Bayesian networks elucidate interactions between fire and other drivers of terrestrial fauna distributions

BRONWYN A. HRADSKY,1,5† TRENT D. PENMAN,1 DAN ABABEL,1,2 ANCA HANEA,3 EUAN G. RITCHIE,4 ALAN YORK,1 AND JULIAN DI STEFANO1

1School of Ecosystem and Forest Sciences, University of Melbourne, 4 Water Street, Creswick, Victoria 3363 Australia
2Light Twist Software, 115 Falconer Street, Fitzroy North, Victoria 3068 Australia
3Centre of Excellence for Biosecurity Risk Analysis, School of BioSciences, University of Melbourne, Parkville, Victoria 3010 Australia
4Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, 221 Burwood Highway, Burwood, Victoria 3125 Australia


Abstract. Fire is a major driver of community composition and habitat structure and is extensively used as an ecological management tool in flammable landscapes. Interactions between fire and other processes that affect animal distributions, however, cause variation in faunal responses to fire and limit our ability to identify appropriate fire management regimes for biodiversity conservation. Bayesian networks (BNs) have not previously been used to examine terrestrial faunal distributions in relation to fire, but offer an alternative statistical framework for modeling complex environmental relationships as they explicitly capture interactions between predictor variables. We developed a conceptual model of the interactions between drivers of faunal distributions in fire-affected landscapes, and then used a non-parametric BN modeling approach to describe and quantify these relationships for a suite of terrestrial native mammal species. We also tested whether BNs could be used to predict these species’ distributions using only remote-sensed or mapped variables. Data were collected at 113 sites across 47,000 ha of continuous eucalypt forest in the Otway Ranges, southeastern Australia; time-since-fire (TSF) ranged from six months to 74 yr. Habitat complexity increased with TSF and forest wetness. Critical-weight-range (35–5500 g) marsupials and rodents were generally more likely to occur at long unburnt sites with high habitat complexity, and in wetter forest types. In contrast, large grazers and browsers preferred less complex habitats and younger or drier forest. Species occurrences were more strongly affected by habitat complexity than TSF, coarse woody debris cover, or invasive predator (Vulpes vulpes or Felis catus) occurrence. Bayesian network models effectively discriminated between the presence and absence of most native mammal species, even when only provided with data on remote-sensed or mapped variables (i.e., without field-assessed data such as habitat complexity). Non-parametric BNs are an effective technique for explicitly modeling the complex and context-dependent influence of fire history on faunal distributions, and may reduce the need to collect extensive field data on habitat structure and other proximate drivers.

Key words: Australia; critical-weight-range mammal; disturbance; Felis catus; fire management; forest; habitat complexity; non-parametric Bayesian network; predator–prey interaction; species distribution (niche) model; Vulpes vulpes.

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† Present address: Quantitative and Applied Ecology Group, School of BioSciences, University of Melbourne, Parkville, Victoria 3010 Australia.
† E-mail: hradskyb@unimelb.edu.au
INTRODUCTION

Fire is a major driver of biome distribution and community composition worldwide (Bond and Keeley 2005, Pastro et al. 2014) and is extensively used as an ecological management tool in flammable landscapes (Bowman et al. 2009, Penman et al. 2011). Fire management objectives for biodiversity conservation are commonly derived from floral vital attributes; for example, management guidelines often include tolerable fire intervals that are based on the time-to-maturation or reproductive mechanisms of key plant species (Burrows 2008, Van Wilgen et al. 2011). Fauna, however, may require very different distributions of post-fire age classes to flora (Di Stefano et al. 2013), and their responses to fire often differ between fire events and locations (Converse et al. 2006, Nimmo et al. 2014). Our ability to predict how fauna will respond to fire and so promote animal diversity through fire management remains weak, partly because the interactions between fire and other drivers of species distributions are poorly understood (Driscoll et al. 2010, Spies et al. 2012).

Faunal responses to fire (positive and negative) are primarily driven by the effects of fire on habitat resources such as food and shelter, rather than direct mortality (Banks et al. 2011, Morris et al. 2011). Loss of vegetation cover after fire, for example, can increase the vulnerability of small and medium-sized mammals to predation, reduce prey abundance or survival, and attract predators to recently burnt areas (Ogen-Odoi and Dilworth 1984, Barnard 1987, Morris et al. 2011, Leahy et al. 2015, Hradsky et al. 2017). Large grazers may also be attracted to recently burnt habitats by a flush of palatable grasses and forbs (Gureja and Owen-Smith 2002, Kutt and Woinarski 2007). Spatial and temporal variations in faunal responses to fire can arise, therefore, when post-fire habitats and processes develop from different baselines or at different rates across the landscape or between fire events (Monamy and Fox 2000, Smucker et al. 2005). Our conceptual model (Fig. 1) summarizes the potentially complex direct and indirect interactions between fire, habitat suitability, predators, vegetation communities, and environmental conditions that may influence faunal distributions in fire-affected landscapes.

Such interactions are likely to be pervasive, and models that use habitat-related variables (such as habitat complexity or vegetation structure) often provide better predictions of faunal occurrence, abundance, or population growth rates than models that use fire-related variables (Di Stefano et al. 2011, Nimmo et al. 2014, Swan et al. 2015, Varner et al. 2015, Santos et al. 2016). Nonetheless, time-since-fire (TSF) and other remote-sensed or mapped predictors that are relatively simple to measure are more suitable metrics for ecological fire management objectives than more proximate predictors such as habitat structure. It is not logistically feasible, for example, to collect fine-scale vegetation structure data across large landscapes when interpolating species distributions; nor are such data available when extrapolating future changes in species distributions in response to proposed management or climate change scenarios. Consequently, there is a need for models that quantify the relationships between fauna populations, proximate predictors, and variables that can be remotely sensed or mapped across fire-affected landscapes.

Such relationships are difficult to capture in regression-based species distribution models that must avoid collinear predictors, such as generalized linear models (Elith and Leathwick 2009). In some cases, researchers have used a series of regression models to examine the relationships between interacting predictors such as TSF, habitat complexity, and vegetation type in a stepwise fashion (Sitters et al. 2014a); in others, variables are so confounded that they preclude formal analysis (Lindenmayer et al. 2008). For example, biotic interactions are usually excluded from species distribution models because predator, competitor, or mutualist data are confounded with environmental parameters (but see Ritchie et al. 2008, Elith and Leathwick 2009). Over-fitting is another potential problem that limits the number of predictors that can be examined with many ecological data sets (Harrell et al. 1996).

Bayesian networks (BNs) provide an alternative statistical framework for addressing these challenges. Bayesian networks explicitly include interactions between variables, and so are suitable for modeling complex environmental systems (McCann et al. 2006, Aguilera et al. 2011). There is a growing interest in the use of BNs to
model species distributions and compare alternative management options (Marcot et al. 2001, Smith et al. 2007, Johnson et al. 2010, Douglas and Newton 2014). In relation to fire and fauna, BNs have recently been used to investigate wildfire scenarios such as salmonid responses to climate change (Roberts et al. 2013, Falke et al. 2015), and the potential ecological risks to a watershed (Ayre and Landis 2012). To our knowledge, however, BNs have not previously been used to model terrestrial faunal distributions in fire-affected landscapes.

In this study, we used a BN modeling approach to investigate the drivers of native mammal distributions in a heterogeneous, fire-affected landscape. This approach enabled us to simultaneously quantify the interdependencies of key drivers depicted in our conceptual model (Fig. 1). Our secondary objective was to examine the potential relevance of these models for conservation management, by reducing the need for intensive collection of fine-scale data when predicting fauna distributions at a landscape scale.

METHODS

Study area

We collected data on habitat structure and native mammal and invasive predator occurrence across 47,000 ha of continuous eucalypt forest in the Otway Ranges, southeastern Australia. The region has a temperate climate, with cool wet winters and dry warm summers. There is an elevation and rainfall gradient across the region, from the relatively flat, dry northeast (150–250 m a.s.l); 800–1000 mm average annual

(Fig. 1. Continued)

References are as follows: 1, Conner et al. (2011); 2, Cross et al. (2015); 3, Clark et al. (2014); 4, Gureja and Owen-Smith (2002); 5, Letnic et al. (2005); 6, Nimmo et al. (2014); 7, Plavsic
rainfall) to the wetter, steeper southwest (400–550 m a.s.l; 1300–1600 mm average annual rainfall). The region encompasses four main forest types: tall mixed forest, foothills forest, forby forest, and wet forest (Fig. 2). These represent broad groupings of vegetation with similar ecological characteristics and fire responses (Cheal 2010) and are ranked in order from the open, dry “tall mixed” forest that occurs at low-elevation locations, to the tall, dense “wet” forest that occurs at high-elevation, high-rainfall locations; detailed descriptions are provided in Appendix S1: Table S1. The forests were extensively burnt by wildfires in 1939 and 1983, and numerous smaller planned burns have subsequently been conducted across the region, particularly in the last decade.

**Study design**

We used a space-for-time approach, assessing native mammal and invasive predator occurrence and habitat variables at 113 sites along a 74-yr post-fire chronosequence. Sites were spatially nested within 23 100-ha circular units (mosaics; Fig. 2). We located three to six (generally five) sites in each mosaic using a stratified random approach to ensure that sites were at least 100 m apart, more than 50 m from roads and the boundaries of neighboring vegetation types and fire age classes, and that different vegetation types and fire age classes were adequately represented. Ultimately, sites within mosaics were 103–955 m apart and mosaics were separated by ≥2.7 km. Details of the site selection procedure are provided in Sitters et al. (2014b), but note that our study did not include their heathland sites. Surveys were conducted between September and November 2012.

**Native mammal distributions.**—We used digital motion-sensing cameras (Reconyx Hyperfire HC500; www.reconyx.com) to survey native terrestrial mammals. These cameras capture images...
of passing animals using a passive infrared motion detector and infrared flash array. At each site, we fastened one camera 30 cm up a tree and faced it toward a bait station 1.6 m away. Cameras were set to maximum sensitivity, and programmed to record images continuously while movement was detected, with five photographs per trigger event. The bait station comprised five tea-strainers (each containing a mix of peanut butter, golden syrup, oats, and pistachio essence) and was tied to a picket approximately 30 cm above the ground. We clipped understory vegetation around the bait station to ensure that animals would be clearly visible. Cameras were deployed for 18 full days at each site, and two researchers with similar levels of experience identified fauna from the photographs. Animals were identified to species level where possible, but Antechinus agilis and Antechinus swainsonii could not reliably be distinguished and so these species were grouped as Antechinus spp. Species were considered to occur (be present) at a site if they were recorded at least once during the survey period.

Interspecific interactions.—Records of predator occurrence (presence/absence) from camera surveys at each site were used to represent predation in our model. Information on competitive or other interactions between native species was insufficient to model these effects. A pilot study indicated that the peanut butter-based lures used in this study were at least as effective at attracting invasive predators as a more typical predator lure, which comprised tuna oil, feathers, and an audio lure (B. Hradsky, unpublished data).

Detection probabilities.—We did not incorporate imperfect detection in the BN models. As an indicator of survey efficacy for each species, however, we calculated the probability that each species would be detected at least once during the survey period given that it was present as 

\[1 - (1 - p)^{18}\]

where \(p\) is the overall detectability estimate for the species. We calculated \(p\) for each species by fitting the single season occupancy model of MacKenzie et al. (2002) using the unmarked package (Fiske and Chandler 2011) in R version 3.2.3 (R Core Team 2015).

Habitat survey.—We derived two measures of habitat structure for each site: understory habitat complexity and coarse woody debris cover (CWD). Both measures were assessed along a 60-m transect, centered on the camera station, and established along a randomly oriented bearing. To quantify habitat complexity, we adapted the approach developed by Newsome and Catling (1979). That is, we assessed the presence of understory vegetation cover in three vertical strata (20–50, 50–100, and 100–200 cm) at 20 evenly spaced points along a 60-m transect using a height pole. We gave each stratum at the site a score from 0 to 3 (corresponding to 0%, 1–30%, 31–70%, or 71–100% vegetation cover, respectively), and summed these scores to give an overall habitat complexity score for the site, ranging from 0 to 9. In our study region, vegetation cover in the 0–20 cm height class is often uniformly high and so it is not an informative predictor (B. Hradsky, unpublished data). Coarse woody debris cover was quantified by measuring the cross-sectional width of each piece of wood (>5 cm diameter and >50 cm in length) that intersected the 60-m transect, summing all lengths and then dividing the sum by the total transect length.

Mapped and remote-sensed variable.—Fire maps dating back to 1939 were used to derive the TSF history of each site. These values were then converted to a time-since-fire index (TSFI) to reflect differences in post-fire growth rates in each vegetation type (Cheal 2010). We calculated the index by deriving a relationship between the rate of succession (x-axis) and a synthetic index ranging between 0 (renewal immediately post-fire) and 1 (waning or senescence) for each vegetation type. This allowed us to model TSF as a continuous variable, and account for different developmental rates in the four vegetation types. A BN modeling approach is capable of incorporating multiple, correlated fire history attributes. However, fire severity data were only available for the most recent fires and so were not included in the model. Fire frequency was also not included because only a narrow range exists within the study area (more than 90% of sites have been burnt no more than three times since 1939).

Other variables that represented the environmental conditions at each site (elevation, average annual rainfall, productivity [normalized difference vegetation index], aspect, slope, and topographic wetness index) were extracted from spatial databases. Data sources, descriptions, and ranges are provided in Appendix S1: Table S2.
Bayesian network development

Non-parametric BNs were used to analyze the relationships presented in the conceptual model. Bayesian networks are directed acyclic graphs that depict logical or causal relationships among a network of variables. Nodes in the BN represent variables, while directed links (arcs) connect input (parent) nodes to response (child) nodes, indicating the direction of influence (Nyberg et al. 2006). Changes to one node can influence all connected (direct and indirect) nodes. We constructed the initial BN based on our conceptual model (Fig. 1), using the variables listed in Appendix S1: Table S2 as nodes. Initially, the model contained all arcs that seemed logical, based on the published literature and our understanding of the study system. After refining the BN structure (see Model construction and refinement), we used the BN to model the distribution of each of the seven native mammal species separately, with the model output (or terminal node) being the probability of species occurrence at each site.

Model construction and refinement.— All BN analyses were conducted using the engine of Uninet (Cooke et al., 2017; www.lighttwist.net/wp/uninet), via R version 3.4.0 (R Core Team 2017), using the package RDCOMClient (Lang 2014). Uninet constructs non-parametric BNs by quantifying nodes using marginal distributions (continuous and/or discrete) and arcs using normal copulas (Nelsen 2006). We manually built the BN, using arcs between nodes to indicate potential relationships between key predictors as identified from the literature (Fig. 1). We then populated the model with data from our 113 sites and used this data to learn relationships between the remote-sensed variables (e.g., elevation, aspect, rainfall, slope, and TSF) to avoid over-saturating the model. We removed arcs between these nodes when the empirical normal rank correlation of the two nodes was <0.1; Uninet calculates these correlations from the data under the assumption of a Gaussian dependence structure (Hanea et al. 2015).

The clustered design of our study (Fig. 2) meant that many data were spatially auto-correlated at distances <2500 m. We therefore calculated a spatially lagged response variable (SLRV; as defined by Haining 2003) for the occurrence of each native mammal species at each site, and added this as a node to the BN. We calculated SLRV as:

$$SLRV_i = \sum_j (W_{ij}Y_j) / \sum_i W_{ij}$$

where $i$ is the site of interest, $j$ is a site within 2500 m of $i$, $W$ is the inverse distance between sites $i$ and $j$ (the weighting), and $Y$ is the response (i.e., presence or absence of the species) at site $j$. To enable the SLRV node to be estimated by the BN if species occurrence data from surrounding sites were not available, the node was connected to the elevation, rainfall, topographic wetness, and productivity nodes (Fig. 3).

We redefined each continuous node of the BN as a beta distribution with parameter estimates (alpha and beta) derived from the raw data using in-built functions in Uninet. The beta distribution model was then used to quantify the influence of predictor variables and assess the fit of predicted distribution models for each species.

Model verification.—Model verification was conducted as per Hanea et al. (2015) using the built-in functions in Uninet. Uninet can test whether joint normal copulas adequately represent the original data by comparing the empirical correlation structures to correlation structures under the normal copula assumption; however, this test is highly conservative. As correlation matrices revealed maximum (element-wise) differences in the order of 0.01, we concluded that the correlation matrix under the normal copula assumption provided an adequate approximation of the empirical correlation matrix. A comparison of the similarity of the correlation matrix of the model to the correlation matrix of the data smoothed by the normal copula assumption indicated that the model provided an acceptable approximation of the smoothed data.

Model inference.—Conditionalization is the process of setting the value of one or more input nodes within a BN to infer how it/they affect the state of other nodes (e.g., if CWD cover is 3% and forest type is tall mixed forest, what is the probability of Rattus fuscipes occurrence?). Conditionalizing one (or more) nodes allows the other (unconditionalized) nodes to vary, based on the relationships defined within the network, and provides uncertainty estimates around these values.

We conducted all model inferences within each forest type, as forest type strongly influences habitat structure and the distribution of some...
native mammals in our study area (Swan et al. 2015). This involved first conditionalizing the forest type node in the model to one of the four types, running all the other conditionalization analyses and then repeating the process for each of the other forest types.

To examine how fire affected habitat structure and predator occurrence within each forest type, we conditionalized the TSFI node across a range of values from the 5% to the 95% quantiles of our field data (at 10% intervals), and recorded the value of the node of interest. We conducted similar conditionalization analyses to compare how the probability of native mammal occurrence was affected by habitat complexity (scores 1–9), CWD cover (5–95% quantiles), and the

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Fig. 3. The final Bayesian network. Arrows indicate the direction of influence from input to response nodes. Colors are consistent with Fig. 1; descriptions of the nodes are provided in Appendix S1: Table S2.
occurrence of each predator species (absent/present), within each forest type. All values in the text and figures are presented as means with upper and lower 95% confidence limits, which were estimated from the model standard deviation using a sample size of 113. We conservatively considered that there was a substantial relationship between an input and a response node if the confidence intervals around the estimated response did not overlap at the minimum and maximum input values. When there was marginal overlap in the confidence intervals and hence some (but not strong) evidence for a relationship, this is indicated in the text.

To assess the ability of our BN models to predict native mammal distributions, we used our survey data to conditionize the predictor nodes, determined the probability of species occurrence at each site, and then assessed model fit using the area under the receiver-operating characteristic curve (AUROC) using the R package pROC (Robin et al. 2011). Area under the receiver-operating characteristic curve compares the true-positive rate to false-positive rate and ranges between 0.5 (indicating no discrimination ability) and 1 (perfect discrimination; Swets 1988). We calculated AUROC separately for each species, conditionizing all nodes.

To understand the potential for these models to be applied by conservation managers in broad-scale land management, we also assessed the model fit when the model was conditionized only with data on mapped and remote-sensed nodes for each species. When data on vegetation cover, habitat complexity, CWD cover, and predator occurrence are not provided to the model, the BN estimates a mean and uncertainty distribution for each of these variables based on rank correlations calculated from the data during model construction. The effectiveness of these models was assessed by comparing the partially conditionized AUROC to the AUROC of the full model.

**Ethics statement**

Our study did not involve direct contact with the study species as data were collected using motion-sensing cameras. All research was conducted with the approval of the Victorian Department of Environment and Primary Industries (research permit numbers 10005514 and 1006882).

**RESULTS**

We recorded 11 native terrestrial mammal species and two invasive predator species across our 113 study sites, as well as four native arboreal mammal and two invasive herbivore species (a full species list is provided in Appendix S1: Table S3). We developed BN models for the seven native terrestrial mammal species that occurred at more than 15% of sites. With the exception of *Tachyglossus aculeatus*, the cumulative detection probabilities for these species were all >0.70 (Table 1). The invasive predators, *Vulpes vulpes* and *Felis catus*, occurred at 12% and 14% of sites, respectively.

| Scientific name | Common name | Sites recorded (n = 113) | Pr (detection|present) |
|-----------------|-------------|-------------------------|----------------|
| Small native mammals (<500 g) | | | |
| *Antechinus* spp. | Antechinus spp. | 54 | 1.00 (0.99, 1.00) |
| *Rattus fuscipes* | Bush rat | 81 | 1.00 (1.00, 1.00) |
| Medium-sized native mammals (0.5–5 kg) | | | |
| *Potorous tridactylus* | Long-nosed potoroo | 21 | 1.00 (1.00, 1.00) |
| *Perameles nasuta* | Long-nosed bandicoot | 34 | 0.74 (0.61, 0.86) |
| *Tachyglossus aculeatus* | Short-beaked echidna | 25 | 0.33 (0.12, 0.60) |
| Large native mammals (>10 kg) | | | |
| *Wallabia bicolor* | Swamp wallaby | 85 | 0.99 (0.98, 0.99) |
| *Macropus giganteus* | Eastern gray kangaroo | 19 | 0.80 (0.65, 0.92) |
| Invasive predators | | | |
| *Vulpes vulpes* | Red fox | 13 | 0.28 (0.08, 0.72) |
| *Felis catus* | Feral cat | 16 | 0.39 (0.17, 0.72) |

*Notes:* Sites recorded is the number of sites where the species was recorded; Pr (detection|present) is the cumulative probability of detection over the 18-d survey period, given the species was present. Numbers in brackets show the lower and upper 95% confidence limits.
There was high uncertainty around the predators’ cumulative detection probabilities (Table 1), but their occurrences were included as nodes in the BN as indicators of potential predation risk. Habitat complexity across the sites ranged from 1 (at a recently burnt site) to the maximum score of 9 (>85% cover in all three height strata). Coarse woody debris cover ranged from <1% to 12%.

The final BN contained 17 nodes (Fig. 3; nodes are described in Appendix S1: Table S2). Model inference showed that habitat complexity was positively associated with time-since-fire (TSFI; Fig. 4a), but that CWD cover did not change with post-fire age (Fig. 4b). Forest type strongly influenced both habitat variables, with values being substantially higher in the wetter forest types (Fig. 4a, b). Time-since-fire, habitat complexity, and forest type did not affect V. vulpes occurrence (Fig. 4c, d). There was some evidence that F. catus occurrence was positively associated with TSF and negatively associated with habitat complexity; F. catus was also more likely to occur in the wetter forest types (Fig. 5). There was some evidence that T. aculeatus was more likely to occur when F. catus was present, with the probability of occurrence increased from 0.53 (0.44, 0.62) to 0.39 (0.30, 0.47) when V. vulpes was present. In contrast, T. aculeatus was more likely to occur when F. catus was present, with the probability of occurrence in tall mixed forest increasing from 0.31 (0.22, 0.40) to 0.49 (0.40, 0.58). For the other native mammal species, estimates around the effects of invasive predator occurrence were associated with large uncertainty, and few consistent patterns could be discerned. Full results are presented in Appendix S1: Fig. S1.

Area under the receiver-operating characteristic curve values indicated that models discriminated between the presence and absence of terrestrial native mammal species with reasonable to good accuracy when conditionalized using the full data set (AUROC range: 0.69–0.86; Fig. 7). Using only mapped and remote-sensed data reduced the discriminative ability of the models by 5.3–16.4%, but AUROCs remained ≥0.70 for R. fuscipes, M. giganteus, Perameles nasuta, and P. tridactylus (Fig. 7).

**Discussion**

Faunal distributions in fire-affected landscapes are potentially influenced by numerous interacting factors (Fig. 1) and can be difficult to predict using fire-related metrics such as TSF or fire severity alone (Nimmo et al. 2014, Varner et al. 2015). A non-parametric BN approach explicitly captured the relationships between multiple, often correlated, drivers of native mammal distributions within a single model. This holistic analysis enabled us to predict native mammal occurrences with reasonable to good accuracy. Moreover, the distributions of four of the seven species could be predicted with reasonable accuracy using only data from remote-sensed and mapped variables such as TSF, vegetation type, and elevation. Further verification with an independent data set is required, but our findings suggest that BNs provide an efficient way of modeling faunal distributions across heterogeneous, fire-affected landscapes, and may reduce...
Fig. 4. Interactions between potential drivers of native mammal occurrence in a fire-affected landscape. The influence of time-since-fire on (a) habitat complexity, (b) coarse woody debris (CWD) cover, (c) Vulpes vulpes occurrence, (e) Felis catus occurrence, and the influence of habitat complexity on (d) V. vulpes occurrence and (f) F. catus occurrence. Results were derived from non-parametric Bayesian networks of data collected at 113 sites, Otway Ranges, Australia. Responses are shown for four different forest types: wet forest (dotted), forby forest (dot-dashes), foothills forest (short dashes), and tall mixed forest (long dashes). Shading indicates 95% confidence intervals.
Fig. 5. Influence of time-since-fire, habitat complexity, and coarse woody debris cover (CWD) on the occurrence of critical-weight-range marsupials and rodents. Results were derived from non-parametric Bayesian networks of data collected at 113 sites, Otway Ranges, Australia. Responses are shown for four different forest types: wet forest (dotted), forby forest (dot-dashes), foothills forest (short dashes), and tall mixed forest (long dashes). Shading indicates 95% confidence intervals. Note difference in scale for *Rattus fuscipes*.
the need to collect extensive field data on habitat structure and other proximate drivers.

The importance of habitat structure for mammal persistence in fire-affected landscapes is well established (Monamy and Fox 2010, Plavsic 2014, Leahy et al. 2015). Habitat structure changes through time after a fire (Coops and Catling 2000, Haslem et al. 2011), but also varies with numerous other factors including topography and rainfall (Keeley et al. 2005, Plavsic 2014).

**Fig. 6.** Influence of time-since-fire, habitat complexity, and coarse woody debris cover (CWD) on the occurrence of (a) *Tachyglossus aculeatus* and (b, c) large macropods. Results were derived from non-parametric Bayesian networks of data collected at 113 sites, Otway Ranges, Australia. Responses are shown for four different forest types: wet forest (dotted), forby forest (dot-dashes), foothills forest (short dashes), and tall mixed forest (long dashes). Shading indicates 95% confidence intervals.
Bayesian network analysis showed that habitat complexity increased with TSF and forest wetness and strongly influenced the distributions of native mammal species in our study landscape. The direction in which habitat complexity influenced native mammal occurrences concurred with current knowledge of the species’ biology. All four small and medium-sized marsupial and rodent species had strong positive associations with habitat complexity and were generally more likely to occur in wetter and long unburnt forests. These taxa are depredated by invasive and native predators (Bilney et al. 2010, Doherty et al. 2015) and preferentially shelter and/or forage in dense vegetation cover to escape from predators. Instead, its occurrence is more likely to reflect the distribution of shelter sites under CWD and the availability of ants (Smith et al. 1989). The low detection rate for this species means that false absences may have contributed to the weakness of its relationships with predictor variables such as CWD in our study.

In contrast, *Tachyglossus aculeatus* (a monotreme) showed very little association with habitat structure or TSF. Although *T. aculeatus* is medium-sized and preyed upon by *V. vulpes* (Hradsky et al. 2017), its spiny coat and ability to dig rapidly means that it does not require dense vegetation cover to escape from predators. Instead, its occurrence is more likely to reflect the distribution of shelter sites under CWD and the availability of ants (Smith et al. 1989). The low detection rate for this species means that false absences may have contributed to the weakness of its relationships with predictor variables such as CWD in our study.

The large herbivore (macropod) species were negatively associated with habitat complexity, and had neutral or negative associations with TSF and forest wetness. Although young macropods are vulnerable to foxes (Banks et al. 2000), these species generally forage in open areas (Banks 2001, Swan et al. 2008) and may be attracted to recently burnt sites by the growth of palatable grasses and herbs after fire (Styger et al. 2011, Tuft et al. 2012).

The relationships between native mammal occurrence, habitat complexity, and fire identified by the BN analyses were qualitatively similar to those from previous regression analyses of species distributions in the same landscape, indicating that BNs represented these relationships appropriately. Swan et al. (2015) used a series of generalized additive mixed models (GAMMs) to determine the relationships between TSFI, vegetation structural variables, and terrestrial native mammal occurrence in the same study area, based on data collected in spring/summer of 2010–2011 and 2011–2012. Key similarities in our findings include the importance of habitat structural variables for native mammals relative to TSFI, positive relationships between *Perameles nasuta* and *Potorous tridactylus* occurrence and dense vegetation cover, and negative relationship between *Macropus giganteus* and understory vegetation.

One substantial difference between the BN and GAMM results, however, was that the GAMMs showed strong interactions between forest type and TSFI for habitat structural variables. Coarse woody debris cover, for example, was not associated with TSFI in tall mixed forest...
but was positively associated with TSFI in wet forest (Swan et al. 2015). In contrast, the BN modeled forest type (which was categorical) as an ordinal variable and found similar relationships between TSFI and habitat structural variables in each vegetation type (Fig. 4a, b). This is likely to be an artifact of the non-parametric BN structure. Alternate model structures could be explored using a larger data set with more samples from each forest type. Fauna distributions may also differ between seasons and years (Hale et al. 2016); further surveys would help clarify this potential source of variation.

Predators are rarely included among the potential drivers of species occurrence or abundance in models of faunal distributions in fire-affected landscapes (although see Arthur et al. 2012), despite their important role in post-fire population dynamics (Morris et al. 2011, Leahy et al. 2015). Our data on the interactions between predators, prey, and fire were limited as they only captured species occurrence (rather than abundance or behavior) and predator detection rates were low. Nonetheless, we found some evidence that *F. catus* was more likely to occur in wet forest, particularly as TSF increased and habitat complexity decreased. The majority of feral cat studies indicate that *F. catus* selects for structurally complex habitats (Doherty et al. 2015a); however, high-resolution telemetry has shown that feral cats select for open habitats in their fine-scale movements (McGregor et al. 2014). A difference in spatial scale of selection may therefore explain the seemingly contradictory preference of *F. catus* for low habitat complexity and wet forests in our study (given that wet forests generally had high habitat complexity)—wet forests also supported more potential prey species. Similarly, differences in temporal scale may explain why broad-scale correlative analyses of *V. vulpes* distributions in fire-affected landscapes such as ours and those of Payne et al. (2014) and Southgate et al. (2007) have found weak or no relationships between fox occurrence and fire history, vegetation type, and/or habitat structure, but telemetry studies have shown that *V. vulpes* uses burnt forest and heathland intensely immediately after fire (Meek and Saunders 2000, Hradsky 2016).

The native rodent *Rattus fuscipes* was less likely to occur when *V. vulpes* was present, perhaps reflecting its avoidance of this predator. Overall, however, we found little consistent evidence of associations between invasive predator and native prey occurrence, and the strength of associations did not reflect the relative prevalence of these prey species in the diet of *V. vulpes* in the Otway Ranges (Hradsky et al. 2017). Surprisingly, *T. aculeatus* was positively associated with *F. catus* occurrence—this relationship should be interpreted cautiously given the low detection rates of both species. Predator manipulation experiments and more detailed data on predation risk are required to better understand the influence of invasive predators on native mammal distributions in fire-affected landscapes. The role of other interspecific interactions also needs further investigation. For example, high levels of herbivory can negatively impact small mammals through the effects on vegetation structure (Foster et al. 2014), and interact with both fire and predators (Dexter et al. 2013, Colman et al. 2015).

The BNs discriminated between the presence and absence of most native mammal species reasonably well, particularly when models were conditionalized using the full variable set. For four species, discrimination was also reasonable when models were conditionalized with only mapped and remote-sensed data, indicating that the BNs effectively captured relationships between proximate and ultimate drivers of distributions for these species. Bayesian networks might therefore be used to predict the distributions of these species at a landscape scale. However, our sample sizes were too small to enable cross-validation testing, and additional testing with independent data sets from the same and other regions is necessary. Fine-scale habitat data sets (and perhaps different survey methods) will be required to predict the distributions of some species such as *T. aculeatus* and *Antechinus* spp. Habitat structure surveys will also continue to be important for understanding how fine-scale habitat complexity and vegetation mosaics influence species distributions, abundance, and behavior.

**Conclusions**

Bayesian networks can be useful for modeling complex systems, but have not been routinely applied in the environmental sciences to date (Aguilera et al. 2011). Recent developments in non-parametric continuous BNs further increase
the potential applicability of BNs for ecological problems, as they reduce the need for large sample sizes and discretization of continuous variables (Aguilera et al. 2011, Hanea et al. 2015). We found that non-parametric BNs provided an effective and efficient method for modeling and predicting native fauna distributions across a heterogeneous landscape, while explicitly incorporating the interactions between habitat structure, fire, invasive predators, and other environmental conditions. Further research and replication is needed to test the ability of BNs to predict species occurrences at interpolated or extrapolated sites. Bayesian networks are likely to be a useful tool for predicting species responses to fire management and identifying appropriate fire regimes for biodiversity conservation in an increasingly fire-prone world.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1926/full