix</i>	<i>naso</i>	Sulawesian shrew rat	2
<i>Paruromys</i>	<i>dominator</i>	giant Sulawesi rat	7
<i>aucidentomys</i>	<i>vermidax</i>	–	2
<i>Rattus</i>	<i>argentiventer</i>	ricefield rat	8
	<i>hoffmanni</i>	Hoffmann's rat	9
	<i>marmosurus</i>	opossum rat	
	<i>rattus</i>	house rat	
	<i>tondanus</i>	–	
<i>Rhynchomys</i>	<i>soriocides</i>	Northern Luzon rhynchomys	10
<i>Sommeromys</i>	<i>macrorhinos</i>	Sommer's Sulawesi rat	2
<i>Taeromys</i>	<i>callithrichus</i>	greater taeromys	7
	<i>celebensis</i>	long-tailed taeromys	

Genus	Species	English name	citation
	<i>hamatus</i>	central mountain taeromys	2
	<i>macrocerus</i>	long-tailed Sulawesi shrew rat	
	<i>rhinogradoides</i>	Tate's Sulawesi shrew rat	
<i>Waiomys</i>	<i>mamasae</i>	Sulawesi water rat	3
Sciuridae			
<i>Hyosciurus</i>	<i>heinrich</i>	montane long-nosed squirrel	11
	<i>ileile</i>	lowland long-nosed squirrel	
<i>Prosciurillus</i>	<i>abstrusus</i>	secretive dwarf squirrel	
	<i>alstoni</i>	Alston's Sulawesi dwarf squirrel	
	<i>leucomus</i>	whitish dwarf squirrel	
	<i>murinus</i>	Celebes dwarf squirrel	
	<i>topapuensis</i>	Mount Topapu squirrel	
<i>Rubriscurus</i>	<i>rubriscurus</i>	Sulawesi giant squirrel	

1. (Musser 2014); 2. (Esselstyn et al. 2015); 3. (Rowe et al. 2016); 4. (Musser 1990); 5. (Mortelli et al. 2012); 6. (Musser 1991); 7. (Fabre et al. 2013); 8. (Musser 1973); 9. (Musser 1971a, 1971b, 1971c); 10. (Musser 1969); 11. (Musser et al. 2010)