

BIOGEOGRAPHY, ECOLOGY AND CONSERVATION OF PARADISAEIDAE:  
CONSEQUENCES OF ENVIRONMENTAL AND CLIMATIC CHANGES

BY

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## **ABSTRACT**

The Paradisaeidae, or birds of paradise (BOPs), comprises 42 species in 17 genera, although these numbers could change as more molecular studies are conducted. BOPs are distributed from the Moluccan Islands east through New Guinea to Tagula Island and northeastern Australia. This analysis set out to develop a multidimensional view of conservation threats to BOP species, looking towards their conservation. For example, under future climatic conditions and considering loss of forest cover, *Astrapia nigra* may face extinction within just 2-4 decades. Generally, under future climatic conditions, BOP distributional areas decrease. Relatively few BOP species face distributional losses owing to sea level rise; however, land use change and future changed climatic conditions present more serious threats. I analyze distributional patterns and likely threats for each species and identify optimal suites of areas for BOP protection based on the results.

## **INTRODUCTION**

The family Paradisaeidae (birds of paradise, or BOPs) comprises 42 species in 17 genera (Frith and Beehler 1998), although some debate exists regarding these numbers. For instance, Dickinson (2003) recognized 39 species in 16 genera, while Sibley and Monroe (1990) recognized 46 species in 17 genera. Cracraft (1992) increased the numbers to ~90 species in 20 genera under the phylogenetic species concept. Heads (2001b) pointed out that Cracraft's phylogenetic species parallel the subspecies of other authors (Iredale 1956; Cooper and Forshaw 1977; Frith and

Beehler 1998) under the biological species concept (Mayr 1962; Gilliard 1969; Diamond 1972). A synthetic understanding of BOPs, including dimensions of geographic distributions, field identification, and speciation studies, would greatly enable proper management and conservation action (Cracraft and Feinstein 2000; Dumbacher et al. 2003; Filardi and Moyle 2005).

Frith and Beehler (1998) reviewed the taxonomic arrangements of the BOPs that have been proposed over the years. Even so, contention still remains regarding relationships within the family, so arrangements of taxa remain a work in progress, as new methods are applied to questions of systematic and phylogenetic relationships in the clade (Cracraft and Feinstein 2000; Scholes 2008). Here, I base discussion and analyses on the Frith and Beehler (1998) classification, except that their inclusion of the genera *Cnemophilus* and *Macgregoria* as sister to the Paradisaeinae has been invalidated: Cracraft and Feinstein (2000), using molecular data, showed that these genera are only distantly related to the BOP clade.

Scholes (2008), using ethological data analyzed in a phylogenetic context, showed that *Parotia* includes 6 species instead of the traditional 4 species: the basal *P. wahnesi*, separation of *P. helenae* as a full species, *P. lawesii*, *P. sefilata*, and two species usually allotted to *P. carolae* (Mt Stolle population and Crater Mountain population). Recent expeditions to the Foya Mountains (Beehler et al. 2007) have also confirmed the distinctiveness of a population, *P. berlepschi*, first described by

Kleinschmidt (1897). Given these recent findings and certainly more to come, we expect the classification of the clade to continue to change.

### *BOP biology*

BOPs have a near-obligate association with closed humid tropical forests, although a few BOP species extend into habitats like second-growth forests, forest edges, and mixed forests including savannah (Bell 1970; Diamond 1972; Frith and Beehler 1998; Grant and Litchfield 2003). Frith and Beehler (1998) presented a detailed summary of habitats used by all BOPs for nesting. As such, BOP habitat use ranges from primary montane and lowland rainforest, e.g., in *Parotia lawesii*, *Paradisaea raggiana*, and *Paradisaea decora* (LeCroy et al. 1980; Pruett-Jones and Pruett-Jones 1988; Frith and Beehler 1998; Frith and Poulsen 1999), second-growth forest as in *Paradisaea rudolphi* (Mack 1992), and mangroves as in *Seleucidis melanoleuca* (Frith and Beehler 1998) and possibly *Semioptera wallacii* (Frith and Poulsen 1999).

BOP habitat use as defined by Frith and Beehler (1998) is good for describing nesting areas, but is restricted in detail and could possibly obscure important behavioral traits important in defining habitat usage as well as accounting for species distributions. For instance, LeCroy (1981), in her monograph of BOP display and evolution, described display areas for different species, and Diamond (1972) found elevational differences in male and female distributions in *Lophorina*. Foraging in most BOPs occurs in the upper portion of the forest canopy, occasionally moving to lower habitats when birds

join mixed flocks (Frith and Beehler 1998). Distributions and habitat usage of BOPs may thus to some extent be associated with foraging strategies and seasonal fruiting of fruit trees (Beehler 1983; Beehler and Dumbacher 1996).

### *BOP biogeography*

BOPs have a wide distribution in the Australo-Papuan region, ranging from sea level to 3500 m (Frith and Beehler 1998; Heads 2001a; 2001b). Most species (18 of 34 species in New Guinea) occur around 1000-2000 m of elevation (Heads 2001a; 2001b); 9 species are found from 0-1000 m; and 7 species occur from 2000-3000 m (Frith and Beehler 1998; Heads 2001a; 2001b). BOP species diversity is concentrated in the areas of Mt. Hagen, Wahgi Valley, and Jimi Valley (including the Mendi area; Heads 2001a; 2001b). Similarly, Beehler et al. (1986) and Pruett-Jones and Pruett-Jones (1986) observed the central highlands region (Victor Emmanuel Mountains, Mt. Giluwe, Mt. Hagen) as the area of highest BOP diversity.

Early authors (Diamond 1972; Diamond 1981; Beehler and Beehler 1986; Whitney 1987, Frith and Beehler 1998) attempted to describe the biogeography of BOPs. However, the most detailed work on BOP biogeography is from a series of papers by Heads (2001a; 2001b; 2002) based on panbiogeographic approaches. BOPs are distributed throughout New Guinea, as well as across eastern Australia, the Moluccas, Yapen Island, the Aru Islands, the Trobriand and D'Entrecasteaux Islands and Sudest Island (Bell 1970; LeCroy et al. 1980; Diamond 1986; Frith 1992; Beehler and Swaby

1991; Frith and Beehler 1998; Frith and Poulsen 1999; Heads 2001a; Heads 2002; Grant and Litchfield 2003). Heads (2002) explained distributions of BOPs as mostly of vicariant origin, and less via dispersal (Frith and Beehler 1998). While this explanation could be true for some species, a more thorough analysis of BOP phylogenetic relationships will clearly reveal more detail on the origins of the various species.

### *Ecological niche modeling*

Ecological niche modeling (ENM) offers a means of predicting geographic distributions of species via estimates of their ecological niches (Peterson et al. 1999; Peterson et al. 2001; Soberón and Peterson 2005). In ENM, the scenopoetic (or abiotic) ecological niche of a species is the range of environmental and physical conditions within which the species is able to maintain populations without immigration (Soberón and Peterson 2005). A species' geographic distribution is defined by its autecological needs, in addition to effects of biotic interactions and historical barriers (Soberón and Peterson 2005).

ENM uses known occurrences of species, in combination with raster map datasets describing relevant environmental characteristics to predict distributional and ecological niches (Soberón and Peterson 2005; Gaubert et al. 2006). Various algorithms have been developed and used to model ecological niches, exploring a range of questions. For instance, Maxent has been used to map species' distributions

(Phillips et al. 2006; Phillips and Dudík 2008) and assess threat status of species (e.g., Sergio et al. 2007); the Genetic Algorithm for Rule-set Prediction (GARP) has been used in mapping species' distributions (Peterson et al. 2001), assessing conservation status of poorly known taxa (Gaubert et al. 2006), locating Pleistocene refugia (Waltari et al. 2007), and assessment of climate change implications for species (Martínez-Meyer 2005; Papeş 2007). Besides GARP and Maxent, other ENM approaches include BIOCLIM, DOMAIN, and HABITAT (Guisan and Zimmerman 2000; Finch et al. 2006; Hernandez et al. 2006) and a variety of statistical approaches (Elith et al. 2006). Comparisons of the different algorithms have been developed, with a variety of results (Elith et al. 2006; Tsoar 2007; Ward 2007).

ENMs have been used to evaluate implications of global climate change for species. Previous studies have assessed mammals (Martínez-Meyer et al. 2004; Gaubert et al. 2006), birds (Peterson et al. 2001; Araújo et al. 2005; Anciães and Peterson 2006), salamanders (Parra-Olea et al. 2005), plants (Peterson et al. 2008), and diseases (Nakazawa et al. 2007). Basically, under changing climatic conditions, a species either shifts spatially to track changing conditions, or adapts in terms of ecological tolerances; otherwise, populations will go extinct (Holt 1990). Since ENMs map the distributional potential of species (Peterson et al. 2001; Pearson and Dawson 2003; Thuiller 2003), climate change effects on species' distributions can be assessed (Martínez-Meyer 2005; Anciães and Peterson 2006) under this rationale. ENMs in a climate change context require explicit assumptions regarding dispersal ability to



produce distributional estimates (Guisan and Zimmerman 2000; Peterson et al. 2001; Parra-Olea et al. 2005; Gaubert et al. 2006; Papeş 2007).

### *Sea level rise*

Sea level rise (SLR) refers to long-term increases in mean sea level, a consequence of several processes of non-linearly coupled components of the Earth system, e.g., global warming and agricultural practices (Bindoff et al. 2007). Currently, SLR is predicted to increase in coming years, which may have serious consequences for living organisms, their habitats, human well-being, and economics (Kennish 2002; Knogge et al. 2004; Gopal and Chauhan 2006; LaFever et al. 2007; Bindoff et al. 2007).

Present rates of ice sheet melt have potential for substantial global SLR impacts (Shepherd and Wingham 2007). The Greenland Ice Sheet contains a volume of water equivalent to 6 m of global sea level rise, and the West Antarctic Ice Sheet contains a volume of water equivalent to 5 m of global sea level rise (Bindschadler 1998). Both are currently showing rapid increases in mass loss that will significantly increase global sea levels if such mass loss continues (Thomas et al. 2004; Rignot and Kanagaratam 2006). Greenland and Antarctica are estimated to contribute 0.35 mm/yr of sea level rise globally, a modest amount compared to the present rate of increase of 3.0 mm/yr of SLR (Shepherd and Wingham 2007). Additionally, increases in current SLR are attributed to anthropogenic changes in land hydrology, changes in the

atmosphere and vertical land movements, tectonics, and sedimentation that occur to influence local measurements (Bindoff et al. 2007).

As SLR effects become more pronounced (Bindschadler 1998; Thomas et al. 2004; Shepherd and Wingham 2007), only very few studies to date have attempted to estimate SLR effects on ecosystems and the wildlife that depend on those ecosystems. At most risk are small island nations that currently confront sea level-related problems more directly. As such, already, Tuvalu and other small islands in Papua New Guinea are experiencing storm-caused over-wash and loss of land area by 20 vertical cm per year; by 2025, some atolls in the Maldivian Islands are expected to be inundated completely by SLR (Ghina 2003). SLR effects in these small island states include loss of estuarine ecosystems, land area, and fresh water (Kennish 2002; Ghina 2003; Knogge et al. 2004; Gilman et al. 2006; Gilman et al. 2007), as well as loss of wildlife (DeVantier et al. 2004; Legra et al. 2008). Although effects on wildlife may seem less critical than socioeconomic impacts on tourism, living areas, and agricultural systems, these phenomena are usually linked, so effects on one ecosystem eventually affect others as well (DeVantier et al. 2004; Gilman et al. 2006).

### *Conservation in New Guinea*

The island of New Guinea comprises Papua New Guinea in the east and the Indonesian provinces of West Papua and Papua in the west (Heads 2002).

Geologically, the island is complex, its formation resulting from a series of events of

drifting, rafting, and sweeping up of islands arcs that combined to form present-day New Guinea (Charles 1991; Heads 2002). Given its isolation, New Guinea is now a biologically diverse region both in terrestrial realms and marine systems surrounding the island. New Guinea holds 700-800 species of birds, including globally unique concentrations of BOPs (38 species), parrots (46 species), and pigeons and doves (45 species; Beehler et al. 1986; Miller et al. 1994; Mack and Dumbacher 2007). Mammal diversity reaches ~200 species, including marsupials, monotremes, rats and bats (Miller et al. 1994; Flannery 1995; Beehler 2007). Sixty of these species are endemic, occupying habitats from lowland rainforest to snow line. The New Guinea flora totals >20,000 species of ferns and flowering plants, including >3000 species of orchids alone (Womersley 1978; Beehler 2007; Takeuchi 2007). As a consequence, New Guinea has been included among the list of megadiverse regions (Mittermeier et al. 2003) and global biodiversity hotspots (Myers et al. 2000).

Included within this diversity are the people that inhabit New Guinea and its satellite islands. In all, >1200 language groups and a hyperdiverse cultural base linked to different systems of beliefs, trade, traditional customs, and land tenure systems sprouted since the settlement of New Guinea ~40,000 years ago (West 2005; Mansoben 2007; Pasveer 2007). Dependency on the surrounding forests, seas, rivers, and wildlife has always been key to the survival and well-being of past and present generations of New Guineans (West 2005; Mansoben 2007). Studies such as those by Carrier and Carrier (1983), Steadman et al. (1999), Foale (2005), Mack and West

(2005), Case et al. (2005), and Cinner et al. (2005) indicate the level of dependency on wildlife and forests for sustenance. Given this dependency, management that leads to sustainable usage of wildlife and their habitats by humans within the region is necessary (Mack and West 2005).

Currently, conservation in Papua New Guinea is done within the framework of wildlife management areas (WMAs), such as the Crater Mountain Wildlife Management Area in Eastern Highlands Province (Johnson et al. 2004; Mack and Wright 1996); marine protected areas (MPAs) such as the Kimbe Bay area (Koczberski et al. 2006; Green et al. 2007) and the Milne Bay area (Kinch 2001; Foale 2005; Baines et al. 2006); integrated conservation and development projects (ICADs), such as the LAK ICAD project in New Ireland (McCallum and Sekhran 1997); national and provincial parks (NPs and PPs) like the Varirata National Park (Gare 1987); and recently conservation areas (CAs), such as the YUS Conservation area in Morobe (Acrenaz et al. 2007; Stabach et al. 2009).

Within New Guinean Indonesia, conservation is also in the form of protected area systems. For instance, the Lorentz National Park, one of the largest and highly diverse park systems in the world, was formed to protect ecosystems and wildlife ranging from glacial mountaintop fauna and habitats to seacoast (Alcorn 2000; Meyers and Hitchcock 2008). Since the Papuan region contains ~50% of Indonesia's biodiversity (McKenna et al. 2002; Richards and Suryadi 2002; Patiselanno 2003; Sheil et al.

2004), protecting and managing this diversity is important. Currently, protected area systems in the region have many flaws: protected areas do not necessarily keep out logging, mining, and large-scale agriculture plantations (Richards and Suryardi 2002; Sheil et al. 2003; Murdiyarso and Kuniyanto 2008). In addition, designating an area as protected without research and follow-up monitoring can lead to impacts not detected until they become a problem, such as introductions of macaques in Papua (Kemp and Burnett 2003) and forest dieback in *Nothofagus* forests (Meyers and Hitchcock 2008).

Given this diversity of degree and manner of protection, is the protected area system sufficient to guarantee adequate protection of biodiversity? Reports on the protected area systems of the countries outline factors that influence (and often hinder) protection of biodiversity: lack of government support, disenfranchising of local communities, mismanagement, minimal policing, and inadequate legislation, lack of management and research capabilities, and increasing pressures from anthropogenic activities (Sheil et al. 2003; WWF PNG 2006; Baines et al. 2006; Dowie 2008).

While the need for protection of biodiversity is growing, given climate change, increasing human populations, and increasing pressures from anthropogenic activities, protection in any form should entail detailed scientific study, good management strategies, collaborative efforts with local communities and other stakeholders, and (minimally) protection that encompasses the distributions of species being conserved (Sarkar et al. 2004; Sánchez-Cordero et al. 2005b).

BOPs are an iconic part of New Guinean biodiversity, so their conservation is of considerable interest. As a result, this study aims to present a multidimensional view of distributions of BOP species, and to develop prioritizations of areas for their optimal protection. Under future climatic conditions and environmental changes, species' distributions may shift, decrease in distribution, or become extinct. I examined the biogeographic patterns of BOPs, using ecological niche models to assess effects of future climate, land use change, and future sea level rise on BOP distributions and diversity.

## **METHODS**

### *BOP distributions*

Biological specimens in museum collections are useful sources of information regarding geographic distributions of species (Ballesteros-Barrera et al. 2007; Peterson 2003; Gaubert et al. 2006; Papeş 2007). BOP locality information was downloaded from the Global Biodiversity Information Facility (GBIF) portal. I also visited two museums to look at specimens and gather locality data (see acknowledgments for a full list). For each species, I collected information on taxonomic identification, collector, date of collection, catalog number, and locality description (country, province/state, and village name). Species lacking sufficiently detailed information to guarantee accurate georeferencing were not included. A total of 986 localities for 37 species, including 3 hybrid “species” (*Diphyllodes guiliemie*, *Paradiseae intermedia* and *P. mariae*; not analyzed), were extracted and

georeferenced to the nearest degree of latitude and longitude and used to create locality maps for each species (Fig. 1).

From the locality dataset above, 686 (the 3 hybrid species excluded) occurrence records were used for building ecological niche models: each of the locality data was georeferenced to within 1' of latitude and longitude using the Geonames geographic database server (<http://www.geonames.org>), including gazetteers and published literature. The final occurrence dataset comprised 2-55 localities for each of 34 species. Species restricted to particular small islands (for instance, *Cicinnurus respublica*, *Manucodia comrii*, *Lycoccorax pyrrhopterus*, *Paradisaea decora* and *Semioptera wallacii*) were excluded from ENM model building.

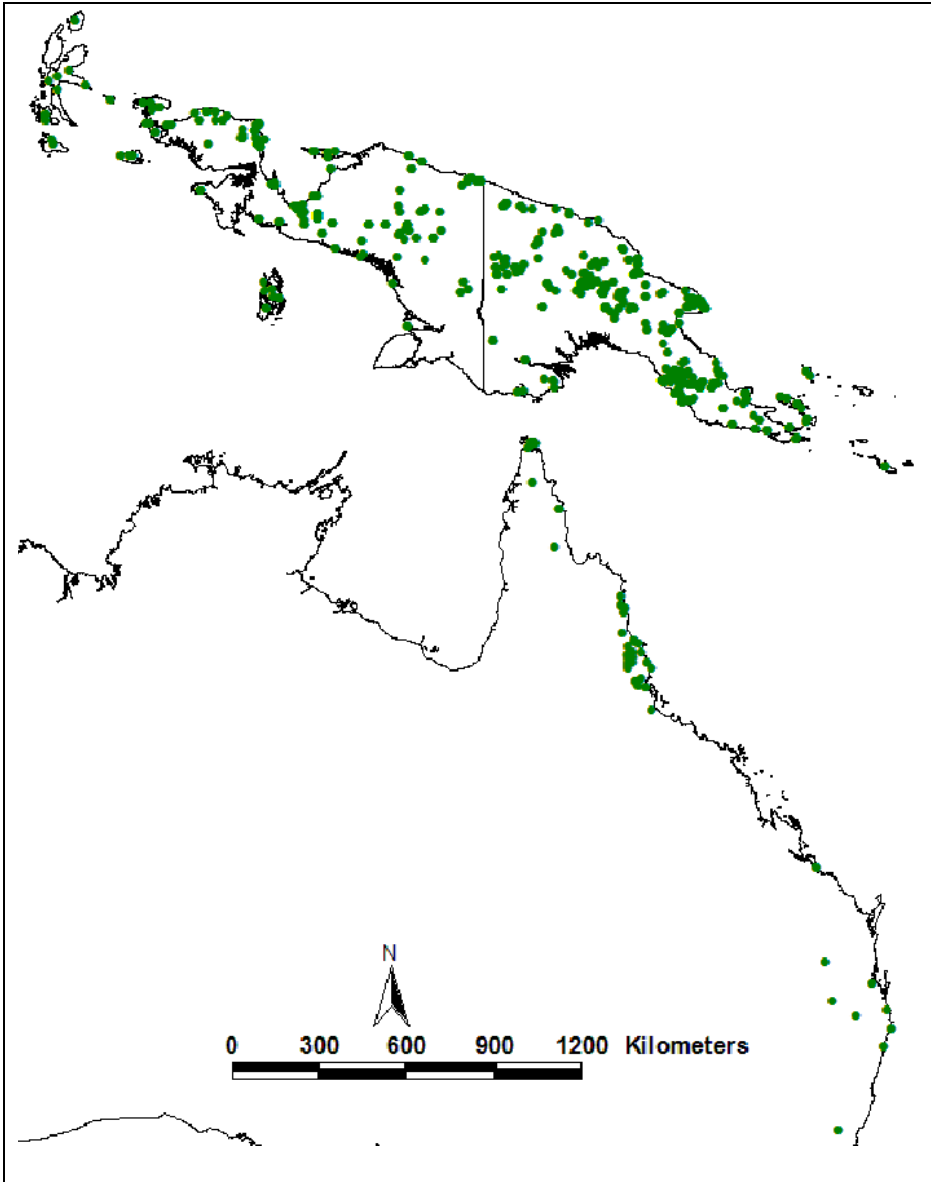


Figure 1. Bird of Paradise occurrence localities across New Guinea, Australia, and the Moluccas islands.

*Ecological niche models- climatic conditions*

ENMs were developed using the Genetic Algorithm for Rule-Set Prediction (GARP; Stockwell and Noble 1992; Stockwell and Peters 1999), specifically the DesktopGarp



software package (<http://www.lifemapper.org/desktopgarp/>); a method that is robust and has seen the broadest application in terms of questions related to ecological niche evolution (Anciães and Peterson 2006; Papeş 2007). GARP uses presence only data; thus, for absence information, absences are derived from the set of pixels where the species has not been detected (Anciães and Peterson 2006; Papeş 2007).

Within GARP processing, data are used to generate initial suites of rules, which then undergo an iterative process of rule selection, evaluation, testing, and incorporation or rejection. First, a method is selected from a range of possibilities, is applied to the training data, and a rule developed; rules may evolve by a number of means (e.g., truncation, point changes, crossing-over among rules) to maximize predictivity. Predictive accuracy for each of the rules is then evaluated based on 1250 points resampled from the test data and another 1250 points randomly selected from the study region as a whole where the species is not known to occur. The change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model, and the algorithm runs either 1000 iterations or until it converges. Projection of GARP models onto landscapes provides an estimate of the geographic distribution of suitable conditions, and allows tests of model predictivity.

In all, 100 models were generated for each species, and the 10 best distribution models were selected using a best-practices procedure for identifying optimal models

(Anderson et al. 2003) based on omission (leaving out true areas of occupation) and commission (including areas not potentially habitable) error statistics. Specifically, I used a soft omission threshold, focusing on the extreme 20% of the distribution of omission values (as measured based on ability to predict held-out subsets of the original input data) across models. I then chose models presenting intermediate levels of commission (i.e., proportional area predicted across the study area).

The 10 best models were summed in ArcView 3.2, as a best and most conservative distribution estimate of the areas in which a species was likely to be present. Finally, because species are often prevented from inhabiting the entire spatial extent of areas presenting appropriate ecological niche conditions by barriers to dispersal (Soberón and Peterson 2005), I reduced modeled distributions for the present to areas to within or contiguous to known current distributions by trimming (Papeş 2007), based on maps presented for each species in Frith and Beehler (1998), effectively adding assumptions regarding dispersal limitations.

#### *ENMs-forest cover*

Studies such as Turner (1996), Schmiegelow and Monkkonen (2002), and Sala et al. (2000), have related reductions in distributions of species ranges to loss of major forest types. I used forest cover data layers spanning BOP distributions from the ESA Global Cover project 2008 (<http://www.esa.int/dua/ionia/globcover>; Bicheron et al. 2008) and intersected them with distributions of species estimated based on climatic

data. GLOBCOVER has a much finer resolution (300 m resolution) than other previous land use/land cover maps (e.g., 1 km<sup>2</sup> spatial resolution in University of Maryland Global Land Cover Facility LULC maps; Giri et al. 2005). Given that land use patterns and species occurrence data do not necessarily come from the same time periods, land cover information could not be included in building niche models (Chapman et al. 2005), but rather were intersected *post hoc* with estimated distributional areas for each species. Since BOP ecological distributions are relatively simple (see text above; Frith and Beehler 1998), I reclassified land cover types (22 classes in GLOBCOVER, Bicheron et al. 2008) into 3 major types: (1) primary forest, (2) secondary forests/scrublands, and (3) grasslands interspersed with sparse vegetation. This simpler map was then used to refine the distributional estimate for each species according to its specific land cover needs.

#### *ENMs- sea level rise*

I mapped effects of SLR on distributions of BOPs by linking species' distributions with spatially explicit projections of marine intrusion caused by SLR. A new GIS analysis by Li et al. (2009) provides detailed marine intrusion projections. These forecasts were derived as follows. Cells that are below a projected SLR are initially flagged. Of the flagged cells, only those that are connected to the ocean are selected. The selected cells are then checked to see whether or not they correspond to existing inland water bodies. Only those cells that connect to the ocean and are not inland

water bodies are designated as inundation cells. The method was implemented for a 6 m SLR scenario; full details of the method are provided in Li et al. (2009).

Already, several studies (Legra et al. 2008; Menon et al. 2009) have used this method with interesting results, and more studies are underway (Legra et al. unpubl. data).

For BOPs, with distributions ranging to low elevations, I intersected predicted distributional areas with the marine intrusion estimates to assess the proportion of distributions lost, focusing on the maximum SLR scenario of 6 m.

#### *Protected areas- Conservation prioritization*

Conservation efforts across Australia and New Guinea are either lacking, or are not necessarily designed optimally for particular species. Many protected areas were developed based on minimal information, which is often quite general, so protection of particular species is not always achieved (Pressey et al. 1994). An approach to solving this problem is objective selection of priority sites for conservation (Eken et al. 2004; Sarkar et al. 2006) based on clear goals. The aim in prioritization for conservation is not necessarily to augment systems of protected areas, but rather to ensure that protected areas are designed and located in best places to conserve biodiversity (UNDP 2004; Urquiza-Hass et al. 2009).

Using place prioritization methods, I evaluated BOP distributions to identify suites of areas most suitable for protecting BOPs. I used the ResNet software package

produced at the University of Texas at Austin (Garson et al. 2007). ResNet is unique in that it uses dynamic memory allocation, and thus is not constrained by the size of the data set used. ResNet uses algorithms modified, verified, and extended from original proposals by Margules et al. (1988).

In ResNet, a particular region is divided into sets of places, either using geographic coordinates (Sarkar et al. 2002; Garson et al. 2007; Illoldi-Rangel et al. 2008) or ecological regions (Sarkar et al. 2002; Sánchez-Cordero et al. 2005; Garson et al. 2007). Algorithms within the program then order places according to their biodiversity content (Sarkar et al. 2002; Garson et al. 2007). The algorithm uses 3 input parameters: (1) an explicit target has been set for adequate representation of each surrogate (here, the number of selected places at which a species must occur), (2) maximum allowed area such that the algorithm orders places until this maximum is reached, and finally (3) the maximum allowed cost of a proposed set of priority places. The goal for such algorithms is to achieve the target as economically as possible; that is, they aim to choose as few places as possible while meeting conservation goals (Margules et al. 1988; Pressey and Nicholls 1989, Sarkar et al. 2004).

Within ResNet, 3 principles or rules are incorporated:

- (i) *Rarity*: surrogates are first ordered inversely by their frequency of appearance in the data set. Places are then ordered by presence of the rarest surrogates (in this case species),
- (ii) *Complementarity*: places are ordered based on numbers of surrogates present that have not met their targeted representation, and
- (iii) *Richness*: places are ordered based on overall number of surrogates present; however, richness is used only in the initial step i.e., selection of first place, since it has been shown previously that reliance on richness results in inefficient place selection (Williams et al. 1996; Csuti et al. 1997; Sánchez-Cordero et al. 2005).

For both initialization and iterative place selection, ties are broken arbitrarily by selecting the first place on the list, so that a unique place is chosen. Iterations continue until all surrogates are adequately represented or the maximum allowed area cost is exceeded. If no explicit target is set, the procedure continues until all places are selected (Sarkar et al. 2002; Garson et al. 2007). The order in which places are selected produces a ranking of places based on their biodiversity content. Biodiversity content is thus implicitly defined by the algorithm, and the intuition behind this approach is that diversity is adequately captured by rarity and complementarity (Sarkar et al. 2002; Sarkar and Margules 2002). As expected, depending on

initialization and iteration criteria chosen, a number of different solutions can thus be achieved (Sarkar et al. 2002).

For BOPs, I divided relevant portions of New Guinea and Australia into 15,738 grid cells (each cell covers  $\sim 123 \text{ km}^2$ ), and then ordered these cells under richness considerations using both distributional and locality data. Since place prioritization differs somewhat in terms of the type of dataset used (Loiselle et al. 2003), I wanted to assess how much of a difference existed in prioritizing places using just locality data versus interpolated distributions of species. Using the prioritized places, I then created a dataset that indicated prioritized places already protected in existing protected areas, and ran ResNet again, this time accounting for existing protected areas (WDPA 2009). [Protected areas were downloaded from the World Database on Protected Area website (<http://www.wdpa.org/>) and edited in ArcView to include only areas contained within the extent of the grid.] For all ResNet runs, both for richness and existing protected areas, I used two target scenarios, 10% and 75%: target scenarios indicate the cells selected when 10% or 75% of species occurrence points or in the case of distributional area, the percentage of grid cells for each species is targeted for protection. Finally, I compared the derived prioritized places under the different targets to assess the effectiveness of using both distributional datasets and locality datasets.

## RESULTS

### *Ecological niche models--BOP distributions*

The ecological niche models (on which all subsequent analyses are based) developed were significantly better at predicting spatial distributions than random for all species (based on random data subsetting;  $\chi^2$  tests,  $P \ll 0.05$ ). Predicted distributions ranged from very large, covering the entire island of New Guinea, for instance, *Cicinnurus regius* (504,891 km<sup>2</sup>, Table 1A), or both New Guinea and large areas of Australia, for instance, *Manucodia keraudrenii* (639,442 km<sup>2</sup>, Table 1A) and *Ptiloris magnificus* (604,126 km<sup>2</sup>, Table 1A), or restricted to a narrow area, such as *Astrapia nigra* (429 km<sup>2</sup>, Table 1A).

Current predicted spatial distributions show certain BOP species to occupy certain altitudinal zones. For instance, *Astrapia rothschildi* is restricted to the Huon Peninsula and the Finisterre Range, and is distributed at lower or middle elevations around both ranges (Fig. 2). In addition, *Epimachus bruijnii* is distributed throughout the Mamberamo Basin, the lower parts of the Van Rees and Foja mountains and the interior floodplains of the Sepik and Green rivers and is found at elevations below 900 m a.s.l.



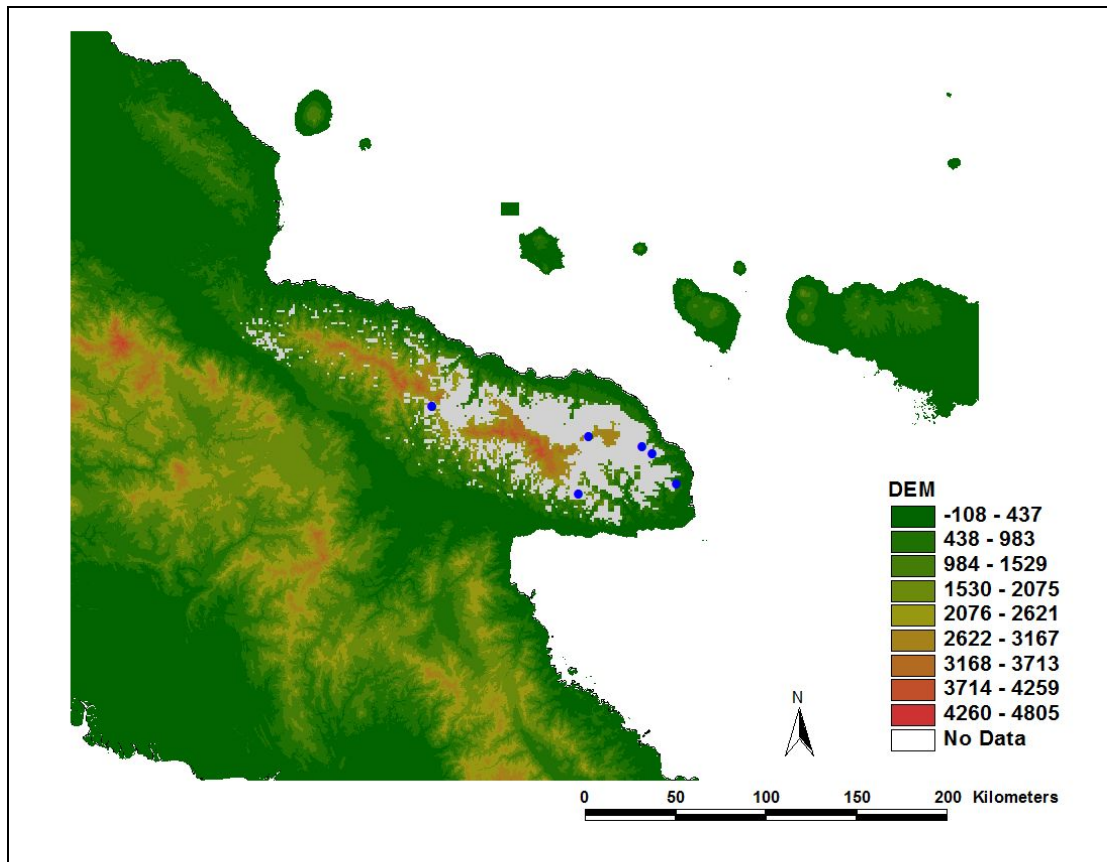


Figure 2. Current predicted distribution of *Astrapia rothschildi* across different elevational zones. Gray shade color shows predicted distribution and blue circles indicate known occurrence points.

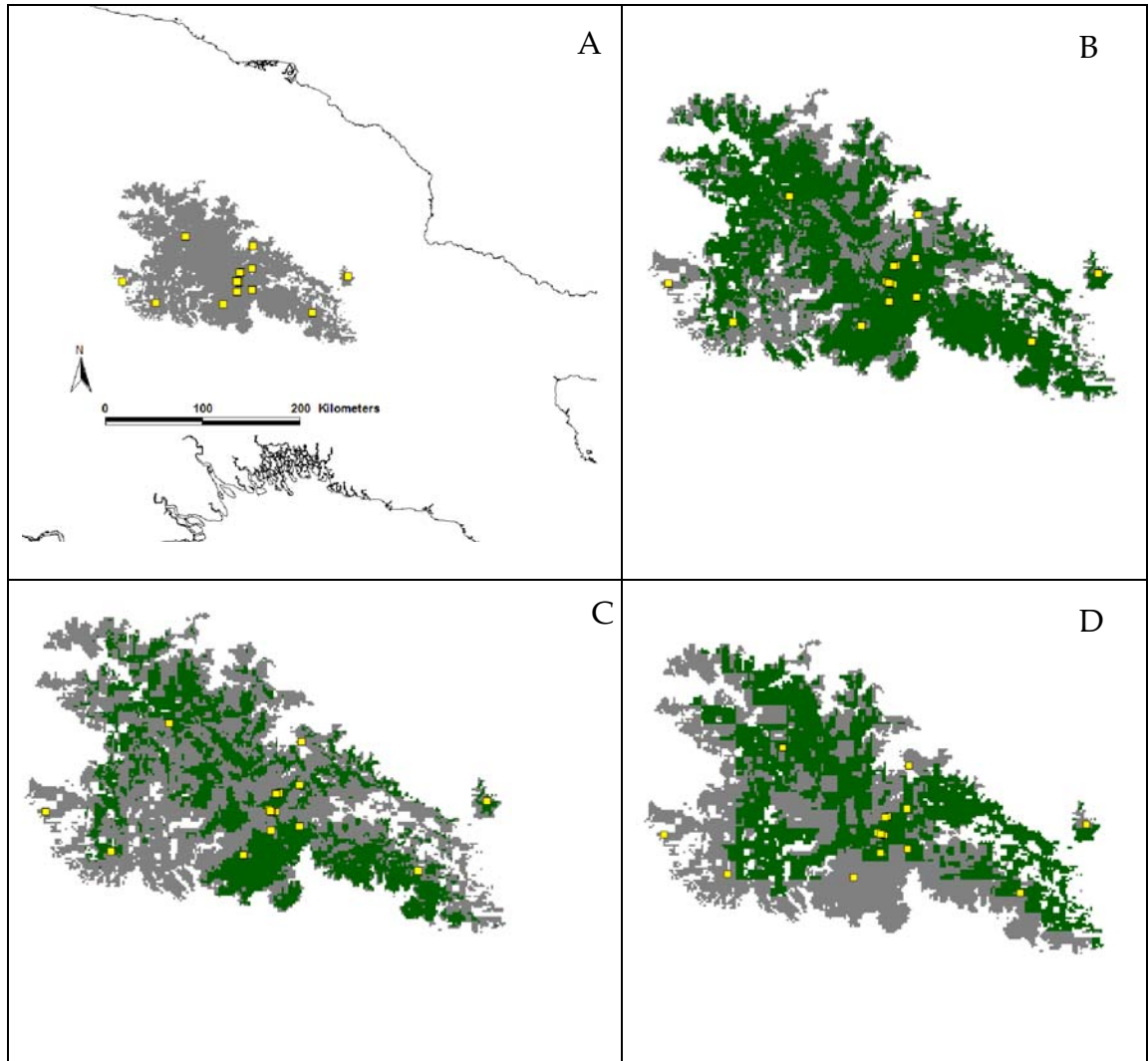


Figure 3. Present distribution of *Astrapia mayeri* (shown in gray, fig A) overlaid with occurrence points (yellow squares, fig A). Future potential distributions of *A. mayeri* given climatic changes are shown in green. A = present distribution, B = distribution at 2020, C = distribution at 2050, and D = distribution at 2080. Green shades in B, C, and D show future predicted distributions while gray shows the present distribution.

Table 1A. Species' distributional areas at present and under projected future climates based on assumptions of no dispersal. Years 2020, 2050, and 2080 show future potential distributions of species using ENM. The column "current" indicates present distributional areas of particular species, with percentages of distributional loss in parenthesis. Forest cover (FC) is given in km<sup>2</sup>, with projected forest cover loss (in parenthesis) under present and future climates (FC\_2020, FC\_2050, and FC\_2080). Dash (-) indicates zero potential distributional area.

Species	Current (km <sup>2</sup> )	2020	2050	2080	Present FC	2020	2050	2080
<i>Astrapia mayeri</i>	15197	10024 (34.04)	5713 (62.41)	7099 (53.29)	15197	10024 (34.04)	5713 (62.41)	7099 (53.29)
<i>Astrapia nigr</i>	429	1 (99.77)	-	-	429	1 (99.77)	-	-
<i>Astrapia notochilii</i>	3799	2638 (30.65)	2494 (34.35)	910 (76.05)	3799	2638 (30.65)	2494 (34.35)	910 (76.05)
<i>Astrapia stephaniae</i>	104880	96983 (7.37)	93791 (10.40)	85973 (17.87)	104880	96983 (7.37)	93791 (10.40)	85973 (17.87)
<i>Astrapia splendissima</i>	92970	75033 (19.29)	66234 (28.76)	57967 (37.65)	92970	75033 (19.29)	66234 (28.76)	57967 (37.65)
<i>Clectornis m. agrifolius</i>	349511	345167 (1.24)	343388 (1.75)	345645 (1.11)	240406	237649 (1.15)	236396 (1.67)	237733 (1.11)
<i>Clectornis regius</i>	504891	484822 (3.97)	500982 (0.78)	490428 (2.86)	504891	484822 (3.97)	500982 (0.78)	490428 (2.86)
<i>Epm. achus albertsi</i>	179013	151202 (1.54)	137947 (22.94)	111268 (37.84)	125976	107797 (14.43)	100104 (20.54)	80934 (35.75)
<i>Epm. achus bruijii</i>	46104	21512 (53.34)	6838 (85.17)	10618 (76.97)	46104	21512 (53.34)	6838 (85.17)	10618 (76.97)
<i>Epm. achus fastuosus</i>	191188	135077 (29.35)	117722 (38.40)	102373 (48.46)	138786	100595 (27.52)	89158 (35.76)	77750 (43.98)
<i>Epm. achus meyeri</i>	219913	203839 (7.31)	192457 (12.48)	192661 (12.39)	219913	203839 (7.31)	192457 (12.48)	192661 (12.39)
<i>Lophortyx superba</i>	168865	156351 (7.89)	149545 (11.34)	142141 (15.73)	168865	156351 (7.89)	149545 (11.34)	142141 (15.73)
<i>Manucodia atra</i>	582289	578994 (0.91)	347356 (40.35)	433882 (25.52)	582289	578994 (0.91)	347456 (40.33)	433882 (25.52)
<i>Manucodia jobiensis</i>	113023	54607 (51.69)	23078 (79.58)	22871 (79.94)	71895	34015 (52.69)	14400 (79.97)	14838 (79.22)
<i>Manucodia kerulouffi</i>	479783	452771 (5.63)	336463 (30.08)	381776 (20.43)	317782	379490 (1.87)	233980 (26.37)	258471 (18.66)
<i>Manucodia leucicauda</i>	639442	615323 (3.77)	608178 (4.89)	629443 (1.56)	383182	302306 (4.87)	370279 (3.37)	380488 (0.70)
<i>Paradisaea apoda</i>	68375	43024 (37.08)	27022 (60.48)	19737 (71.13)	47561	29617 (37.73)	20198 (67.53)	14819 (68.84)
<i>Paradisaea brevicauda</i>	103096	71458 (30.69)	75295 (28.97)	54535 (47.10)	103096	71458 (30.69)	75295 (28.97)	54535 (47.10)
<i>Paradisaea carunculata</i>	1997	1437 (28.04)	1407 (29.54)	384 (80.77)	1855	1346 (27.44)	1324 (28.63)	366 (80.27)
<i>Paradisaea guillemii</i>	792	304 (61.62)	230 (70.96)	44 (94.44)	448	166 (62.95)	189 (62.28)	11 (97.54)
<i>Paradisaea minor</i>	360388	344528 (4.40)	268972 (25.37)	278350 (22.76)	360388	344528 (4.40)	268972 (25.37)	278350 (22.76)
<i>Parotis carolae</i>	173908	133198 (23.41)	120613 (30.65)	109662 (39.94)	173908	133198 (23.41)	120613 (30.65)	109662 (39.94)
<i>Parotis helena</i>	22808	15851 (30.50)	13088 (42.70)	5802 (74.56)	18818	13231 (26.69)	10973 (41.69)	4777 (74.61)
<i>Parotis javanica</i>	108989	98434 (8.00)	96420 (9.88)	81934 (23.42)	108989	98434 (8.00)	96420 (9.88)	81934 (23.42)
<i>Parotis seiffersi</i>	11522	6177 (49.39)	6823 (40.78)	4257 (63.05)	11522	6177 (49.39)	6823 (40.78)	4257 (63.05)
<i>Paradisaea raggiana</i>	160780	156815 (12.47)	146915 (8.62)	145320 (9.62)	160780	156815 (12.47)	146915 (8.62)	145320 (9.62)
<i>Paradisaea rufolophi</i>	56757	50755 (10.57)	50621 (10.81)	32997 (41.86)	56757	50755 (10.57)	50621 (10.81)	32997 (41.86)
<i>Ptilinopus alberti</i>	102105	94554 (7.40)	90741 (11.13)	88484 (13.34)	102105	94554 (7.40)	90741 (11.13)	88484 (13.34)
<i>Ptilinopus intercedens</i>	62472	56238 (9.98)	50383 (19.38)	47653 (23.72)	62472	56238 (9.98)	50383 (19.38)	47653 (23.72)
<i>Ptilinopus agrifolius</i>	604126	573550 (5.06)	540662 (10.51)	584205 (3.30)	382445	370886 (3.02)	349252 (8.68)	372161 (2.69)
<i>Ptilinopus perdisseus</i>	61707	40228 (34.81)	28016 (57.84)	34053 (44.82)	61707	40228 (34.81)	28016 (57.84)	34053 (44.82)
<i>Ptilinopus victoriae</i>	21603	13019 (39.74)	14072 (34.86)	11851 (45.14)	21603	13019 (39.74)	14072 (34.86)	11851 (45.14)
<i>Selaeuclidia melanoleuca</i>	385443	301094 (21.88)	173988 (54.94)	161805 (58.02)	253274	200492 (20.84)	117059 (53.78)	109288 (56.85)

Table 1B. Loss of projected species distributional areas under 6 m of sea level rise. Total areal losses are shown here as percentages at different time periods, i.e., areal loss under present projected distributions (current), future projected distributions (2020, 2050, and 2080) and areal loss under projected present (Present FC) and future forest cover (FC\_2020, FC\_2050, and FC\_2080). Dashes (-) indicate no loss of area under sea level rise predictions.

Species	Current	2020	2050	2080	Present FC	FC_2020	FC_2050	FC_2080
<i>Astragale mayeri</i>	-	-	-	-	-	-	-	-
<i>Astragale nigra</i>	-	-	-	-	-	-	-	-
<i>Astragale rotundifolia</i>	15.96	14.79	-	-	15.96	14.79	-	-
<i>Astragale stephaniae</i>	14.18	11.44	10.1	-	14.18	11.44	10.1	-
<i>Ochnopus magnificus</i>	52.93	51.71	51.4	51.76	36.25	35.85	35.65	35.86
<i>Ochnopus regius</i>	62.96	61.26	62.51	61.23	62.94	61.25	62.48	61.21
<i>Epimachus alberti</i>	27.27	23.06	21.04	16.97	19.2	16.44	15.27	12.34
<i>Epimachus brylioni</i>	6.52	3.03	0.99	1.59	6.52	3.03	0.99	1.59
<i>Epimachus fastuosus</i>	29.13	20.6	17.96	15.61	21.15	15.34	13.6	11.86
<i>Epimachus mayeri</i>	33.49	31.08	29.35	29.38	33.49	31.08	29.35	29.38
<i>Lophodina supereba</i>	-	-	-	-	-	-	-	-
<i>Menucco alba</i>	73.61	72.89	49.55	57.9	73.58	72.86	49.55	57.88
<i>Menucco jobeensis</i>	16	8.12	3.46	3.43	10.13	5.06	2.16	2.27
<i>Menucco charjoata</i>	69.75	65.8	50.73	57.16	46.71	44.41	35.46	38.94
<i>Menucco newbouldi</i>	36.07	34.18	34	35.01	21.36	21.18	20.74	21.25
<i>Paradisaea aenea</i>	9.8	6.54	4.12	-	6.84	4.51	-	-
<i>Paradisaea brevicauda</i>	15.71	10.9	11.48	8.32	15.72	10.9	11.48	8.32
<i>Paradisaea cauruculata</i>	-	-	-	-	-	-	-	-
<i>Paradisaea guillemoti</i>	-	-	-	-	-	-	-	-
<i>Paradisaea minor</i>	53.03	50.68	40.28	41.61	53.02	50.67	40.27	41.6
<i>Paradisaea canibe</i>	26.35	20.31	18.39	16.72	26.35	20.31	18.39	16.72
<i>Paradisaea melanae</i>	-	-	-	-	-	-	-	-
<i>Paradisaea lavei</i>	16.29	15.01	14.71	-	16.29	15.01	14.71	-
<i>Paradisaea sentia</i>	-	-	-	-	-	-	-	-
<i>Paradisaea wainae</i>	-	-	-	-	-	-	-	-
<i>Paradisaea reggiana</i>	24.06	23.51	22.24	21.94	24.06	23.51	22.24	21.94
<i>Paradisaea rufopalmi</i>	-	-	-	-	-	-	-	-
<i>Paradisaea alberti</i>	-	-	-	-	-	-	-	-
<i>Ptilotis intercedens</i>	9.37	8.47	7.64	7.18	9.37	0.92	7.65	7.18
<i>Ptilotis magnificus</i>	32.54	30.85	29.93	31.58	20.41	19.89	19.31	20.06
<i>Ptilotis paradisaeus</i>	3.73	2.46	1.58	2.08	3.73	2.46	1.58	2.08
<i>Ptilotis victorae</i>	1.3	0.79	0.85	0.72	1.3	0.79	0.85	0.72
<i>Selaucidia melanocephala</i>	49.62	39.61	26.23	24.3	32.3	26.03	17.69	16.4

### *Ecological niche model--climatic effects*

Under climate changes, BOP species are projected to lose varying amounts of their distributions, and in one case experience extinction, under assumptions of no dispersal. For instance, *Astrapia mayeri*, is projected to lose 34% (5173 km<sup>2</sup>) by 2020, 62% (9484 km<sup>2</sup>) by 2050, and 53% (8098 km<sup>2</sup>) of its distributional area by 2080 (Fig. 3A-D). By 2020, *Astrapia nigra* is projected to experience total loss (100%, 428 km<sup>2</sup> Table 1A), with *Manucodia atra* projected to experience the smallest loss (1%, 5295 km<sup>2</sup>, Table 1A) in distributional area. By 2050, aside from *Astrapia nigra*, *Epimachus bruijnii* and *Cicinnurus regius* are projected to experience the biggest (85%, 39,266 km<sup>2</sup>, Table 1A) and smallest (1%, 3929 km<sup>2</sup>, Table 1A) loss in distributional areas, respectively. Finally by 2080, *Parotia wahnesii* is projected to see the biggest (95%, 1089 km<sup>2</sup>, Table 1A) loss, with *Cicinnurus magnificus* projected to experience the smallest (1%, 3866 km<sup>2</sup>, Table 1A) loss in distributional area.

Taking into account climate change and present land cover, results ranged from large losses (100%) to negligible losses (1%). For instance, by 2050, *Astrapia nigra* is projected to go extinct, *Epimachus bruijnii* is projected to experience the next biggest loss (85%, 39,266 km<sup>2</sup>, Table 1A), with *Cicinnurus regius* projected to experience the smallest loss (1%, 3929 km<sup>2</sup>, Table 1A). By 2080, *Paradiseae guilielmi* is projected

to experience a loss of 98% (437 km<sup>2</sup>, Table 1A) of its distribution, while *Manucodia keraudrenii* will experience the least loss (1%, 2694 km<sup>2</sup>, Table 1A).

#### *Ecological niche model--sea level rise effects*

Under sea level rise predictions, 32% (N = 11) of BOP species will experience no effect of marine intrusion on their distributional areas, such as in *Astrapia mayeri*, *A. nigra*, and *A. rothschildi* (Table 1B). Within present distributional areas, *Manucodia atra* is projected to experience the largest loss (74%, 99,646 km<sup>2</sup>, Table 1B) in its' distributional area to marine intrusion, with *Ptiloris victoriae* projected to experience the smallest loss (1%, 458 km<sup>2</sup>, Table 1B) of its distributional area to marine intrusion. Species that experienced no loss in distributional areas due to marine intrusion generally also experience no loss owing to forest cover (i.e., 32%, N = 11 species). Forest cover marine intrusion losses across BOP species' distributions ranged from 74% to 1% (Table 1B) of present distributional areas.

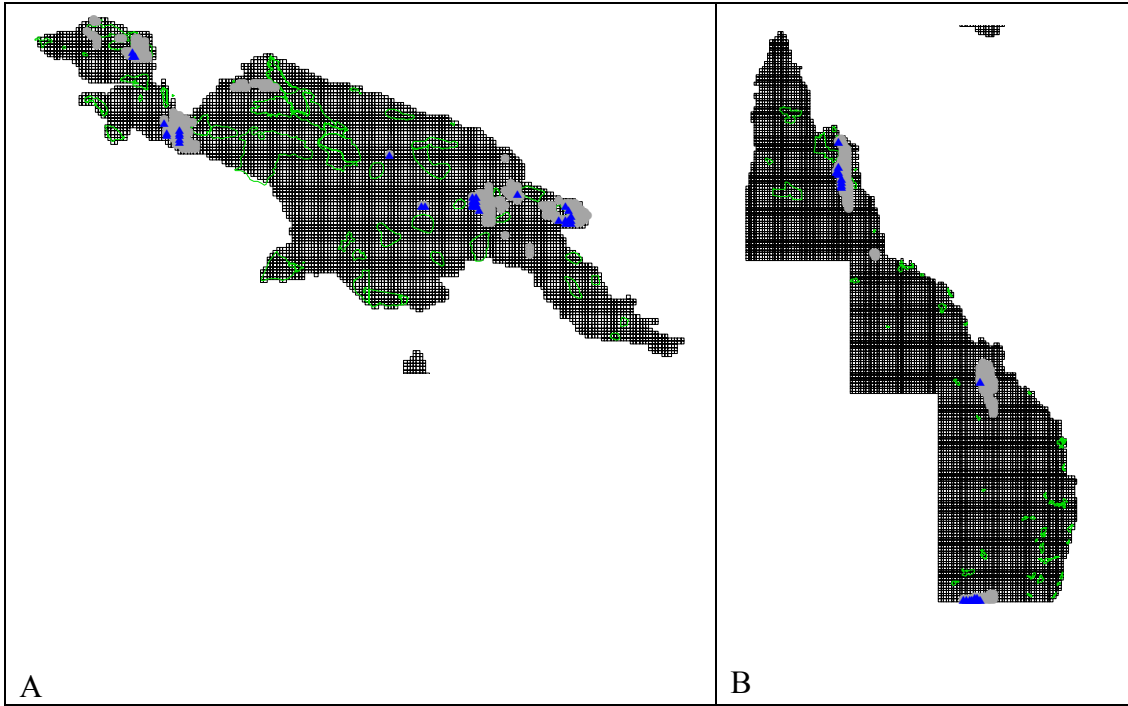
#### *BOP conservation- Place-prioritization*

BOPs distributions overlapped one or more existing protected areas, obviously. Current protected area systems within the study region cover only ~8% (153,141 km<sup>2</sup>) of total area (1,993,077 km<sup>2</sup>), but represented 74% and 100% of BOP species for both BOP occurrence and projected present distributional data respectively. For BOP localities, under a target representing 10% of a species occurrence records, 0.5% (N = 79 prioritized cells, 9976 km<sup>2</sup>) of area was prioritized whereas at a 75% target,

1.2% (N = 190 prioritized cells, 23,993 km<sup>2</sup>; Fig. 4A-C) of area was prioritized.

Using present day distributional data, 0.3% (N = 53 prioritized cells, 6693 km<sup>2</sup>) of distributional area was prioritized under a target representing 10% of a species distribution, while at 75% target scenario; an area covering 3% (N = 406 prioritized cells, 51,2670 km<sup>2</sup>) was prioritized (Fig. 4D-F).

For BOP localities, 10 prioritized cells covering an area of 1230 km<sup>2</sup> are needed to represent all species of BOPs under a 10% target scenario. For a 75% target scenario, 13 (1599 km<sup>2</sup>) prioritized cells are needed to fully represent all species. Under present day distributions, 7 (861 km<sup>2</sup>) prioritized cells are needed to represent all species of BOPs under both 10 and 75% target scenarios.





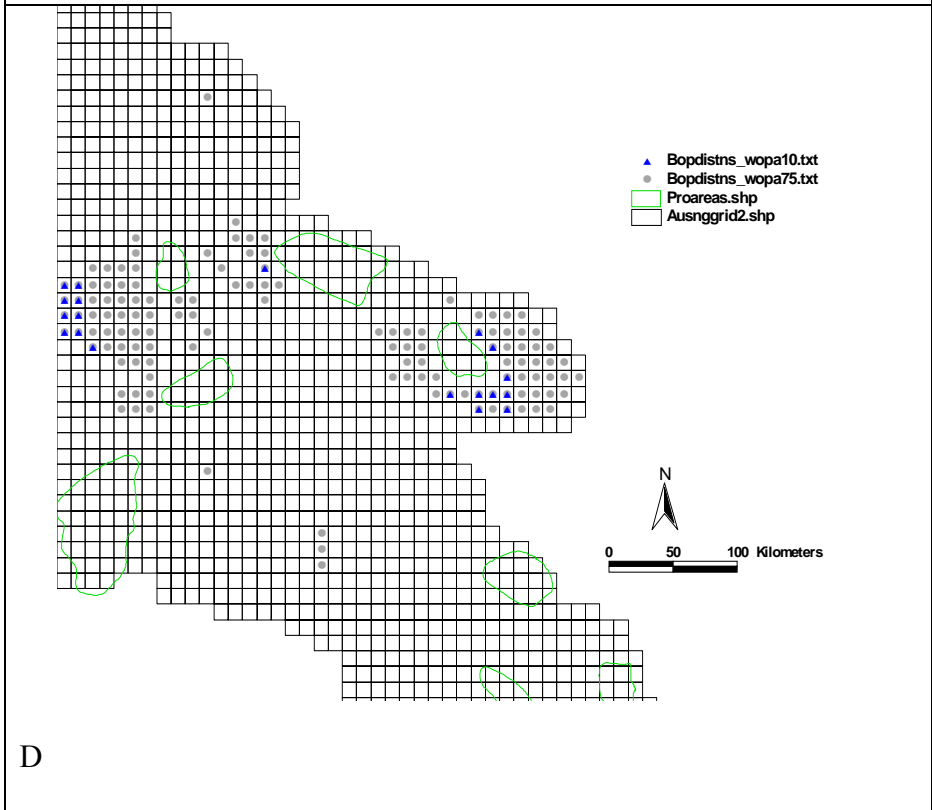
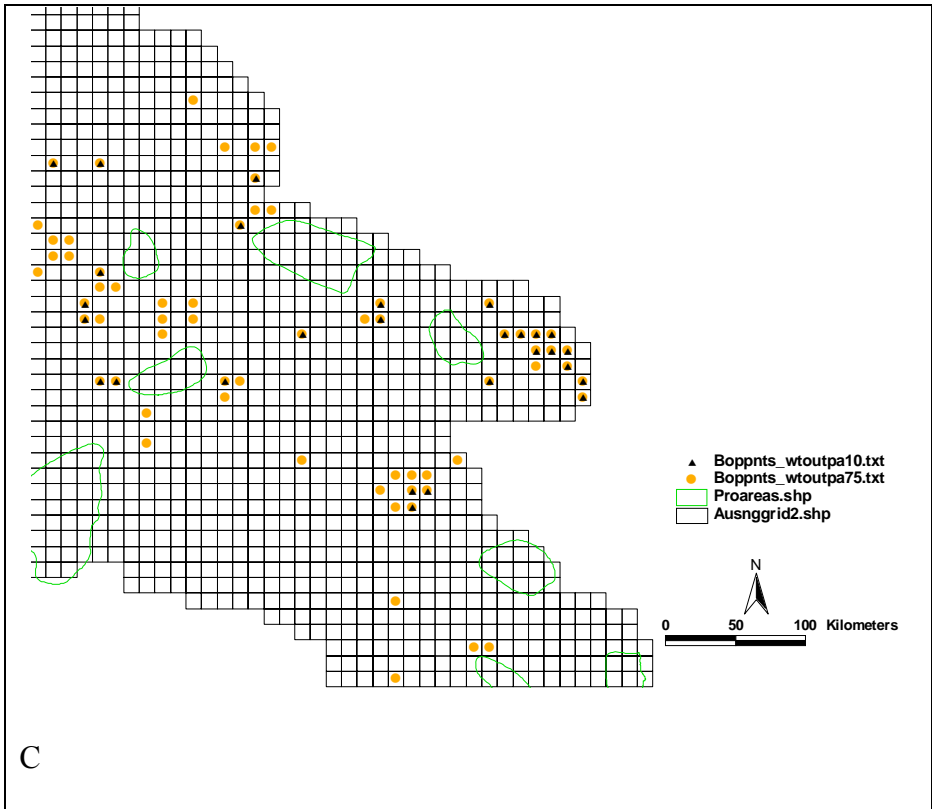


Figure 4. All prioritized cells across BOP distributional areas (A-B). C and D show sections (Huon Peninsula region) of the prioritized cells under 10 and 75% target scenarios. C shows prioritized cells using BOP localities and D shows prioritized cells using BOP distributions. Green polygons show current protected area networks; black triangles (10%) and orange circles (75%) in C show different target scenarios. In D target scenarios are indicated as blue triangles (10%) and gray circles (75%).

## **DISCUSSION**

ENMs have been widely used to map species' distributions (Anderson et al. 2003; Raxworthy et al. 2003; Meynard and Quinn 2007) and predict responses to climatic changes (Pearson and Dawson 2003; Martínez-Meyer 2005; Anciães and Peterson 2006). While ENMs have been widely used (see Phillips et al. 2006 and Phillips and Dudík 2008), applications of ENMs specific to New Guinea are lacking. A factor hindering use of ENMs for New Guinea fauna is the lack of biodiversity datasets that could be used to develop niche models; even if such data do exist, they are not recent or are spread throughout many museums, and are not easily accessible. Secondly environmental layers are often based at global scales and thus reprojecting of environmental layers to specific scales can compromise fine-scale predictability of models (see Pearson and Dawson 2003; Martínez-Meyer 2005 and Phillips and Dudík 2008). Given these caveats, recent efforts to make natural history collections available electronically (see Brooke 2000; Graham et al. 2004) and much higher-resolution environmental datasets (see Pearson and Dawson 2003; Martínez-Meyer

2005), make it possible to do bioinformatics type research on New Guinea flora and fauna.

I present here distributional data for 34 BOP species using ENMs. BOP distributional estimates developed herein complement earlier biogeographic descriptions of BOP distributions. This study also provides clear distributional patterns of species, unlike earlier summaries (see Heads 2001a; 2001b; 2002) that mostly outlined only general patterns. BOPs distributions ranged from narrow, as seen for *Astrapia nigra*, to very large, i.e., spanning the entire island of New Guinea, such as for *Cicinnurus regius*, or both New Guinea and Australia, as seen in *Manucodia atra*. However, for certain species of BOPs, the paucity of recent locality data made validation of species distributional predictions (see Thuiller 2003; Guisan and Thuiller 2005; Phillips et al. 2006) impossible, so certain estimates may not be as accurate as expected (see Anderson and Martínez-Meyer 2004; Martínez-Meyer 2005).

Under climate change effects, BOPs will experience loss of distributional areas, and probable extinction for *Astrapia nigra*. Species such as *Manucodia atra*, *Cicinnurus regius*, and *C. magnificus* are projected to experience smallest losses in distributional areas, while *A. nigra*, *Epimachus bruijnii* and *Parotia wahnesii* are projected to see big losses within their distributional ranges. Taking into account land use change (in the present) and the effects of marine intrusion, BOPs are likely to see further losses in distributional ranges over time.

Prioritization of areas using distributional data can enhance and effectively aid conservation efforts. Here I used BOP distributions and locality data to prioritize cells. Prioritization of cells differed with use of locality or distributional data; i.e., prioritization with locality data required more cells (see Loiselle et al. 2003) to represent all 34 species than prioritizations based on interpolated distributional data. Conservation efforts using as few areas as possible that fully represent a suite of species (Margules et al. 1998; Sarkar et al. 2004); in this case to the extent that my interpolations are correct, the prioritization for BOPs would greatly enhance species conservation across New Guinea, i.e., with few areas conservation of species can be achieved at minimal cost and with a concentrated effort. However due care must be taken in implementing conservation using areas developed under prioritization procedures because prioritization can be affected by the occurrence datasets used in developing distribution models and thus could potentially misdirect conservation action. Prioritization using an array of biodiversity surrogates across New Guinea would greatly improve prioritization efforts, identify gaps in existing networks, and help strengthen existing networks by specifically prioritizing areas that represent a variety of biodiversity surrogates (Pawar et al. 2007; Urquiza-Haas et al. 2009).

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