Vulnerability of megapodes (Megapodiidae, Aves) to climate change and related threats

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SUMMARY

Aspects of species life histories may increase their susceptibility to climate change. Owing to their exclusive reliance on environmental sources of heat for incubation, megapodes may be especially vulnerable. We employed a trait-based vulnerability assessment to weigh their exposure to projected climate variables of increasing temperatures, fluctuating rainfall and sea level rise and their biological sensitivity and capacity to adapt. While all 21 species were predicted to experience at least a 2 °C increase in mean annual temperature, 12 to experience a moderate or greater fluctuation in rainfall and 16 to experience rising seas, the most vulnerable megapodes are intrinsically rare and range restricted. Species that employ microbial decomposition for incubation may have an adaptive advantage over those that do not and may be more resilient to climate change. The moderate microclimate necessary for mound incubation, however, may in some areas be threatened by anthropogenic habitat loss exacerbated by warmer and seasonally drier conditions. As with many avian species, little is known about the capacity of megapodes to adapt to a changing climate. We therefore recommend that future research efforts investigate megapode fecundity, gene flow and genetic connectivity at the population level to better determine their adaptive capacity.

Keywords: Megapodiidae, megapodes, Indo–Pacific, climate change, sea level rise, trait-based vulnerability assessment

INTRODUCTION

Climate change is predicted to have profound consequences for global biodiversity (Dawson *et al.* 2011; Bellard *et al.* 2012; Wetzel *et al.* 2013). While such change is not novel in a geological timeframe, human modification of landscapes is, and this may hinder species' abilities to seek refuge from the results of a changing climate, possibly increasing their risk of extinction (Lovejoy 2008; Taylor & Kumar 2016). Integrating the exposure of landbirds to projected future climate and land-use changes, Jetz *et al.* (2007) estimated that 10–20% of the world's 8750 species would be threatened with extinction by 2100. Species most at risk are relatively sedentary tropical endemics that are confined to restricted ranges such as mountain tops, coastal forests or islands (Jetz *et al.* 2007; Sekercioglu *et al.* 2012). Owing to high rates of endemism, inherent species range restrictions and high vulnerability to stochastic and anthropogenic impacts, terrestrial island biota is perhaps more acutely imperilled by climate change than those of any other ecosystem (Fordham & Brook 2010; Kingsford & Watson 2011; Keppel *et al.* 2012; Harter *et al.* 2015).

Aspects of both a species' life history and ecology can lead them to be disproportionately sensitive to environmental change (Williams *et al.* 2008). Such species may be more vulnerable to and adversely affected by the predicted outcomes (Foden & Young 2016). Many of the 22 species within the avian family Megapodiidae exhibit both life history and ecological traits that may render them particularly susceptible to the adverse effects of climate change. The ground-nesting megapodes are distributed throughout the central Indo–Pacific and Australasia (Fig. 1), where all but two are confined to the tropics, and they occur everywhere from small oceanic islands to large continent-sized landmasses (Jones *et al.* 1995). At least 16 species range well below 2000 m elevation and most utilize moist lowland to montane forest, but some depend on cover types ranging from dry forest to coastal and strand forest in supratidal areas (Jones *et al.* 1995; IUCN 2016). Regardless of where they are found, megapodes are best known for their unique breeding strategy of employing only environmentally derived heat to incubate their eggs as opposed to body heat (Jones *et al.* 1995).

Despite their unique life history traits, megapodes are a comparatively poorly known group that face multiple conservation threats (Jones 1999; IUCN 2016). Half of all species fall within an International Union for the Conservation of Nature (IUCN) Red List category of concern and all but three exhibit declining populations (IUCN 2016). Ten species

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Figure 1 The global distribution of 21 species of megapodes. Dark grey indicates the actual cumulative distribution for all species. For more detail and species-level range descriptions, refer to Jones *et al.* (1995), Harris *et al.* (2014) or IUCN (2016).
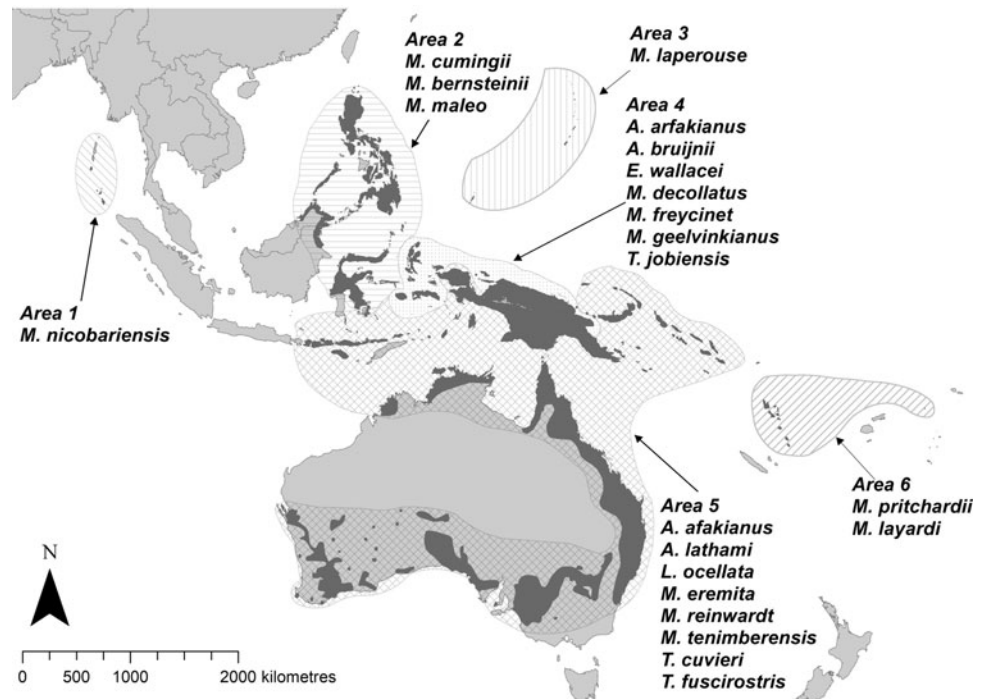
of concern range at least to some extent across relatively small islands and most megapodes are deterministically threatened by hunting, egg collecting, introduced predators and habitat destruction or degradation (Jones *et al.* 1995; IUCN 2016). Only two species are known to be directly threatened by stochastic events including cyclones and possible shifting of geothermal activity rendering incubation sites unusable (IUCN 2016). A major stochastic event not yet adequately quantified for this unique family is climate change (Dekker *et al.* 2000; IUCN 2016). The environmental manifestations of climate change, which could be exacerbated by human activity (Brook *et al.* 2008), may pose serious and exceptional challenges to the productivity of a family of birds that relies directly and exclusively on elements of the environment for reproduction.

Species vulnerability is defined by the Intergovernmental Panel for Climate Change (IPCC 2007) as the 'degree to which a system (or species) is susceptible to, and unable to cope with, adverse effects of climate change, including climate variability and extremes.' Based on a variety of biological and ecological traits, not all species will respond in the same way to climate change (Foden *et al.* 2013; Foden & Young 2016). Here, we employ a trait-based vulnerability assessment (Foden & Young 2016) to investigate the susceptibility of megapodes to potential environmental change caused by predicted increases in temperature, fluctuations in rainfall and sea level rise. We further assess effects of other known extrinsic threats (both anthropogenic and stochastic) to megapodes and any protections afforded by contemporary conservation actions. Lastly, we discuss caveats to our approach and highlight gaps in knowledge that hinder a more effective vulnerability assessment.

METHODS

Study group and geographic range

Megapodes use three biological or environmental sources of heat to incubate their eggs: (1) microbial decomposition of organic matter; (2) volcanic or geothermal activity; and (3) passive solar radiation (Jones *et al.* 1995; Sinclair 2002). This monophyletic family is composed of two clades: 'brush-turkeys' and 'scrubfowl' (Harris *et al.* 2014). Although other taxonomies list 22 species for the family, BirdLife International considers Forsten's megapode (*Megapodius forstenii*) a subspecies of the dusky megapode (*Megapodius freycinet*) (IUCN 2016). As we relied on IUCN data for much of our assessment, we likewise assumed that the two clades together comprise 21 species. Brush-turkeys are relatively sedentary, occur mostly on larger landmasses and exclusively use microbial decomposition to incubate their eggs in mounds made of organic matter (Jones *et al.* 1995). Scrubfowl use all three sources of environmental heat for incubation in both burrows and mounds, many are capable of flying long distances (*Macrocephalon* excluded) and many (particularly *Megapodius*) occur on numerous small and oceanic islands (Jones *et al.* 1995; Harris *et al.* 2014). Together, the megapodes range broadly west to east from the Nicobar Islands in the Indian Ocean to Tonga in the Pacific, and north to south from Uracus in the Northern Mariana archipelago to very southern portions of Australia ([Fig. 1]) (Jones *et al.* 1995).

Trait-based vulnerability assessment

Following the general methodologies of Williams *et al.* (2008), Gardali *et al.* (2012) and Foden *et al.* (2013), we assessed the

Table 1 Criteria for scoring vulnerability to climate change and the level of extrinsic threats and conservation actions for 21 species of megapodes. Scoring measures were used to calculate the level of each category by species based on best fit by individual criterion. The higher the number scored for each criterion, the greater the level of sensitivity, exposure, other threats and conservation actions and the lower the level of adaptive capacity.

	Criteria group	*Criteria*	*Scoring measures*
Sensitivity	Habitat specialization	Habitat plasticity	1 = uses ≥4 cover types, 2 = uses 2–3 cover types, 3 = uses 1 cover type
	Rarity	Population size (no. of individuals)	1 = >100 000, 2 = 30 000–10 ,000, 3 = 10 000–30 000, 4 = <10 000
		Population trend	1 = stable, 2 = declining
	Restricted ranges	Range size (km^2)	1 = >100 000, 2 = 20 000–100 000, 3 = <20 000
		No. of islands or landmasses	1 = >30 or on large landmass, 2 = occurs on 10–30, 3 = occurs on <10
	Incubation strategy	Localized or dispersed	0 = non-colonial, 1 = many smaller colonies, 2 = few large colonies
		Coastal areas	0 = strictly inland, 1 = some coastal, 2 = mostly coastal
		Heat source	0 = only microbial decomposition, 1 = some microbial decomposition, 2 = no microbial decomposition
		Method plasticity	1 = uses all 3 strategies, 2 = uses 2 strategies, 3 = uses only 1 strategy
Adaptive capacity		Extrinsic barriers to dispersal	0 = not isolated, 1 = moderately isolated, 2 = greatly isolated
Exposure	Sea level rise	Inundation threat (to breeding habitat)	0 = not exposed, 1 = minimally exposed, 2 = moderately exposed, 3 = highly exposed
	Change in precipitation	Total annual increase	0 = none, 1 = up to 100 mm increase, 2 = 101–300 mm increase, 3 = >300 mm increase
		Total annual decrease	0 = none, 1 = up to 25-mm decrease, 2 = 26–50-mm decrease, 3 = >50-mm decrease
		Wet season increase	0 = none, 1 = up to 100-mm increase, 2 = 101–200-mm increase, 3 = >200-mm increase
		Wet season decrease	0 = none, 1 = up to 20-mm decrease, 2 = >20-mm decrease
		Dry season increase	0 = none, 1 = up to 20-mm increase, 2 = >20-mm increase
		Dry season decrease	0 = none, 1 = up to 25-mm decrease, 2 = 26–50-mm decrease, 3 = >50-mm decrease
	Change in temperature	Yearly mean increase	0 = none, 1 = up to 1.0 °C increase, 2 = 1.1–2.0 °C increase, 3 = ≥2.1 °C increase
Other extrinsic threats		Introduced predators	0 = none, 1 = minimal threats, 2 = multiple threats
		Anthropogenic	0 = none, 1 = ≤2 threats, 2 = 3–4 threats, 3 = ≥5 threats
		Stochastic	0 = none, 1 = 1 threat, 2 = 2–3 threats
Conservation actions		Current/underway	0 = none, 1 = 1–2 established, 2 = 3–4 established, 3 = 5–6 established
		Proposed	0 = none, 1 = 1–3 actions proposed, 2 = 4–6 actions proposed, 3 = >6 actions proposed

vulnerability of megapodes based on their intrinsic sensitivity to climate change, their extrinsic exposure to its environmental pressures and their ability to adapt to these pressures (i.e., adaptive capacity). Other assessments focus on species that occur well outside our focal region (e.g., Gardali *et al.* 2012), were designed to rank more than one taxonomic group (e.g., Foden *et al.* 2013) or require data that simply are not available for most megapodes (e.g., NatureServe). This results in criteria and ranking schemes that were not entirely useful to us. A small number of our sensitivity and adaptive capacity criteria, however, were adopted from these schemes and modified to meet our needs. Others we developed to reflect the novel and key traits of megapode life history and the smaller

species-level scale of our assessment. In all instances, however, we chose or formulated criteria based on how climate change might affect these specific traits and how species would in turn be affected (Table 1).

To determine and score species sensitivity and adaptive capacity based on our criteria, we drew on published literature on the Megapodiidae (e.g., Dekker *et al.* 2000; Sivakumar & Sankaran 2012) and relied heavily on current data made available by the IUCN (2016). To determine exposure, we used relevant climate data from the IPCC (2014) and the Commonwealth Science and Industrial Research Organisation (CSIRO). We reviewed literature using Web of Science, Scopus and Google Scholar to find published data on

the effects of climate change and sea level rise across the geographic range of the megapodes.

Assessment criteria

To weigh sensitivity, we identified nine biological or ecological traits within four criteria groups relevant to megapodes: habitat specialization, species rarity, restricted ranges and incubation strategy. We assessed and scored species for these criteria with various measures (Table 1). Habitat specialists tend to be more sensitive to environmental perturbations than generalists (Jiguet *et al.* 2007). We scored specialization based on a list of 16 habitat cover types provided by the IUCN (2016) known to be suitable for megapode breeding and foraging. Scoring species rarity was based on IUCN (2016)-determined population size and stability for each, assuming that vulnerability was greater for smaller and declining populations (Foden *et al.* 2013). For restricted ranges, we scored species based on overall range size and the number islands or landmasses (representing discreet populations) on which each occur, assuming that inhabiting smaller ranges that encompass fewer small landmasses increased vulnerability (Jetz *et al.* 2007). We scored incubation strategy for species by the proximity of their incubation sites to coastal areas, which would most likely be affected by even the current conservative estimates of sea level rise (Church *et al.* 2013). We further scored species by their tendency to breed in a colonial or aggregated manner, assuming this would incur greater climate vulnerability (e.g., Barve *et al.* 2012) than breeding in a more dispersed nature. We lastly scored species by their use of microbial decomposition for incubation and their incubation method plasticity or their ability to employ more than one method across their range. We assumed that less reliance on microbial decomposition and less incubation method plasticity would increase vulnerability for species predicted to experience warmer and seasonally drier climatic conditions caused by climate change.

Adult dispersal ability served as the sole criterion to define adaptive capacity and we scored species following the measures in Table 1. Most island species of megapodes are known to have the ability to disperse over water, while those occurring on large landmasses do not need to disperse by flying (Jones *et al.* 1995). To account for their dispersal ability, we therefore scored species by their relative isolation to reflect the existence of extrinsic barriers to dispersal (Table 1). Species occurring on larger landmasses were thus not considered isolated, while those on small islands were and their level of isolation was determined by the relative proximity and number of landmasses potentially within reach.

We identified change in temperature, change in precipitation and sea level rise as criteria groups to assess climate exposure of megapodes and scored species by the measures in Table 1. We calculated values for mean annual temperature, total annual precipitation and wet and dry season precipitation based on data extracted from CSIRO's ACCESS 1.0 model (Bi *et al.* 2013), the University of Tokyo's National

Institute for Environmental Studies MIROC 5 model (Watanabe *et al.* 2011) and the Met Office Hadley Centre's HadGEM2-AO model (Baek *et al.* 2013). Models were accessed from the WorldClim website (www.worldclim.org) at 30-second resolution. They were selected for their rigorous construction and testing and their cumulative fit to the most likely climate change scenarios for the Indo–Pacific and Australasia (Baek *et al.* 2013; CSIRO and Bureau of Meteorology 2015).

Bioclimatic data were extracted at 79 reference points that were layered over climate models in ArcGIS (ESRI 2015). To create these points, spatial data acquired from the IUCN (2016) for each megapode species were layered over an Environmental Systems Research Institute (ESRI) world base-map. A data layer was built by distributing points at 200–400-km intervals across the range of each species, taking into account the size of their ranges; those that covered larger areas received more points than those that occurred on small islands, which generally received only one point. This layer was then placed over baseline bioclimatic projections and future climate scenarios for all three climate models. Climate change variables were extracted from Representative Concentration Pathway (RCP) 8.5 emission scenarios from projections for 2070. To assess the increase in temperature and level of change and fluctuation in precipitation by 2070, four categories of bioclimatic variables were used for extraction: 'yearly mean temperature', 'annual precipitation', 'precipitation at wettest quarter' and 'precipitation at driest quarter' (Booth *et al.* 2014). Data extracted from baseline projections (taken from 1980–2000 climate averages) were subtracted from the 2070 bioclimatic data, yielding change values by category for each climate model. These values were then summed and averaged to produce the change values for temperature and precipitation we used for each reference point across species ranges. Values from all points within each species' range ($\bar{x}$ = 5.05 points per species, range = 1–20) were averaged to provide a mean level of change each species is predicted to experience by at least 2070. For the purpose of scoring species, those predicted to experience greater levels of change in local climate variables were considered more highly exposed (Table 1).

Sea level rise is complex and involves many uncertainties at the local level (Church *et al.* 2013). We therefore scored megapodes based on their primary breeding habitat, where areas more likely to be affected by rising seas served as proxies for high exposure (Foden *et al.* 2013).

Quantifying vulnerability and assessing added stressors to climate change

We quantified vulnerability for each species by multiplying the sum scores across criteria for sensitivity and adaptive capacity with those of exposure (Gardali *et al.* 2012) to produce an index, with higher scores signifying increased vulnerability. To illustrate the effect of added stressors to climate change, we scored megapodes by the effects of all known anthropogenic and non–climate change–related

Table 2 Climate change sensitivity (S), adaptive capacity (AC) and exposure (E) points accrued (out of a total of 24, 2 and 22 possible, respectively), vulnerability scores and ranking for 21 species megapodes. Vulnerability scores were calculated as (S + AC) × E. Climate change vulnerability is compared with the degree of other known threats (both anthropogenic and stochastic) and level of conservation actions taken for individual species.

Common name	Scientific name	S	AC	E	Vulnerability score	Other threats	Conservation actions
Nicobar megapode[a]	*Megapodius nicobariensis*	20	1	13	273	Many	Many
Moluccan megapode	*Eulipoa wallacei*	18	1	10	190	Many	Moderate
Vanuatu megapode[a]	*Megapodius layardi*	17	2	10	190	Many	Moderate
Waigeo brush-turkey[a]	*Aepypodius bruijnii*	17	1	10	180	Many	Moderate
Polynesian megapode[a]	*Megapodius pritchardii*	20	2	7	154	Few	Few
Melanesian megapode	*Megapodius eremita*	13	1	11	154	Few	Few
Micronesian megapode[a]	*Megapodius laperouse*	15	2	9	153	Many	Many
Tanimbar megapode[a]	*Megapodius tenimberensis*	17	1	8	144	Few	Few
Sula megapode[a]	*Megapodius bernsteinii*	13	1	10	140	Many	Few
Maleo	*Macrocephalon maleo*	16	1	8	136	Many	Many
Biak megapode[a,b]	*Megapodius geelvinkianus*	12	1	9	117	Few	Few
Dusky megapode	*Megapodius freycinet*	12	1	8	104	Unknown	None
Wattled brush-turkey	*Aepypodius arfakianus*	10	0	10	100	Few	Few
New Guinea megapode	*Megapodius decollatus*	9	0	10	90	Unknown	None
Collared brush-turkey	*Talegalla jobiensis*	10	0	9	90	Unknown	Few
Red-billed brush-turkey	*Talegalla cuvieri*	11	0	8	88	Few	Few
Australian brush-turkey	*Alectura lathami*	9	0	8	72	Few	Few
Black-billed brush-turkey	*Talegalla fuscirostris*	9	0	8	72	Unknown	Few
Malleefowl	*Leipoa ocellata*	9	1	7	70	Many	Many
Philippine megapode	*Megapodius cumingii*	10	0	7	70	Moderate	Moderate
Orange-footed megapode	*Megapodius reinwardt*	9	0	7	63	Unknown	None

[a] Species that are confined to small islands with ranges under 20 000 km^2 (Table 1).

[b] Species for which data are deficient.

stochastic threats faced by each (Table 1) (IUCN 2016). To reflect possible mitigation of these stressors, we additionally scored for all current and planned conservation actions intended as megapode protection throughout their ranges (Table 1) (IUCN 2016). These two categories were scored separately from vulnerability and assigned ranks. The level of both other extrinsic threats and conservation actions were ranked by species as 'many', 'moderate' or 'few' based on the total points accrued by scoring. Under both categories, 'many' was assigned to species that scored from five to seven points, 'moderate' for those that scored three to four points and 'few' for those that scored one to two points.

RESULTS

The Nicobar (*Megapodius nicobariensis*), Moluccan (*Eulipoa wallacei*) and Vanuatu (*Megapodius layardi*) megapodes and the Waigeo (or Bruijn's) brush-turkey (*Aepypodius bruijnii*) were ranked most vulnerable to climate change, while the orange-footed (*Megapodius reinwardt*) and Philippine (*Megapodius cumingii*) megapodes, malleefowl (*Leipoa ocellata*) and black-billed (*Talegalla fuscirostris*) and Australian (*Alectura lathami*) brush-turkeys were ranked least vulnerable (Table 2). Sensitivity was the most important factor contributing to the vulnerability of seven species and played the largest role in the susceptibility of the Waigeo brush-

turkey and the Polynesian (*Megapodius pritchardii*) and Tanimbar (*Megapodius tenimberensis*) megapodes (Fig. 2). The two most important criteria groups under this category were species rarity and range restrictedness, ranking high for eight and seven species, respectively (Table 3). Exposure was the most important factor for the remaining species and played an important role in the vulnerability of only the black-billed brush-turkey (Fig. 2).

The most pertinent of the three exposure criteria groups was temperature change, which increased for all species and scored 98.4% of available points, followed by sea level rise (43.3%) and precipitation change (29.5%). The individual exposure criterion (Table 1) that scored highest was increase in yearly mean temperature followed by increases in wet season and total annual precipitation, respectively. The sensitivity criteria group that contributed most to vulnerability was species rarity (scoring 66.7% of points), for which 12 species ranked at least moderate to high (Table 3). Ten of these ranked at least moderate to high for restricted ranges (Table 3), the second most important sensitivity criteria group scoring 60.3% of available points, which was followed by habitat specialization (scoring 58.7%). The individual sensitivity criteria (Table 1) that scored highest were, in descending order, nesting plasticity, population size, range size and population status. Quantitatively, adaptive capacity had little influence on the vulnerability ranking of megapodes (Fig. 2).

Figure 2 Comparison of the effects of species sensitivity, adaptive capacity, and exposure in our assessment of the vulnerability to climate change across 21 species of megapodes. Values reflect the average of scores across individual criteria within criteria groups for each category.
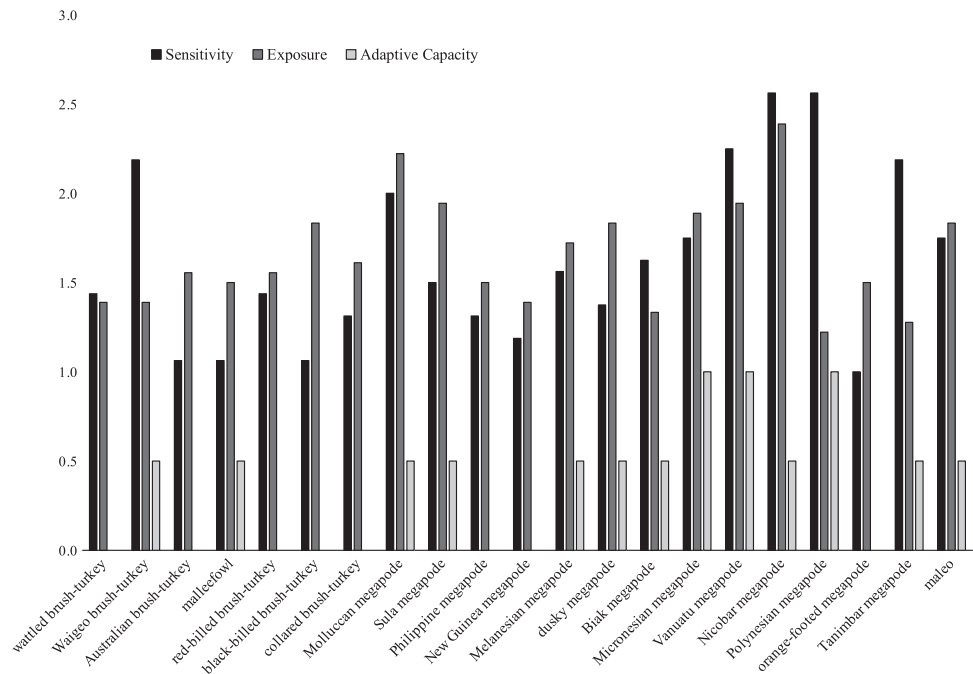
Extrinsic barriers to dispersal exist for 12 of the species, of which one brush-turkey and three scrubfowl were determined to be highly isolated (Table 3).

Comparing across species, our assessment suggests that the most important exposure criterion is annual mean temperature increase (range = 2.0–3.0, RCP 8.5) by 2070. All but the Polynesian megapode were predicted to experience a temperature increase of ≥2.1 °C (Table 3), a level of increase over baseline that served as the highest score for this criterion. Sixteen species will be exposed to rising sea levels, eight of which will be at least moderately affected (Table 3). Both the Moluccan and Nicobar megapodes will be the most vulnerable to inundation (Table 3). While 15 species will be exposed to an increase in mean annual rainfall, seven of these will also experience at least a moderate decease in dry season rainfall, resulting in increased seasonality in precipitation (Table 3) characterized by longer and more intense dry seasons. The wattled brush-turkey (*Aepypodius arfakianus*) and New Guinea megapode (*Megapodius decollatus*) will experience the highest average increase in annual rainfall over baseline (range = 27.8–395.9 mm, RCP 8.5), while the Tanimbar megapode will be exposed to the greatest average decrease (range = –21.2 to –157.3 mm, RCP 8.5). In terms of sensitivity to climate change, the Nicobar and Polynesian megapodes both scored highest in our assessment and received the most points possible for three of four categories: habitat specialization, rarity and range restriction (Table 3). The Biak (*Megapodius geelvinkianus*) and Tanimbar megapodes and the Waigeo brush-turkey proved to be equally range restricted, with the latter two likewise receiving the most points possible for rarity (Table 3).

Comparing between clades, scrubfowl accrued 59.8% of available points for sensitivity and the brush-turkeys 44.7%, a difference that was statistically significant (*t*-test, $p = 0.026$). Within sensitivity, points accrued by scrubfowl for rarity were likewise not significantly different from those acquired by brush-turkeys (71.4% and 57.1%, respectively). Scrubfowl did, however, accrue significantly ($p = 0.045$) more points for restricted ranges (69.0% vs. 42.9%). Comparing exposure by clade shows no significance ($p > 0.05$) in points accrued, with scrubfowl securing 41.2% of available points and the brush-turkeys 38.9%.

Eight megapodes were determined to be subject to many extrinsic threats (Table 2). Four of these were protected, or proposed to be protected, by many conservation actions, while 13 others were protected by few or none (Table 2). Seven species were scored as experiencing few extrinsic threats, one a moderate level, and threats to the remaining five were either unknown or not reported by IUCN (2016) (Table 2). Three of these latter species were protected by no conservation measures.

DISCUSSION

Our results suggest that most megapodes are at least moderately vulnerable to current projections of future climate change. While sea level rise may pose a threat to two species, all will be exposed to an increase in temperature of at least 2 °C over baseline projections and most will be subjected to fluctuations in average annual and seasonal rainfall. Many species are intrinsically rare (Table 3), which may increase their susceptibility to both stochastic and anthropogenic

Table 3 Comparison of the effect of climate change, by category, across 21 species of megapodes. All ranks (H = high, M/H = moderate to high, M = moderate, L = low) are based on the percentage of points scored for each species per category out of the total available and reflect the level of exposure, sensitivity and adaptive capacity as scored for criteria under each in Table 1. Data deficiency is indicated by 'dd' and a null value is indicated by '–'.

| | Sensitivity | | | | Adaptive capacity | Exposure | | | | | | | |
| | | | | | | | | Increased rainfall | | | Decreased rainfall | | |
	Habitat specialist	Rarity	Restricted ranges	Incubation strategy	Dispersal barriers	Sea level rise	Annual	Wet season	Dry season	Annual	Wet season	Dry season	Increased temperature
Brush-turkeys													
A. arfakianus	H	L	L	L[a]	–	–	H	M	H	–	–	–	H
A. bruijnii	M/H	H	H	L[a]	M	–	M	M	–	–	–	H	H
A. lathami	L	M	L	L[a]	–	L	–	L	–	M	–	L	H
L. ocellata	L	M	L	L	M	L	–	–	–	L	M	L	H
T. cuvieri	M/H	M/H	L	L[a]	–	L	M	L	M	–	–	–	H
T. fuscirostris	L	M	L	L[a]	–	M/H	L	L	–	–	–	L	H
T. jobiensis	M/H	M	L	L[a]	–	L	M	M	M	–	–	–	H
Scrubfowl													
E. wallacei	M/H	M/H	M/H	H	M	H	–	–	–	M	M	L	H
M. bernsteinii	L	M/H	M/H	M[a]	M	M/H	–	L	–	M	–	M	H
M. cumingii	M/H	M	L	L	–	L	M	L	–	–	–	–	H
M. decollatus	M/H	L	M	L[a]	–	–	H	M	H	–	–	–	H
M. eremita	M/H	M	M	M	M	L	M	M	–	–	–	H	H
M. freycinet	L	M/H	M	M[a]	M	M/H	L	L	–	–	–	L	H
M. geelvinkianus	L	H	H	dd	M	dd	M	M	–	–	–	M	H
M. laperouse	L	H	H	M	H	M/H	M	M	–	–	–	–	H
M. layardi	H	H	H	M	H	M/H	L	M	–	–	–	M	H
M. nicobariensis	H	H	H	M[a]	M	H	M	H	–	–	–	M	H
M. pritchardii	H	H	H	M	H	L	L	L	–	–	–	M	M/H
M. reinwardt	L	L	L	M[a]	–	L	–	L	–	L	–	L	H
M. tenimberensis	M/H	H	H	L[a]	M	–	–	L	M	H	–	–	H
M. maleo	L	H	M/H	M	M	M/H	L	L	–	–	–	L	H

[a] Species that rely exclusively on microbial decomposition and on one incubation strategy.

threats (Simberloff 2000). Our results further suggest that scrubfowl may be more sensitive to climate change than brush-turkeys, owing not only to their rarity, but perhaps more so to their relatively restricted ranges. Excepting the Moluccan and Melanesian (*Megapodius eremita*) megapodes, seven of the top nine most climate-sensitive species (Table 2) are confined to ranges of less than 6500 km^2 (range = 70−6452 km^2) (IUCN 2016). All of these are scrubfowl, aside for the Waigeo brush-turkey, another range-restricted species. The four most vulnerable megapodes (Table 2) are additionally subjected to many other extrinsic, primarily anthropogenic threats, which may amplify the effects of climate change (Brook *et al.* 2008). Regardless of their apparent ability to fly long distances over water, scrubfowl face the greatest barriers to dispersal, with all but three ranked as at least moderately isolated (Table 3). Although over-water dispersal is apparently lacking for the brush-turkeys (Harris *et al.* 2014), the majority may have the option of dispersing by foot or relatively short over-land flights to higher elevations (Tingley *et al.* 2012).

Other tropical island landbirds show a similar vulnerability to climate change with increasing rarity and range restriction (Taylor & Kumar 2016). These species will also be exposed to many of the same climate change-induced environmental pressures as megapodes (Sekercioglu *et al.* 2012) and face similar extrinsic threats (Hughes 2017). One trait, however, may make megapodes uniquely vulnerable to climate change, namely their evolutionary strategy of relying solely on environmental sources of heat to incubate their eggs (Jones *et al.* 1995).

The majority of megapodes (62%) rely exclusively on microbial decomposition for a heat source, particularly brush-turkeys, which are strict mound builders. All but three species of megapodes included in our assessment employ microbial decomposition as at least one incubation strategy (Jones *et al.* 1995). Findings for three mound building species in New Guinea suggest that megapodes construct mounds that maintain stable core temperatures regardless of ambient air temperatures (Sinclair 2001). Malleefowl are known to possess the ability to actively regulate the temperature of their mounds during incubation, and evidence suggests that other species may do likewise (Jones *et al.* 1995; Sinclair 2001). Findings for the Australian brush-turkey additionally suggest that megapode embryos can withstand temperature fluctuations of 6 °C above and 9 °C below optimal incubation temperatures (34 °C) for extended periods (Eiby & Booth 2008). Species that rely on microbial decomposition, therefore, may be at a greater adaptive advantage than those that do not in the context of increasing temperatures and changes in rainfall.

Mound-building megapodes occur predominantly in moist montane or lowland forests (Jones *et al.* 1995). These species tend to select incubation sites with densely closed canopies, readily available sources of fine organic matter and a thermally stable sub-canopy microclimate that facilitates vegetative decomposition and requires relatively little effort to maintain proper incubation temperatures (Jones *et al.* 1995;

Sinclair 2002; Sinclair *et al.* 2002). The overall increase in warmth and moisture predicted for the Indo-Pacific and Australasia as a result of climate change (Collins *et al.* 2013) would likely lead to an increase in forest biomass and organic matter for mound incubation. Synergies between increased temperatures, seasonal fluctuations in rainfall and contemporary human forestry practices, however, may limit the future availability of these habitat elements and increase the vulnerability of those species that rely on them (Jetz *et al.* 2007; Brook *et al.* 2008).

Indonesia, the Philippines and Timor-Leste experience some of the world's highest rates of deforestation (Sodhi *et al.* 2010) and support populations of 13 megapode species (Fig. 1), ten of which are at least moderately vulnerable to climate change (Table 2). Ten species in this region are mound builders that rely on microbial decomposition (Table 3) (Jones *et al.* 1995). Our study assessed vulnerability based on exposure variables averaged across species ranges and does not fully reflect the decreased rainfall some local populations of more broadly ranging species may be subjected to (Collins *et al.* 2013). For areas predicted to experience more seasonal rainfall, with increased wet and decreased dry season precipitation (Table 3), moisture may fall rapidly in intense storms, leading to greater runoff and dryer soil conditions overall (Trenberth 2011). Given their reliance on rainfall to initiate microbial decomposition, mound-building species in some areas would likely need to shift their breeding seasons in response to an increase in rainfall seasonality (Jones *et al.* 1995; Imansyah *et al.* 2009). Ultimately, however, a trend towards hotter and seasonally drier conditions, coupled with regionally ubiquitous human-ignited wildfires, may exacerbate loss of habitat and essential biomass (Cochrane 2003; Brodie *et al.* 2012; Diffenbaugh & Giorgi 2012). Where ecosystems are not entirely devastated, the moderate and stable microclimate necessary for megapode breeding may be drastically modified to one that is far hotter and drier (Cochrane 2003; Brodie *et al.* 2012), rendering affected areas unconducive to mound incubation.

Three species of megapodes in the Pacific south of the equator (Fig. 1) are likewise predicted to face a warmer climate with more seasonality in rainfall (Widlansky *et al.* 2013). For reasons similar to those that affect mound-nesting species faced with habitat loss in Indonesia, the mound-nesting Vanuatu megapode may potentially be the most vulnerable to these changes (O'Brien *et al.* 2003). Fluctuations in rainfall, however, may have consequences for the productivity and adult apparent survival of other endemic landbirds throughout the tropical Pacific (Saracco *et al.* 2016).

Some criteria groups employed in our assessment under sensitivity and exposure contain more criteria and scoring measures than others and may add more to sum scores for each species (e.g., under change in precipitation, Table 2). Given that the total points possible for sensitivity and exposure (24 and 22, respectively) were quite close and that all species were weighed by these criteria, we felt that this was not a particular concern. Ultimately, we focused on cumulative scores for

species and judged it important to include the criteria we did in order to reflect the potential effects of various climate change scenarios.

One caveat of our assessment is the relatively course nature of extraction of bioclimatic data from the climate models we used to calculate exposure change values. Increasing the number of reference points for data extraction would increase the accuracy of mean estimates for temperature increases and changes in annual and seasonal precipitation. Our change value calculations, however, adequately and appropriately fit the trends predicted for the Indo-Pacific and Australasia by the IPCC (Collins *et al.* 2013). Likewise, our approach to assessing the effect of sea level rise on species tends to assume that coastal breeding areas for some species are fixed and does not take into account the shift and replacement of habitat that may be possible for some species during the relatively slow inundation of ocean waters.

Knowledge gaps and research priorities

Little is known about the nesting and habitat preferences of the Biak megapode, and some ecological data are lacking for the dusky, Sula (*Megapodius bernsteinii*), Vanuatu and Tanimbar megapodes. In some instances, this reduced our ability to score their vulnerability (Table 2). Molecular life history data are lacking altogether for some species, precluding us from assessing evolvability in terms of adapting to climate change (Foden & Young 2016). We suggest future research places an emphasis on: (1) megapode habitat use and ecology, including recruitment, survival and dispersal; and (2) gene flow and genetic connectivity at the population level to identify bottlenecks and other anomalies that lower evolvability (Jones 1999). Although investigations of megapode fecundity are challenging (Jones *et al.* 1995), studies regarding the output, speed and success of reproduction should be pursued; the findings would serve as indirect measures of evolvability that could enhance molecular findings and indicate the rate at which advantageous novel genotypes are added to and accrued within sensitive populations (Foden & Young 2016).

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