

# An ecological regime shift resulting from disrupted predator–prey interactions in Holocene Australia

THOMAS A. A. PROWSE,<sup>1,4</sup> CHRISTOPHER N. JOHNSON,<sup>2</sup> COREY J. A. BRADSHAW,<sup>1,3</sup> AND BARRY W. BROOK<sup>1</sup>

<sup>1</sup>The Environment Institute and School of Earth and Environmental Science, University of Adelaide, Adelaide, South Australia 5005 Australia

<sup>2</sup>School of Zoology, University of Tasmania, Hobart, Tasmania 7005 Australia

<sup>3</sup>South Australian Research and Development Institute, P.O. Box 120, Henley Beach, South Australia 5022 Australia

**Abstract.** The mass extinction events during human prehistory are striking examples of ecological regime shifts, the causes of which are still hotly debated. In Australia, human arrival approximately 50 thousand years ago was associated with the continental-scale extinction of numerous marsupial megafauna species and a permanent change in vegetation structure. An alternative stable state persisted until a second regime shift occurred during the late Holocene, when the largest two remaining marsupial carnivores, the thylacine and devil, disappeared from mainland Australia. These extinctions have been widely attributed to the human-assisted invasion of a competing predator, the dingo. In this unusual case, the simultaneous effects of human “intensification” (population growth and technological advances) and climate change (particularly increased ENSO variability) have been largely overlooked. We developed a dynamic model system capable of simulating the complex interactions between the main predators (humans, thylacines, devils, dingoes) and their marsupial prey (macropods), which we coupled with reconstructions of human population growth and climate change for late-Holocene Australia. Because the strength of important interspecific interactions cannot be estimated directly, we used detailed scenario testing and sensitivity analysis to identify robust model outcomes and investigate competing explanations for the Holocene regime shift. This approach identified human intensification as the most probable cause, while also demonstrating the potential importance of synergies with the effects of climate change. Our models indicate that the prehistoric impact of humans on Australian mammals was not limited to the late Pleistocene (i.e., the megafaunal extinctions) but extended into the late Holocene.

**Key words:** Australia; climate change; Holocene extinction; human intensification; kangaroos; marsupials; megafauna; paleoecology; regime shift; Tasmanian devil; thylacines.

## INTRODUCTION

Regime shifts can occur in ecological systems when the modification or addition of a single component results in fundamental changes to core ecosystem functions and processes, causing the transition to alternative stable states (Scheffer et al. 2001, Folke et al. 2004, Anderson et al. 2009). Contemporary regime shifts have been triggered by human-driven perturbations, including the overharvesting and suppression of important predators (Edmunds and Carpenter 2001), the introduction of invasive species (Nicholls 2011), and climate disruption (deYoung et al. 2008). Perhaps the most striking examples of ecological regime shifts are the mass extinction events of human prehistory, the causes of which are still hotly debated (Prideaux et al. 2007, Roberts and Brook 2010, Lorenzen et al. 2011).

In Australia, most recent evidence implicates the arrival of humans with the continental-scale extinction of about 50 large mammal species by 45 thousand years

ago (Prideaux et al. 2007, Prideaux et al. 2010, Roberts and Brook 2010). Prehistoric human hunting probably threatened the viability of large herbivores (Roberts and Brook 2010), with the resulting trophic cascades possibly contributing to the extinction of top marsupial predators and causing an irreversible change in the structure of the dominant vegetation (Folke et al. 2004, Rule et al. 2012). The ensuing alternative stable state consisted of a depauperate predator guild dominated by thylacines (marsupial “tigers” or “wolves,” *Thylacinus cynocephalus*) and devils (*Sarcophilus harrisii*). The thylacine was a medium-sized (~20 kg) predator that was specialized for consuming freshly killed vertebrate prey, whereas the devil was smaller (~8 kg) and took live prey but was also specialized for scavenging the carcasses of large vertebrates (Jones and Stoddart 1998, Lachish et al. 2009).

It has been commonly assumed, but never established, that a subsequent regime shift was triggered in the late Holocene by the invasion of the dingo (*Canis lupus dingo*), an early domesticated dog from Asia (Corbett 1995, Johnson and Wroe 2003). Dingoes were introduced by humans into northern Australia about 4000

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Corresponding Editor: F. A. Smith.

<sup>4</sup> E-mail: thomas.prowse@adelaide.edu.au

years before present (yr BP), after which they spread rapidly throughout the Australian mainland (Savolainen et al. 2004, Johnson 2006). Thylacines and devils apparently disappeared soon afterward—the latest reliable radiocarbon dates for mainland fossils of these species are approximately 3400 and 3100 yr BP, respectively (Brown 2006, Johnson 2006). The demise of these specialist predators left dingoes (generalist predators) and humans (versatile omnivores) as the only mainland predators capable of hunting large herbivore prey. Thylacines and devils persisted on the island of Tasmania, which was never colonized by dingoes due to its isolation following late-Pleistocene sea-level rise, although thylacines also went extinct there in the early 1900s (Prowse et al. 2013).

Although this circumstantial evidence implicates the dingo invasion in the Holocene regime shift on the mainland, climate change and human “intensification” (i.e., human population growth and technological advances on the mainland) provide two alternative (or synergistic) explanations (Lourandos 1997, Johnson and Wroe 2003, Brown 2006). Following the relatively wet and stable climate of the Holocene optimum (~8000–5000 yr BP), orbitally forced changes in solar irradiance strengthened the El Niño–Southern Oscillation (ENSO) and Australia’s climate shifted to a drier, more El Niño-dominated state, with current conditions setting in about 2000 yr BP (Donders et al. 2008). Human population growth during the Holocene, particularly after 4000 yr BP, has been inferred from archaeological rock-shelter records from different regions of mainland Australia (Ross 1985, Lourandos 1997, Lourandos and David 2002). Although taphonomic (decay process) biases complicate the interpretation of such trends, recent treatments conclude that there is strong evidence for a broadscale increase in human occupation intensity through the Holocene (Johnson and Brook 2011, Williams 2012). Johnson and Brook (2011) demonstrated that, after removing preservation biases, a threefold increase in human population growth after 5000 yr BP best accounts for the observed increase in the number of occupied rock-shelter sites.

Ecological regime shifts (including loss of species) can be triggered by slowly changing variables once a threshold is exceeded (Anderson et al. 2009, Takimoto 2009), and the viability of thylacines and devils on the Australian mainland might have been compromised once human density surpassed such a threshold. However, most analyses of the mainland thylacine and devil extinctions to date have focused on the potentially negative influence of dingoes through exploitation competition (competition for prey) and interference competition (time wasted on interspecific interactions), as well as direct predation by dingoes on the native carnivores (Corbett 1995, Johnson 2006, Fillios et al. 2010). Greater development of cooperative hunting and territorial behavior, together with a semi-

commensal relationship with humans, might have given dingoes an advantage in some or all of these interactions (Corbett 1995, Johnson and Wroe 2003, Johnson 2006). However, humans also competed with and hunted the native carnivores (Marshall and Corruccini 1978, Flannery 1994, Flood 1995, Paddle 2000), and these pressures would have strengthened as the human population grew. Increased ENSO variability after 5000 yr BP probably modified all of these interactions, for instance by causing boom-and-bust dynamics in vegetation and herbivore populations (Brown 2006, Letnic and Dickman 2006).

Combining ecological theory with simulation models provides the tools with which to explore these prehistoric interspecific interactions and population processes (Choquenot and Bowman 1998, Holdaway and Jacomb 2000), and to evaluate their potential additive and synergistic effects on thylacine and devil populations. To this end, we constructed a complex model system to recreate the dynamic interaction between the postulated extinction drivers (dingoes, climate, and humans), the long-term response of macropod prey, and the viability of thylacine and devil populations, between 5000 yr BP and the arrival of Europeans (~200 years before present). We designed our model structure to incorporate the key stressors that are implicated in the Holocene extinctions by accommodating top-down ecological processes resulting from predatory interactions and competition between predators, and the bottom-up influence of climate on vegetation and prey population dynamics. Because the strength of important interspecific interactions cannot be estimated directly (Holdaway and Jacomb 2000, Brook and Bowman 2002), we instead use detailed scenario testing and sensitivity analysis (of species carrying capacities, vital rates, maximum population growth rates, attack rates, and competition coefficients) to sift the likely parameter space and investigate single-cause and multicausal explanations for the Holocene extinctions. In particular, we ask whether the dingo invasion is supported as the main and most probable extinction driver after reconstructions of human population growth are taken into account. Contrary to popular wisdom, our models identify human intensification as the most likely cause of the mainland thylacine and devil extinctions, thereby indicating that the impact of prehistoric humans on Australian mammals was not limited to the late Pleistocene extinction event.

#### METHODS

We coded the aspatial, multispecies model in the R computing environment (R Development Core Team 2011), and assumed an arbitrary simulation area of one million km<sup>2</sup> of grassland habitat (~13% of the total area of mainland Australia) for the purposes of calculating population densities. We initiated stochastic model iterations at 5500 yr BP and terminated at 200 yr BP

(approximating the timing of European settlement). With the exception of humans, we simulated all species using matrix population models, a seasonal time step, and a pre-breeding census design (Caswell 2001).

*Macropod prey dynamics*

We assumed a prey base consisting of a generic macropod herbivore based on the red kangaroo (*Macropus rufus*), and underpinned our simulations with Pople and colleagues' (2010) interactive kangaroo-vegetation-rainfall model. Kangaroo population dynamics are modeled over a seasonal time step as a function of vegetation biomass, where vegetation growth is determined by simulated rainfall and previous vegetation biomass, and the density of kangaroos consuming the vegetation. Seasonal vegetation growth ( $\Delta V$ ; kg/ha) and daily vegetation ingestion by kangaroos ( $I$ ; kg/d) are given by:

$$\Delta V = -55.12 - 0.01535V - 0.00056V^2 + 2.5R$$

$$I = 0.086(1 - e^{-V/34}) \times W^{0.75} \times H_i$$

where  $V$  is vegetation biomass (kg/ha),  $R$  is simulated seasonal rainfall (mm),  $W$  is the average body mass of a red kangaroo (26 kg), and  $H_i$  is kangaroo density (individuals/ha). Vegetation growth is drawn from a normal distribution with mean  $\Delta V$  and standard deviation of 52 kg/ha. The numerical response of kangaroos is mediated through age-structured survival rates. Survival of juveniles <1 year old ( $S_J$ ), and subadults and adults  $\geq 1$  year old ( $S_A$ ), is modeled in seasonal time steps as a logistic function of vegetation biomass:

$$S_J = 0.80 \times e^{(-6.610+0.017V)} / [1 + e^{(-6.610+0.017V)}]$$

$$S_A = 0.99 \times e^{(-0.397+0.02V)} / [1 + e^{(-0.397+0.02V)}].$$

The model assumes an equal sex ratio and that female kangaroos produce 0.39 offspring each season, on average.

*Predator dynamics*

Exploring the full range of competing explanations for the mainland thylacine and devil extinctions necessitated a model structure that included eight predatory interactions (Table 1). To govern predation of kangaroo prey by each carnivore (humans, thylacines, devils, dingoes), we adopted Type I functional responses that incorporated both intra- and interspecific interference competition (de Villemereuil and Lopez-Sepulcre 2011). The functional response ( $f$ ) of a predator was modeled as the inverse of the average time ( $T$ ) between consuming two kangaroo prey items, where  $T$  equals the sum of time spent searching for prey ( $T_S$ ) and time wasted due to interference by conspecifics ( $T_{WI}$ ) and competing predator species ( $T_{WC}$ ). In a system with  $m$  predators

$$f(N, F, C) = \frac{1}{(T_S + T_{WI} + T_{WC})} = \frac{aN}{\left(1 + cF + \sum_{i=1}^m c_m C_m\right)}$$

where  $a$  is the focal predator's attack rate on the prey species with density  $N$ ,  $c$  is the intraspecific interference competition coefficient,  $F$  is the focal predator density, and  $c_m$  is the interspecific competition coefficient with predator  $m$  that has density  $C_m$ . Given that devils do not hunt large macropod prey, we limited them in the simulation to hunting kangaroos that were less than two years old. We used simple, Type I functional responses to permit the direct killing of thylacines and devils by humans or dingoes, thereby allowing for the possibility that the latter species might have engaged in surplus killing of the native carnivores.

We assumed an annual breeding cycle, and fixed maximum life spans and age-structured fertility rates for each predator species, with parameter estimates based on a combination of species-specific observations and ecological analogues (Appendix A). We assumed logistic population growth, mediated through variation in survival rates for two age classes, juveniles (<1 year old) and subadults/adults (>1 year old). We reduced seasonal, age-structured survival rates linearly from a maximum when population density was zero to rates required for a stable population when the population was at carrying capacity (Caswell 2001). To link the numerical and functional responses of a predator species, we: (1) set the per capita rate of prey consumption that was required for a stable predator population, (2) calculated the realized per capita prey consumption rate each season, and (3) using those two values, calculated the proportion of the predation requirement that was met for that season. We then adjusted carrying capacities seasonally by weighting the starting predator density by the latter proportion (e.g., if the seasonal predation rate was higher than that required for a stable population, the seasonal carrying capacity exceeded the starting density). Carrying capacity calculations for dingoes (if introduced) used the starting population density for thylacines.

*Scenario testing*

We tested models that included and/or excluded the follow three processes:

- 1) *Dingo introduction.* We assumed an introduction date of 4000 yr BP (Johnson 2006) and a propagule size of 500 individuals.
- 2) *Climate change.* To simulate natural climate change from the wetter mid-Holocene conditions before 5000 yr BP to the drier recent conditions (2000 to 200 yr BP; Donders et al. 2008), we generated past and current rainfall distributions and transitioned between these states. For current rainfall patterns, we sampled seasonal rainfall from lognormal distributions fitted to data for Menindee, New South Wales

TABLE 1. Binary factors and uniform-distribution parameter ranges (for continuous variables) tested using Latin hypercube sampling for models of mainland thylacine and devil extinctions based on interactions of humans, thylacines, devils, and dingoes and their kangaroo prey.

Parameter	Range
Scenarios†	
Dingo introduction	yes/no
Climate change	yes/no
Human intensification	yes/no
Starting densities (individuals/km <sup>2</sup> )	
Kangaroo	5 to 30‡
Thylacine	0.02 to 0.3§
Devil	1 to 12¶
Human	0.02 to 0.21#
Juvenile survival (at carrying capacity)	
Thylacine, devil, dingo	0.15 to 0.5
Maximum population growth rates ( $r_m$ )	
Thylacine	0.24 to 0.44
Devil	0.29 to 0.49
Dingo	0.26 to 0.46
Predation rate for stable population (prey-predator <sup>-1</sup> ·d <sup>-1</sup> )	
Thylacine, dingo	0.1 to 0.5
Devils	0.02 to 0.5
Attack rates on kangaroos	
Thylacine, dingo, human	0.00005 to 0.005
Devils	0.00002 to 0.002
Attack rates on thylacines/devils	
Dingo, human	0 to 0.005
Interference competition coefficients	
Dingo–dingo, dingo–human, human–human	–0.02 to 0.02
All other predator combinations	0 to 0.02

† We considered the relative influence of the three extinction drivers on model output through three binary factors (reflecting the inclusion/exclusion of each process from a simulation), resulting in a total of eight scenarios tested.

‡ Typical density range for the red kangaroo in the absence of main predators (Pople et al. 2010).

§ Pre-European population size for thylacines in Tasmania is estimated at 2000–4000 individuals, equating to 0.036–0.071 individuals/km<sup>2</sup> (Guiler and Godard 1998).

¶ Recorded devil densities in Tasmania range from 1.74 individuals/km<sup>2</sup> (Pemberton 1990) to 11.58 individuals/km<sup>2</sup> (Guiler 1970).

# Likely range for Pleistocene human densities (Brook and Bowman 2004).

(32°23' S, 142°25' E), where the vegetation component of the interactive kangaroo model was parameterized (Pople et al. 2010). To generate past rainfall distributions, we first removed data for seasons coinciding with El Niño events (Australian Bureau of Meteorology 2011) and refit the lognormal distributions. We then adjusted log(mean) parameters so that expected seasonal rainfall was 30% higher than for the current distributions (Kershaw 1995).

- 3) *Human intensification*. We modeled intensification solely as exponential human population growth ( $r = 4.01 \times 10^{-4}$ ) after 5000 yr BP, according to the best-fitting model of Johnson and Brook (2011).

#### Sensitivity analysis

We used the R package lhs (Carnell 2009) to sample from three binary factors (representing the inclusion/exclusion of each putative extinction driver) and wide, but plausible, ranges for 31 parameters (including initial

species densities, vital rates, maximum population growth rates, attack rates, and competition coefficients), thereby constructing a 34-dimension Latin hypercube with 100 000 divisions for sensitivity analysis (Table 1). To allow adequate coverage of the multidimensional parameter space, we ran a single simulation per hypercube division (Prowse et al. 2013). Given the importance of species demography to extinction risk, we varied juvenile survival rates for stable predator populations at carrying capacity (necessitating corresponding adjustments to adult mortality). For each predator, we derived two estimates of maximum annual population growth rate ( $r_m$ ) using established allometric relationships (Hennemann 1983) or age at first reproduction (Hone et al. 2010). We varied  $r_m$  within  $\pm 0.1$  of the mean estimate for each species (thylacines, 0.34; devils, 0.39; dingoes: 0.36). We assumed that the predation rate required for a stable predator population ranged from one prey killed every 2–10 days (thylacines,

dingoes) or 2–50 days (devils). We set maximum values for interference competition coefficients so that, when averaged across the full range of starting conditions,  $T_{WI} + T_{WC}$  ranged up to 25% of  $T_S$ . We also permitted negative coefficients to allow for the benefits of cooperative hunting between dingoes and humans. With the exception of attack rates governing predation on kangaroos, the tested ranges for all other attack rates and competition coefficients encompassed zero, so that our models effectively tested scenarios that included and excluded certain interactions. We did not subject the starting propagule size for dingoes to sensitivity analysis because, given that we assumed carrying capacities for dingoes in excess of any plausibly sized invasion event, the dingo population always grew in the years immediately following the simulation introduction.

#### *Model output and statistical analysis*

We used a quasi-extinction threshold of fewer than 500 individuals to define extinction, because we did not model small population phenomena such as demographic stochasticity, inbreeding depression, loss of genetic diversity, and Allee effects (Shaffer 1981). We discarded simulation results if kangaroos or dingoes (if introduced) went extinct, or if thylacine or devil extinctions occurred prior to 4000 yr BP. We classified the remainder as “plausible” models and categorized them as “successes” or “failures.” Because the fossil record cannot provide an exact date for the mainland thylacine and devil extinctions, we defined successful simulations as those for which both species went extinct between 4000 yr BP and European settlement.

To evaluate the influence of different model inputs on the probability of achieving a simulation success, we analyzed the simulation output using boosted regression trees (BRT) (Elith et al. 2008), implemented via functions in the R package *dismo* (Hijmans et al. 2011). BRTs can include different types of predictors (e.g., categorical and continuous), can fit complex, nonlinear relationships, and automatically handle interactions between predictors (Elith et al. 2008), so this technique is particularly useful for exploring and summarizing the output from complex model systems (Prowse et al. 2013). Because model scenarios that included the dingo introduction required specification of additional parameters, we first split the set of plausible models based on this factor. For each resulting data set, we evaluated a candidate set of BRT models that included the main factor effects, various combinations of parameters grouped according to their relevance to the native carnivores, humans and/or dingoes, and at least first-order interactions (i.e., minimum tree complexity = 2). We fit all BRT models with the routine *gbm.step*, using a binomial error and logit link, a learning rate of 0.01, and a bag fraction of 0.5. We compared candidate model performance using 10-fold, out-of-sample, cross-validation deviance (where lower values indicate better model performance). Because

models including dingo-specific parameters as predictors were not well-supported, we repeated the model selection process using output from all plausible models. We used the best-performing model to evaluate the relative influence of each predictor (Friedman and Meulman 2003).

## RESULTS

Using this dynamic model system, we produced “successful” simulations resulting from single processes (Fig. 1a) as well as more complex, multicausal scenarios (Fig. 1b), but at different relative likelihoods. From 100 000 Latin hypercube divisions, we derived 6130 plausible simulations of the late-Holocene ecosystem in Australia (i.e., no incorrect extinctions), of which 993 simulations were deemed successes (i.e., both thylacines and devils went extinct between 4000 yr BP and European settlement). Human intensification, as modeled using Johnson and Brook’s (2011) reconstruction of human population growth after 5000 yr BP, was overwhelmingly supported as the most probable driver of the mainland extinctions. Intensification was included in 80% of successful simulations, whereas climate change and the dingo invasion were modeled in only 44% and 16% of successes, respectively. No successful simulations were produced unless at least one of these factors was included in the models.

Although scenarios including the dingo introduction were more likely to simulate rapid extinction of the native carnivores, human intensification and/or climate change were sufficient to produce both extinctions prior to 3000 yr BP, representing the earliest dates supported by the fossil record (Brown 2006, Johnson 2006; see Fig. 2). From the subset of simulations we classified as successful, the extinction of thylacines and devils was simulated to occur between 4000 and 3000 yr BP in 21% and 11% of cases, respectively. Further, 74% of successful models simulated that the thylacine’s extinction preceded the devil’s, which is consistent with the relative order of events indicated by the available fossil evidence.

The ability of BRT models to predict simulation success/failure (based on out-of-sample cross-validation) was optimized with a predictor set including the main effects (three binary factors representing the inclusion/exclusion of each extinction driver) and human-specific parameters only (Fig. 3a; Appendix B). For this selected BRT model, metrics of relative influence confirmed human intensification as the primary process responsible for successful simulation outcomes (Fig. 3a). Although climate change impacts also had some support, the dingo introduction was a poor predictor of model success (Fig. 3a). When human intensification was included, the probability of a successful model outcome exceeded 50% for all initial human densities above 0.08 individuals/km<sup>2</sup>, assuming that continuous predictors were set at their mean values (Fig. 3b). The primary simulated interactions involved two binary factors

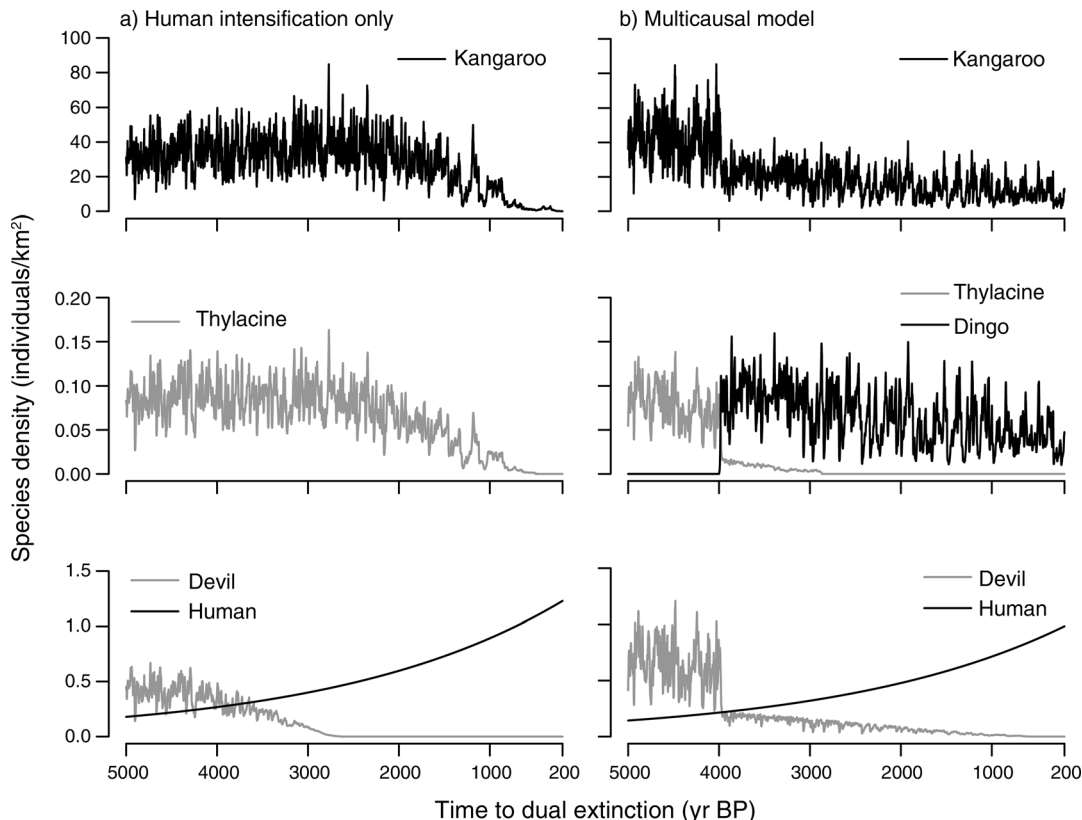


FIG. 1. Examples of “successful” simulations in which both thylacines and devils went extinct on the Australian mainland between 4000 years before present (yr BP) and European settlement. (a) Scenario of human intensification, where humans exert strong, direct hunting pressure on devils and rapidly cause their extinction as human densities increase; thylacines are driven extinct much later, primarily due to exploitation competition. (b) A multicausal model that includes the effects of the dingo invasion, climate change, and human intensification. The dingo population grows rapidly following introduction and quickly drives thylacines extinct due to direct predation and interference competition; the devil extinction occurs much later, arising from a combination of climate-change effects on kangaroo densities, increased competition, and direct mortality associated with the growing human population.

(human intensification, climate change) and two continuous predictors (initial human density, human attack rate on kangaroos). Simulation scenarios that included climate change magnified human impacts, allowing thylacine and devil extinctions to occur when human density and/or hunting efficiency were lower (Fig. 3b).

#### DISCUSSION

Challenging popular wisdom, our simulations overwhelmingly support human intensification as the most probable cause of the Holocene regime shift on mainland Australia. For scenarios including prehistoric intensification of human density, as modeled using Johnson and Brook’s (2011) reconstruction of population growth post-5000 yr BP, the probability of simulating these extinctions prior to European arrival exceeded 50% for all initial (pre-5000 yr BP) human densities above 0.08 individuals/km<sup>2</sup> (Fig. 3b). This equates to a human density of only 0.55 individuals/km<sup>2</sup> at European settlement, which is a plausible estimate of the actual figure for a technologically sophisticated

hunter–gatherer society (Thomson 2001). This predicted probability is based on BRT analysis of model output (Appendix B) and is calculated by assuming mean values for other predictors, including human attack rates on the native carnivores that equate to one thylacine and devil killed per human every 7 and 0.17 years, respectively (at the average starting densities tested). These rates are ecologically reasonable, given that Aborigines hunted both thylacines and devils for food and/or ceremonial purposes (Flood 1995, Paddle 2000).

In our simulations, the attack rate of humans on kangaroos was a more influential predictor of simulation success than human attack rates on thylacines or devils, indicating a principal role for exploitation competition in recreating the Holocene extinctions (Fig. 3). However, our models assumed a simplified, single-species prey base and therefore complete dietary overlap between all predators. This model structure might exaggerate anthropogenic impacts to some extent if, in reality, resource partitioning reduced the potential for exploitation competition between humans and the

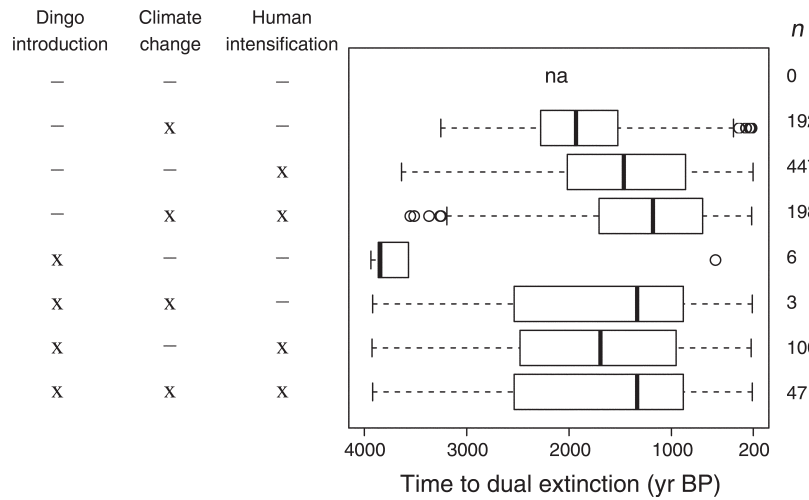


FIG. 2. Box-and-whisker plots of time to dual extinction of thylacines and devils; x symbols indicate that the relevant extinction driver (on the left) was included in the models; minus symbols indicate no inclusion. Scenarios including human intensification were more likely to produce successful simulations; scenarios including the dingo introduction were more likely to simulate rapid extinctions post-4000 yr BP for the thylacine and devil. Sample sizes ( $n$ ) for each scenario (i.e., number of simulations that successfully reproduced the actual historical outcome) are shown on the right. Where no extinction drivers were included (top row), there were no extinctions (na, not applicable). Boxplots show the median time at which dual extinction occurred (lines within boxes), the interquartile range (boxes), dual extinction times falling within 1.5 times the interquartile range from the box ends (whiskers), and outliers beyond the whiskers (points).

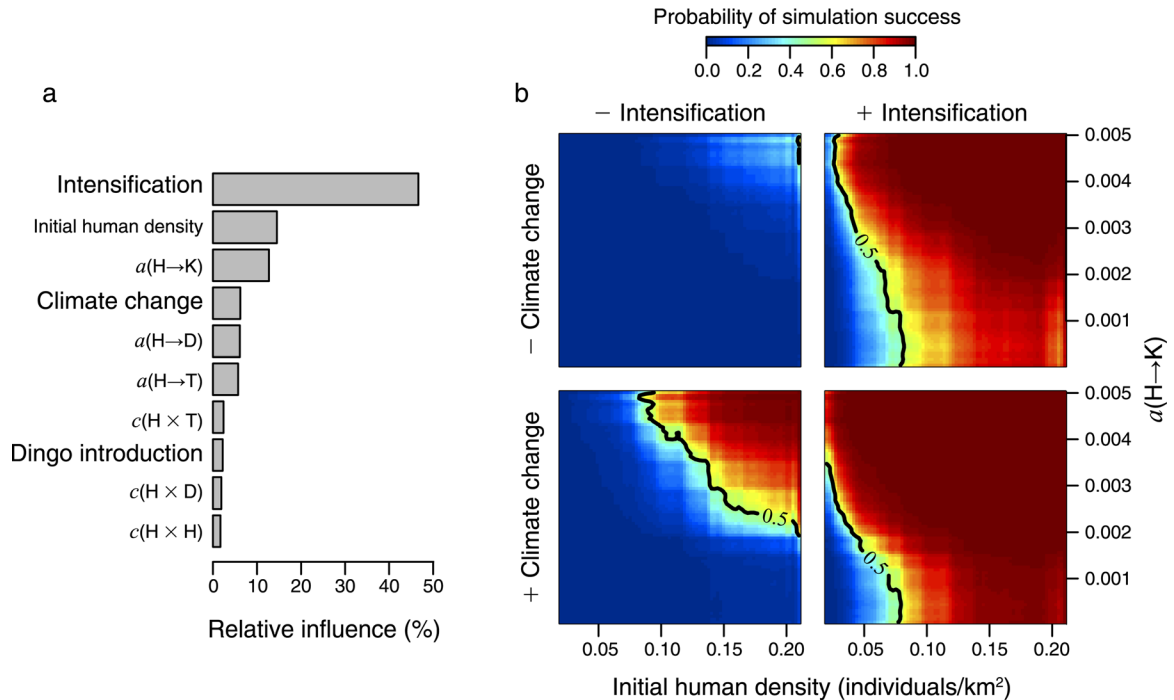


FIG. 3. Boosted regression tree (BRT) analysis of the plausible model subset. (a) Relative influence of model factors and parameters on the probability of a successful simulation outcome for the best-performing BRT model (see Appendix B). Attack rates “ $a$ ” of species  $X$  on species  $Y$  are denoted  $a(X \rightarrow Y)$ ; interference competition coefficients “ $c$ ” between species  $X$  and  $Y$  are denoted  $c(X \times Y)$ . Species and their abbreviations are: kangaroo, *Macropus rufus* (K); thylacine, *Thylacinus cynocephalus* (T); devil, *Sarcophilus harrisii* (D); and humans (H). (b) Interaction plots illustrating simulated interactions between extinction drivers (human intensification, climate change, where + indicates that the driver is included in the model simulations and – indicates that it is not) and continuous variables (initial human density, human attack rate on kangaroos [ $a(H \times K)$ ]). Plot color shading shows interpolated probabilities of simulation success using the best-performing BRT model.

native carnivores. In our sensitivity analysis, lower attack rates of humans on kangaroos mimicked a lower dependence of humans on that prey and were associated with smaller probabilities of simulating the thylacine and devil extinctions (Fig. 3). Although some resource partitioning between humans and the native carnivores seems likely, there is abundant evidence that indigenous Australians hunted and consumed essentially all marsupial, reptile, and bird species available to them (Miller et al. 1993, Flannery 1994). The potential for exploitation competition with native predators therefore seems high; indeed, the selective pressure of human hunting is thought to have caused the dwarfing of many marsupial species (Marshall and Corruccini 1978, Flannery 1994, Johnson 2006).

We modeled human intensification as an exponential, monotonic increase in human population density after 5000 yr BP, which is supported by the rock-shelter records (Johnson and Brook 2011). Although oscillations or variability in human population dynamics over the late Holocene might have temporarily released certain native species from persecution, the ability of humans to use different prey types and plant-based foods suggests that they would have been less affected by ENSO cycling. We should note also that the scenario of human intensification used here might be considered conservative, because it fails to account for technological advances. Over the mid-late Holocene, many new tool types appeared (including spear throwers, hafted axes, and backed blades) and major changes in resource use occurred (e.g., grinding of grass seed to make flour, permanent fish traps) (Lourandos 1997, Mulvaney and Kamminga 1999). These advances could have allowed the extension of semipermanent human settlements into habitats that, until then, had been exploited intermittently, despite the negative effects of a drier, more variable climate after 5000 yr BP.

Late-Holocene climatic change was minor compared to preceding climate shifts associated with Pleistocene glacial–interglacial cycles (Donders et al. 2008), and is not usually invoked as an explanation for the mainland thylacine and devil extinctions (Brown 2006). In contrast, it is widely recognized that modern extinctions typically involve a number of interacting stressors that, in combination, can raise the probability of extinction above that expected due to additive effects (Brook et al. 2008). We simulated the transition from the Holocene optimum to an ENSO-dominated rainfall pattern after 5000 yr BP, finding that this relatively moderate climate change could plausibly account for the thylacine and devil extinctions (Fig. 1), but only provided that human impacts (particularly human density and hunting efficiency) were also of sufficient magnitude (Fig. 3b). Increased ENSO cycling probably favored boom-and-bust dynamics in herbivore populations (Brown 2006, Letnic and Dickman 2006), a phenomenon captured by the kangaroo–vegetation–rainfall component of our simulations. For scenarios including both climate

change and human intensification, the former magnified human impacts by effecting smaller, more variable kangaroo populations, thereby reducing the influence of human hunting efficiency on model success rates.

Our multispecies models support recent claims that the dingo's role in Australia's Holocene extinctions has been overstated (Johnson and Wroe 2003, Brown 2006, Johnson 2006). In our simulations, dingoes could reduce thylacine and devil populations through a combination of exploitation and interference competition, as well as direct predation (Fig. 1b). However, when we included the dingo introduction as the sole extinction driver, dingoes rarely drove thylacines and devils to extinction in the time frame required (only 5% of the plausible simulations for which dingoes were introduced). This is despite our assumptions of: (1) complete dietary overlap between dingoes and the native species which maximizes the potential for exploitation competition; and (2) Type I functional responses governing dingo predation on thylacines and devils that should cause more system instability than if saturating responses were used. The apparent connection between the dingo invasion and the subsequent mammal extinctions might be no more than a coincidence (i.e., a result of greater contact and trade between northern Australia and the people of southern Asia, which also might have spurred the technological innovations that facilitated intensification). By extension, our results support the proposal that thylacines and devils persisted on the island of Tasmania not because the dingo was absent, but because human density remained low and/or climate change differed substantially from the mainland (Johnson 2006). There are no trends apparent in the size of the Tasmanian human population, nor any evidence of mainland contact or technology transfer over the Holocene (Mulvaney and Kamminga 1999, Johnson 2006). Furthermore, Tasmania lies permanently within a rain-bearing belt of westerly winds and is less affected by ENSO dynamics than the mainland. We should note, however, that our models could underestimate dingo impacts by omitting two processes: (1) more frequent, El Niño-induced droughts after 5000 yr BP might have forced animals toward watering points and increased the potential for competition between dingoes and native carnivores, and (2) dingoes might have introduced a heretofore unidentified disease that afflicted thylacines and devils (Johnson 2006).

The arrival of humans in Australia appears to have triggered a regime shift that involved two major environmental changes: the rapid extinction of the megafauna (e.g., giant Diprotodontid “wombats,” flightless *Genyornis* birds, large *Procoptodon* kangaroos, marsupial “hippos” *Zygomaturus*) (Johnson 2006, Roberts and Brook 2010), and a subsequent rearrangement of the vegetation as a consequence of that extinction event (Rule et al. 2012). It is most often assumed, however, that an ensuing ecological equilibrium was upset by a second regime shift following the introduc-



tion of the dingo around 4000 yr BP (Johnson and Wroe 2003). We have made the first quantitative exploration of the processes responsible for the Holocene extinction of thylacines and devils on mainland Australia. Our results indicate that although dingoes might have hastened these extinctions, human intensification, possibly aided by synergistic climate change effects, is the most likely extinction driver. Holocene intensification parallels in some ways the development of agriculture on other continents, but in a culture that retained a hunter-gatherer economy, and would similarly have impacted negatively on the wildlife exploited for human use (Johnson and Wroe 2003). It seems probable that human impacts on the structure and composition of Australian biodiversity were not limited to the late Pleistocene, but extended into the late Holocene.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Fixed demographic parameters used in the matrix population models for devils, thylacines, and dingoes ([Ecological Archives E095-057-A1](#)).

### Appendix B

Evaluation of candidate boosted regression tree models fitted to the simulation output ([Ecological Archives E095-057-A2](#)).

### Supplement

R script files to run the multispecies simulations in parallel, and two data files containing monthly rainfall records for Medindee, New South Wales, Australia (with and without El Niño events) ([Ecological Archives E095-057-S1](#)).