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Occupancy and habitat associations of European hares and rabbits in mesic forests of the Northern Tablelands, New South Wales, Australia

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ABSTRACT

Context. Globally, invasive species contribute to ecological decline by outcompeting native fauna. Effective management of invasive species' impacts should be informed by context-specific data. In Australia, the European hare (*Lepus europaeus*) remains poorly understood, especially in terms of distribution and ecological impacts, while the European rabbit (*Oryctolagus cuniculus*) is a well-researched pest, particularly in agricultural landscapes. Research has not sufficiently addressed the ecology of hares and rabbits in Australia's forested environments. **Aims.** We assessed the occupancy of hares and rabbits in the Northern Tablelands forests of New South Wales and identified factors associated with their occurrence. **Methods.** In a single-season survey, we deployed 300 cameras, across four study sites, in Guy Fawkes River National Park and Oxley Wild Rivers National Park, to gather data on hare and rabbit distributions. We quantified temporal activity patterns and analysed site occupancy of hares and rabbits using single season occupancy models. Detection data were pooled to estimate landscape-scale occupancy and to generalise results within a mesic system. **Key results.** Across 12,303 camera trap nights, hares and rabbits were detected infrequently. Hare occupancy decreased with increasing distance from non-native vegetation and increased with elevation and topographic wetness index. Rabbit occupancy also decreased with increasing distance from non-native vegetation and elevation. Hares and rabbits exhibited high temporal activity overlap (>80%). **Conclusions.** Our study provides insight into habitat associations and potential drivers of hare and rabbit distribution in mesic forests. The observed relationships between occupancy, proximity to non-native vegetation, and elevation establish a baseline for understanding hare and rabbit ecology in forested landscapes, where their ecological roles remain poorly documented. **Implications.** This study improves understanding of hare and rabbit occupancy in forested landscapes and highlights the need for monitoring approaches to be tailored for the target species. Although our survey design aligns with standard methods for native fauna, the unique behaviours and detectability of hares and rabbits may require tailored approaches. Refining these methods is crucial for deepening our understanding of these species' ecology and impacts, as well as supporting more effective and targeted management.

Keywords: detection, European hare (*Lepus europaeus*), European rabbit (*Oryctolagus cuniculus*), invasive species, lagomorph, mesic forest, occupancy, predator.

Introduction

Invasive species threaten ecosystems worldwide by disrupting native biodiversity and ecosystem function (Simberloff *et al.* 2013). Their impacts extend beyond direct competition with native species, sometimes leading to cascading effects throughout the ecosystem (Mack *et al.* 2000). These effects can include land degradation through soil erosion (Eldridge and Simpson 2002); weed infestation and seed dispersal (Twigg *et al.* 2009); and predation, including hyper-predation (Smith and Quin 1996) or prey naivety (Sih *et al.* 2010). In addition to ecological impacts, invasive species can have significant economic repercussions, with estimates of costs exceeding billions of dollars annually

(Hoffmann and Broadhurst 2016). Effective management strategies are therefore essential to mitigate the adverse effects of invasive species; however, it is often best for management decisions to be driven by context-specific data that permit an informed, adaptive approach (Davis *et al.* 2011).

Australia hosts a broad variety of invasive vertebrate pest species (Bomford and Hart 2002). Among these are two sympatric lagomorphs, the European hare (*Lepus europaeus*; henceforth 'hare') and the European rabbit (*Oryctolagus cuniculus*; henceforth 'rabbit'). Both species were introduced during European settlement of the continent (Williams *et al.* 1995; Stott 2015). Historically, hares were predominantly found in the integrated wheat and sheep agricultural systems of southeast Australia (Jarman 1986; Stott and Harris 2006), with their distribution spanning ~700,000 km^2 (Jarman 1986). There has been little subsequent examination of their distribution and they are not generally considered to be a significant pest (e.g. Northern Tablelands Local Land Service 2024; NSW Government 2025). Rabbits are widespread across all Australian states and territories, occurring in a range of habitat types with an estimated distribution covering ~70% (4,500,000 km^2) of mainland Australia (West 2018).

Hares and rabbits thrive within agricultural environments, benefitting from habitat modifications associated with farming and from the abundance of grasses that form the main component of their diet (Chapuis 1990; Lush *et al.* 2017). The impacts of rabbits on agricultural systems, including semi-arid and arid regions of Australia, are well documented, with extensive reviews highlighting their ecological and economic influence (e.g. Lees and Bell 2008; Cooke 2012). In agricultural landscapes, rabbit impacts include crop damage, soil degradation, and competition with livestock for forage resources (Saunders *et al.* 2002). In semi-arid and arid ecosystems, rabbits contribute to widespread vegetation loss, alteration of native plant communities, and declines in soil quality, primarily through overgrazing and warren formation (Eldridge and Koen 2008; Cooke 2012).

Hares and rabbits can also be found in forested systems, particularly in fragmented landscapes where land use changes create a mosaic of open and wooded environments (Parker *et al.* 1976; Towerton *et al.* 2011). While not their primary habitat, these areas may serve as temporary refuges during dispersal or movement between cleared areas. However, hares and rabbits are typically detected at lower rates in forested ecosystems than in cleared areas (e.g. Towerton *et al.* 2011), with their presence in these habitats currently understudied. This has resulted in a significant gap in our understanding of how hares and rabbits interact with, and affect, forested habitats. Consequently, there is a need for more focused research to explore their roles, potential competition with native species, impacts on vegetation, and overall contributions to ecosystem dynamics in forested systems.

While rabbits are less cryptic than hares, both species are primarily nocturnal and crepuscular (Villafuerte *et al.* 1993; Pépin and Cargnelutti 1994; Schai-Braun *et al.* 2012), making them difficult to monitor effectively. Typically, hare and rabbit densities have been indexed using standard spotlight count methods (Poole *et al.* 2003), faecal pellet counts (Wood 1988; Cooke and McPhee 2007), and warren counting (rabbits only; Parer and Wood 1986; Jansen *et al.* 2023). Such techniques can be popular due to simplicity and affordability (Delibes-Mateos *et al.* 2023). However, they have limitations related to minimum required effort and terrain (Parkes 2001), habitat conditions (Burnham *et al.* 1980), and population densities (Parkes 2001). Other influences, such as the probability of detection and the alertness, interest, and training of the observers may also hinder more traditional 'on the ground' survey methods (Burnham *et al.* 1980). Such problems with these techniques are likely to be amplified in heavily vegetated areas, such as the forests and grassy woodlands of Australia.

In more complex habitats, indirect monitoring methods, such as camera trapping, are favoured for observing elusive species (Grotta-Neto *et al.* 2020). This non-invasive approach to monitoring allows continuous surveillance with minimal disturbance to target species, providing data throughout the day and night, for extended periods in a variety of weather conditions. This is particularly valuable for studying nocturnal and crepuscular species like hares and rabbits. Camera traps can also be effective for studying species interactions, such as predation risk or competition, and can capture rare or cryptic behaviours that are challenging to document through traditional field methods (Caravaggi *et al.* 2016).

We used a lured array of camera traps to monitor hare and rabbit populations in the Northern Tablelands of New South Wales (NSW), Australia. This region is a mesic area where hares and rabbits are present. However, little is known about their ecology and distribution in local systems. Thus, our aim was to examine hare and rabbit distributions and to complete an exploratory investigation into their site occupancy and habitat associations. We asked the following:

1. What are the probabilities of detecting hares and rabbits in mesic forests?
2. What environmental and habitat covariates are associated with the occupancy of hares and rabbits in mesic forests?
3. Do the daily activity patterns of co-occurring hares and rabbits overlap?

Materials and methods

We conducted camera trapping surveys in two conservation reserves: Guy Fawkes River National Park and Oxley Wild Rivers National Park. Guy Fawkes River National Park comprises 100,590 ha located on the eastern edge of the New England Tablelands and the western edge of the Dorrigo Plateau, in north-eastern NSW (NSW National Parks and Wildlife Service 2023*a*). Its vegetation communities are predominantly tall

open forest; however, woodlands, heaths, sedge lands, shrublands, and closed forest also occur. This Park is of high conservation significance, hosting at least 24 threatened species including brush-tailed rock wallabies (*Petrogale penicillata*) and spotted-tailed quolls (*Dasyurus maculatus*) (NSW National Parks and Wildlife Service 2023*a*).

Oxley Wild Rivers National Park forms an integral part of the Gondwana Rainforests of Australia World Heritage Area (NSW National Parks and Wildlife Service 2023*b*). It comprises 145,223 ha of wet and dry eucalypt forests, grassy woodlands, and heathlands, and lies along the Great Escarpment between the Northern Tablelands and the east coast. The Park is also of high conservation significance, hosting the largest confirmed population of brush-tailed rock wallabies (Thurtell *et al.* 2022).

In this study we collected data from two study sites in Guy Fawkes River National Park (henceforth, Paddysland and Glen Nevis) and two study sites in Oxley Wild Rivers National Park (henceforth, Front Tableland and Tabletop) (Supplementary Fig. S1). Each study site was approximately 20,000 ha in area.

Camera trapping

Camera monitoring was conducted using Reconyx™ HP2X cameras set to take 10 Rapid Fire™ motion pictures per trigger. Cameras were set to operate on a 24-h schedule, using a high-flash output setting. At each study site, 75 cameras were placed 500 m apart, and 50 m from the road. Each camera was secured to a steel post, approximately 0.5 m above ground, focused on a peanut butter and oat bait ball inside a plastic canister, 4 m away. Cameras were set up facing a southerly direction to reduce the impact of sun-induced lens flare. Vegetation was removed within each camera's field of view to decrease false triggers and increase the detection of target species. Cameras were deployed for 6 weeks (42 days) from late October to mid-December of 2021. Where possible, animals in each image were manually assigned species' specific metadata tags using 'Field Guide to Mammals of Australia' (Knight and Menkhorst 2010) and an in-house reference guide of common species known to occur at each study site. All faunal surveys were approved by the Department of Primary Industries, Orange Animal Ethics Committee (Animal Research Authority: ORA 19/22/027; Approval period: 30 January 2020 to 29 January 2023).

Vegetation assessments

We measured vegetation structure at each individual camera's location using a habitat complexity score adapted from Newsome and Catling (1979). Vegetation structure surveys were conducted at the beginning of the camera monitoring period. Vegetation structure was measured using each of the following five categories: 'tree cover' (>10 m in height, live canopy cover, excluding epicormic growth), 'shrub cover' (1–10 m in height, must be living vegetation), 'ground cover' (<1 m in height, includes grass, herbs, forbs, sedges, rushes, and vines), 'logs' (must be >30 cm in diameter), and 'other woody debris' (any dead wood plant material such as bark, branches, and shrubs with no foliage). For each category, vegetation was given a score of 0–3 for a 20 m × 50 m plot based on the following metrics: '0' represents no vegetation of that category within the plot around the camera, '1' represents low (i.e. 1–30% cover) of that vegetation category within the plot, '2' represents mid (i.e. 31–70% cover) of that vegetation category within the plot, and '3' represents high (i.e. 71–100% cover) of that vegetation category within the plot.

Due to large similarities in vegetation structure for some of these categories across the study site, all variables were tested for near zero variance using the 'caret' package in R (ver. 6.0.94; Kuhn 2008). Following this test, the categories for 'logs' and 'other woody debris' were removed from further analysis across all four study sites. Additionally, high tree cover ('3') represented too few camera locations and exhibited large standard error. To improve model stability, mid tree cover ('2') was combined with high tree cover into a single category (mid to high) prior to model fitting.

Occupancy covariates

To improve our understanding of the factors associated with hare and rabbit distributions in a forested system, we modelled the effects of various ecological and environmental covariates (Table S1). Occupancy of hares and rabbits is expected to vary with vegetation cover and structural complexity (Scharine *et al.* 2011; Bison *et al.* 2024). To account for this, vegetation structure covariates as described above were examined, as these can influence shelter availability and foraging opportunities for ground-dwelling mammals (Arthur *et al.* 2012).

Environmental covariates including distance to non-native vegetation, elevation, topographic wetness index (TWI), and soil type were derived from geospatial data. We measured distance to non-native vegetation, including cleared areas such as those currently or previously used for livestock grazing, to reflect the proximity of hares and rabbits to open foraging habitat and refuge patches. We measured distance to non-native vegetation in ArcGIS utilising the NSW State Vegetation Type Map (SVTM; ver. C1.1.M1.1), by extracting the non-vegetated category (State Government of NSW and NSW Department of Climate Change, Energy, the Environment and Water 2020). At each study site we visually verified each patch of non-native vegetation against satellite imagery and manually added any missing patches by modifying the layer in ArcGIS.

We also included covariates to test the importance of different environmental gradients in forested ecosystems. Elevation was included because it can influence hare and rabbit distribution. Hares and rabbits have been documented to occupy distinct elevational ranges in mountainous regions (Foster *et al.* 2022). We tested the impact of elevation to

determine whether hares and rabbits in our study sites exhibit similar responses.

In arid-zone habitats, water availability is the primary factor influencing rabbit distribution (Myers and Parker 1965), but we found no comparable research on hares. Rabbits in these environments obtain most of their water requirements from moisture contained in plants (Myers and Parker 1965). Similarly, in more temperate environments, rabbits consume plant species with higher water content, particularly in warmer months (Martin *et al.* 2007). Water sources at our study sites are often in highly ephemeral surface depressions, small waterbodies and creeks, and consequently there is a lack of suitable spatial data for water sources at our study sites. Therefore, we used TWI as an indicator of water availability. Elevation and TWI were calculated using a Digital Elevation Model (DEM) derived from LiDAR 5 Metre Grid (Geoscience Australia 2019). The TWI was calculated in ArcGIS Pro using the standard wetness index formula: $\mathrm{TWI} = \ln(\alpha/\tan\beta)$, where α denotes the specific catchment area (obtained from a flow accumulation grid) and β is the slope angle in radians calculated from the DEM (Beven and Kirkby 1979).

Soil type has also been shown to influence rabbit distribution, primarily relating to warren construction, with rabbits preferring well drained soils that facilitate burrowing (Parker *et al.* 1976; Williams *et al.* 1995). Similarly, hares in agricultural habitats in Italy exhibited higher densities on well-drained soils compared to those with higher clay content (Santilli and Ferretti 2008), thus we included soil type to assess whether a similar response occurs in forested ecosystems. Soil type was calculated using eSPADE (NSW's soil spatial viewer) State Government of NSW and NSW Department of Climate Change, Energy, the Environment and Water 2012.

All covariates were calculated at each camera location. To account for the heterogeneous distribution of the data across the study sites, data standardisation was performed on the geospatial covariates (distance to non-native vegetation, elevation, and TWI) using the 'scales' package in R (ver. 1.3.0; Wickham *et al.* 2023). Due to lack of variability, soil type was excluded from further analysis (Fig. S2). We tested for collinearity in our retained predictor variables by calculating Pearson's correlation coefficient using the R package 'correlation' (ver. 0.8.6; Makowski *et al.* 2022). No predictor variables had correlations $> |0.7|$, so all retained predictors were used in subsequent analysis.

Detection covariates

We modelled the impact of predator presence, the interspecies interactions between hares and rabbits, and potential changes in detectability associated with vegetation recovery following camera deployment (as days since deployment) on species detection probability. Predator presence was obtained from camera detections across the same 42-night trap surveys used to generate the hare and rabbit data. Predator detections were collapsed into a single presence/absence matrix including detections of feral cats (*Felis catus*), spotted-tailed quolls, red foxes (*Vulpes vulpes*), and dingoes (*Canis familiaris*). Other known predators of hares and rabbits, such as birds of prey and snakes are rarely and unreliably detected on camera at our study sites, so were not included.

Occupancy analysis

Occupancy modelling is a statistical tool used to estimate the probability that a species occupies a particular site, accounting for the possibility that the species might be present but remain undetected during surveys. This approach was deemed most appropriate due to the elusive nature of hares and rabbits in forested systems. We used single-season occupancy modelling, as described by MacKenzie *et al.* (2017), to estimate the site occupancy (ψ) and detection probability (P) for hares and rabbits within a mesic system. Analyses were conducted using the 'unmarked' R package (ver. 1.5.0; Fiske and Chandler 2011; Kellner *et al.* 2023). All analyses and data processing were conducted using R (ver. 4.3.3; R Core Team 2024).

We assumed a closed population during the sampling period. For each species, we generated a detection history matrix, where each location corresponded to one of the 75 cameras deployed within each of the four study sites. Each 'occasion' was defined as a 24-h period from midday to midday, aligning with the temporal activity patterns of hares and rabbits. Detection data from all four study sites were pooled for each species to estimate landscape-scale occupancy, with a random intercept for study site to account for unmeasured heterogeneity among areas.

We adopted an ecologically informed but exploratory modelling approach, as all predictors had plausible ecological relevance but uncertain relationships with species occupancy. Occupancy (ψ) level covariates included vegetation structure (ground, shrub cover, and tree cover), topographic variables (elevation and TWI), and distance to non-native vegetation (as an index of landscape openness). Detection (P) covariates included predator presence and hare or rabbit presence (for interspecies interaction effects on detectability) and days since camera deployment. We focused our examination of interspecies interactions on the detection model only to assess whether the presence of predators and hares or rabbits impacted the species detectability through either avoidance or attraction of co-occurring individuals. We did not model these interactions as occupancy covariates as we wanted to focus on habitat and environmental predictors only.

As noted above, while all predictors have plausible ecological justification, the nature of their relationships in these ecosystems remains uncertain. To account for this, model selection using all possible combinations of covariates was performed using the 'MuMIn' package (ver. 1.48.4; Bartoń 2024). Model support was evaluated using Akaike Information Criterion (AIC; Akaike 1973) and corresponding

model weights. Models within ΔAIC ≤ 6 of the top model were considered to have substantial support and when competing models were nested, the simpler model was retained (Richards 2008, 2015). Covariates appearing in all supported models were interpreted as having strong support, those occurring in more than 50% of the supported models as having moderate support, and those present in <50% of the supported models as having weak support (Richards *et al.* 2011; Richards 2015).

Model fit was evaluated for the top ranked models for each species using the MacKenzie–Bailey parametric bootstrap goodness-of-fit test (MacKenzie and Bailey 2004), with $P > 0.05$ indicating no evidence of lack of fit or overdispersion (Table S2). Covariate effects were visualised by generating predicted occupancy and detection probabilities from model-averaged coefficients across all models within ΔAIC ≤ 6. Predictions were based on the fixed-effect component of the model, with the random intercept set to zero, thus representing population-level relationships rather than site-specific predictions. Fixed-effect uncertainty was estimated using Monte Carlo simulation by sampling from the model-averaged coefficients and their variance–covariance matrix, with predictions back-transformed to the probability scale. The 95% confidence intervals were defined as the 2.5th and 97.5th percentiles of simulated predictions. Intervals reflect fixed-effect uncertainty only and do not incorporate among-site random-effect variance. Predicted relationships were visualised using 'ggplot2' in R (Wickham 2016).

Temporal analysis

To analyse the daily activity patterns of hares and rabbits, we used the timestamps of all camera trap detections for each species. We reduced temporal dependence associated with repeat triggers from the same individual by separating consecutive records by 1 min, an arbitrary but conservative threshold. All detection timestamps were then included (rather than applying a larger time-to-independence filter), because time-to-independence filtering can bias camera-trap-derived activity curves and overlap estimates (Peral *et al.* 2022). These timestamps were used to construct kernel density estimates of activity across the 24-h cycle. We calculated the coefficient of overlap (Δ) using non-parametric methods outlined by Ridout and Linkie (2009), applying the Δ4 estimator (Dhat4), as sample sizes for both species exceeded 75 independent detections. The overlap coefficient ranges from 0 (no temporal overlap) to 1 (complete overlap) Analyses were conducted using the 'overlap' R package (ver. 0.3.9; Meredith *et al.* 2024).

Results

Across all study sites, we recorded 698 detection events for hares and 163 detection events for rabbits, from 12,303 camera trap nights. Hares were detected on 99 cameras, with the greatest number of detections at Paddysland ($N = 383$), followed by Tabletop ($N = 281$), Front Tableland ($N = 22$), and Glen Nevis ($N = 12$). Rabbits were detected on 44 cameras, with detections greatest at Tabletop ($N = 127$), followed by Paddysland ($N = 30$), Glen Nevis ($N = 5$), and Front Tableland ($N = 1$). The number of survey days required for effective hare detection was less than our 42-night survey period but was marginally greater for rabbits (Fig. S3). Occupancy varied strongly among study sites, with large standard deviations (>1) remaining after accounting for occupancy and detection covariates (hare s.d. = 1.716; rabbit s.d. = 1.365 on the logit scale).

Hare occupancy

The estimated detection probability was 0.170 (95% CI: 0.159–0.182) and the estimated occupancy probability was 0.331 (95% CI: 0.280–0.386). Model selection indicated support for multiple competing models, justifying model-averaged inference (Table 1). The top model for hares was ψ ~ distance to non-native vegetation + elevation + shrub cover + TWI + (1| site), P ~ rabbit + predator (Table 1). During covariate screening, occupancy was moderately supported by distance to non-native vegetation (12 of 13 supported models; Table S3), elevation (10 of 13 supported models), topographic wetness (9 of 13 supported models), and shrub cover (9 of 13 supported models). Tree cover received weak support (2 of 13 supported models). Detection probability was moderately supported by rabbit presence (11 of 13 supported models) and predator presence (10 of 13 supported models).

Model-averaged coefficients indicated that hare occupancy declined significantly with increasing distance to non-native vegetation (Table 2, Fig. 1*a*), while showing non-significant positive associations with elevation (Fig. 1*b*) and TWI (Fig. 1*c*). Hare occupancy was highest at low shrub cover and declined at higher shrub cover levels (Fig. 1*d*). However, confidence intervals for mid and high shrub cover overlapped substantially and were not significant. Detection probability was higher when rabbits (Fig. 1*e*) and predators (Fig. 1*f*) were present.

Rabbit occupancy

The estimated detection probability was 0.088 (95% CI: 0.076–0.103) and the estimated occupancy probability was 0.151 (95% CI: 0.114–0.197). Model selection indicated support for multiple competing models, justifying model-averaged inference (Table 1). The top model for rabbits was ψ ~ distance to non-native vegetation + elevation + (1|site), P ~ day + predator (Table 1). During covariate screening, occupancy was moderately supported by distance to non-native vegetation (7 of 13 supported models; Table S3) and elevation (7 of 13 supported models). Detection probability was moderately supported by predator presence (8 of 13

Table 1. Covariates used to estimate the probability of occupancy for hares and rabbits.

Species	Model	d.f.	logLik	AIC	delta	weight
Hare	ψ(nnv + elv + shrub + TWI + 1|site), *P*(pred + rabbit)	10	−1988.849	3997.699	0.000	0.360
	ψ(nnv + elv + TWI + 1|site), *P*(pred + rabbit)	8	−1991.558	3999.116	1.418	0.177
	ψ(nnv + elv + shrub + 1|site), *P*(pred + rabbit)	9	−1991.184	4000.368	2.669	0.095
	ψ(nnv + elv + shrub + TWI + 1|site), *P*(rabbit)	9	−1991.432	4000.863	3.164	0.074
	ψ(nnv + elv + shrub + TWI + 1|site), *P*(pred)	9	−1991.853	4001.707	4.008	0.049
	ψ(nnv + elv + 1|site), *P*(pred + rabbit)	7	−1993.940	4001.880	4.182	0.045
	ψ(nnv + shrub + tree + TWI + 1|site), *P*(pred + rabbit)	11	−1989.962	4001.924	4.226	0.044
	ψ(nnv + elv + TWI + 1|site), *P*(rabbit)	7	−1994.139	4002.277	4.579	0.037
	ψ(nnv + shrub + TWI + 1|site), *P*(pred + rabbit)	9	−1992.179	4002.358	4.660	0.035
	ψ(nnv + elv + TWI + 1|site), *P*(pred)	7	−1994.554	4003.109	5.410	0.024
	ψ(nnv + shrub + tree + 1|site), *P*(pred + rabbit)	10	−1991.588	4003.176	5.477	0.023
	ψ(nnv + elv + shrub + 1|site), *P*(rabbit)	8	−1993.762	4003.523	5.825	0.020
	ψ(elv + shrub + TWI + 1|site), *P*(pred + rabbit)	9	−1992.849	4003.698	6.00	0.018
Rabbit	ψ(nnv + elv + 1|site), *P*(day + pred)	7	−648.749	1311.498	0.000	0.264
	ψ(nnv + 1|site), *P*(day + pred)	6	−649.986	1311.972	0.473	0.208
	ψ(elv + 1|site), *P*(day + pred)	6	−650.492	1312.984	1.485	0.125
	ψ(. + 1|site), *P*(day + pred)	5	−651.940	1313.880	2.382	0.080
	ψ(nnv + elv + 1|site), *P*(pred)	6	−650.992	1313.985	2.486	0.076
	ψ(nnv + 1|site), *P*(pred)	5	−652.239	1314.479	2.980	0.059
	ψ(nnv + elv + 1|site), *P*(day)	6	−651.537	1315.075	3.576	0.044
	ψ(elv + 1|site), *P*(pred)	5	−652.742	1315.484	3.985	0.036
	ψ(nnv + 1|site), *P*(day)	5	−652.774	1315.547	4.049	0.035
	ψ(. + 1|site), *P*(pred)	4	−654.199	1316.399	4.900	0.023
	ψ(elv + 1|site), *P*(day)	5	−653.271	1316.542	5.044	0.021
	ψ(nnv + elv + 1|site), *P*(.)	5	−653.596	1317.193	5.694	0.015
	ψ(. + 1|site), *P*(day)	4	−654.722	1317.444	5.946	0.013

All models include a random intercept for study site (1|site). Model: Occupancy (ψ) covariates: nnv, distance to non-native vegetation from camera trap point; elv, elevation at camera trap point; TWI, topographic wetness index at camera trap point; tree, tree cover; shrub, shrub cover; ground, ground cover. Detection (*P*) covariates: pred, predator presence; hare, hare presence; rabbit, rabbit presence; day, days since camera deployment.

supported models) and days since camera deployment (8 of 13 supported models).

Model-averaged coefficients indicated that rabbit occupancy declined with increasing distance to non-native vegetation (Table 2, Fig. 2*a*), although this effect was not significant. Rabbit occupancy also showed a non-significant negative association with elevation (Fig. 2*b*). Detection probability was higher when predators were present (Fig. 1*c*) and declined with survey period duration (Fig. 2*d*).

Temporal analysis

Temporal analysis indicated substantial overlap in activity patterns between hares and rabbits, with both species being primarily nocturnal and crepuscular with peak activity occurring around dawn and dusk. The activity overlap between the two species was 82.6% (Fig. 3).

Discussion

Our study assessed the occupancy of hares and rabbits within mesic forests of the NSW Northern Tablelands and examined how habitat and landscape attributes influence patterns of occurrence. All models included a random intercept for study site, accounting for unmeasured heterogeneity among sites and supporting inference at the landscape scale rather than at individual sites.

Hare occupancy

Hares exhibited a strong association with proximity to non-native vegetation, with occupancy declining as the distance from non-native vegetation and cleared areas increased. This pattern is consistent with evidence that hares preferentially exploit anthropogenically modified environments (e.g. Towerton *et al.* 2011). Habitat modifications, such as the

Table 2. Model averaged coefficients and relative variable importance for fixed effects in occupancy (ψ) and detection covariates (P) and for the random intercept of study site from models within $\Delta AIC \leq 6$.

Species	Coefficient			
	Fixed effects	**Estimate**	**s.e.**	***P*-value**
Hare	ψ(intercept)	−1.102	0.905	0.223
	ψ(non-native veg)	−0.619	0.242	0.011*
	ψ(elevation)	0.421	0.223	0.059
	ψ(shrub cover mid)	−0.037	0.373	0.921
	ψ(shrub cover high)	−0.843	0.713	0.237
	ψ(TWI)	0.304	0.220	0.167
	ψ(tree cover low)	−0.070	0.304	0.817
	ψ(tree cover mid-high)	−0.033	0.222	0.880
	P(intercept)	−1.618	0.044	<0.001*
	P(predator)	0.394	0.235	0.093
	P(rabbit)	0.569	0.278	0.041*
	Random effects	**Variance**	**s.d.**	–
	Study site (intercept)	2.945	1.716	–
Species	**Coefficient**			
	Fixed effects	**Estimate**	**s.e.**	***P*-value**
Rabbit	ψ(intercept)	−2.242	0.702	0.001*
	ψ(non-native veg)	−0.302	0.279	0.279
	ψ(elevation)	−0.173	0.205	0.398
	P(intercept)	−1.971	0.309	<0.001*
	P(day)	−0.149	0.109	0.172
	P(predator)	0.674	0.386	0.081
	Random effects	**Variance**	**s.d.**	–
	Study site (intercept)	1.864	1.365	–

The random intercept indicates the level of unexplained heterogeneity in baseline occupancy probability among sites. Asterisk (*) indicates $P < 0.05$.

conversion of natural habitats to agricultural landscapes, create niche opportunities to facilitate hare range expansion (Pasqualotto *et al.* 2021). Fragmentation of forested areas may further assist the dispersal of hares into environments where they were previously undetected or absent. This could help us better understand hare presence within National Parks and other mesic environments where cleared areas are common by-products of historic livestock grazing practices.

Hare occupancy was also positively associated with increasing elevation. In New Zealand's South Island, hares have been recorded at elevations exceeding 2000 m (Foster *et al.* 2022), which is substantially higher than the maximum elevation sampled within our study area (1256.8 m). This broad elevational range indicates considerable tolerance to variation in climatic and environmental conditions. Similar flexibility along altitudinal gradients has been documented elsewhere, with hares adjusting foraging behaviour and diet composition in response to reduced resource availability at higher elevations (Puig *et al.* 2017). Additional research across wider elevational gradients within mesic forest systems in Australia would help clarify the mechanisms underlying this pattern.

Hares showed a moderate association with increasing TWI, indicating that hydrology was not a strong determinant of occupancy, at the scale examined. Although higher TWI values indicate a greater potential for water accumulation in the landscape (e.g. valleys or depressions) (Ågren *et al.* 2014; Mattivi *et al.* 2019), the absence of statistical support suggests that moisture gradients within mesic forest have limited influence on hare occupancy. A study in an Australian alpine environment reported that hare occurrence increased with distance from waterbodies (Hartley *et al.* 2022). In our study, we were unable to directly measure waterbodies due to the mostly ephemeral nature of local water sources, which are highly dependent on rainfall, and the lack of detailed, reliable spatial mapping for the area. Differences among studies highlight the potential role of local hydrological conditions in shaping habitat associations of hares and indicate further research is needed to clarify the underlying mechanisms.

Hare occupancy was only weakly associated with vegetation structure, with predicted occupancy highest at low shrub cover. This weak association is unexpected, as hares do not dig burrows and therefore depend on vertical structural complexity for refuge (Bock 2020). The absence of significant detectable effects may reflect limited variability in structural attributes across camera locations, or the preference for fine-scale features that provide functional shelter which were not measured in our broad-scale vegetation survey. It is also possible that landscape-scale predictors, such as elevation and non-native vegetation, have a stronger influence on occupancy, which may obscure more localised structural influences. Interpretation of the relationship between species and their environment can be scale-dependent (Wiens 1989). Therefore, fine-scale investigation examining vegetation structure and refuge availability is needed to further understand the vegetation communities that hares require to persist in forested systems.

Rabbit occupancy

Rabbit occupancy exhibited weak and uncertain associations with landscape variables. Although occupancy decreased with increasing distance to non-native vegetation, this relationship was poorly supported, with the null occupancy model remaining competitive. This pattern suggests that broad-scale landscape covariates alone may have limited explanatory power for rabbit occupancy within forested systems. Previous studies have reported higher rabbit abundance in continuous landscapes, combining open foraging areas and nearby shelter, rather than fragmented environments (Virgós *et al.* 2003). In our study, non-native vegetation mostly represented smaller

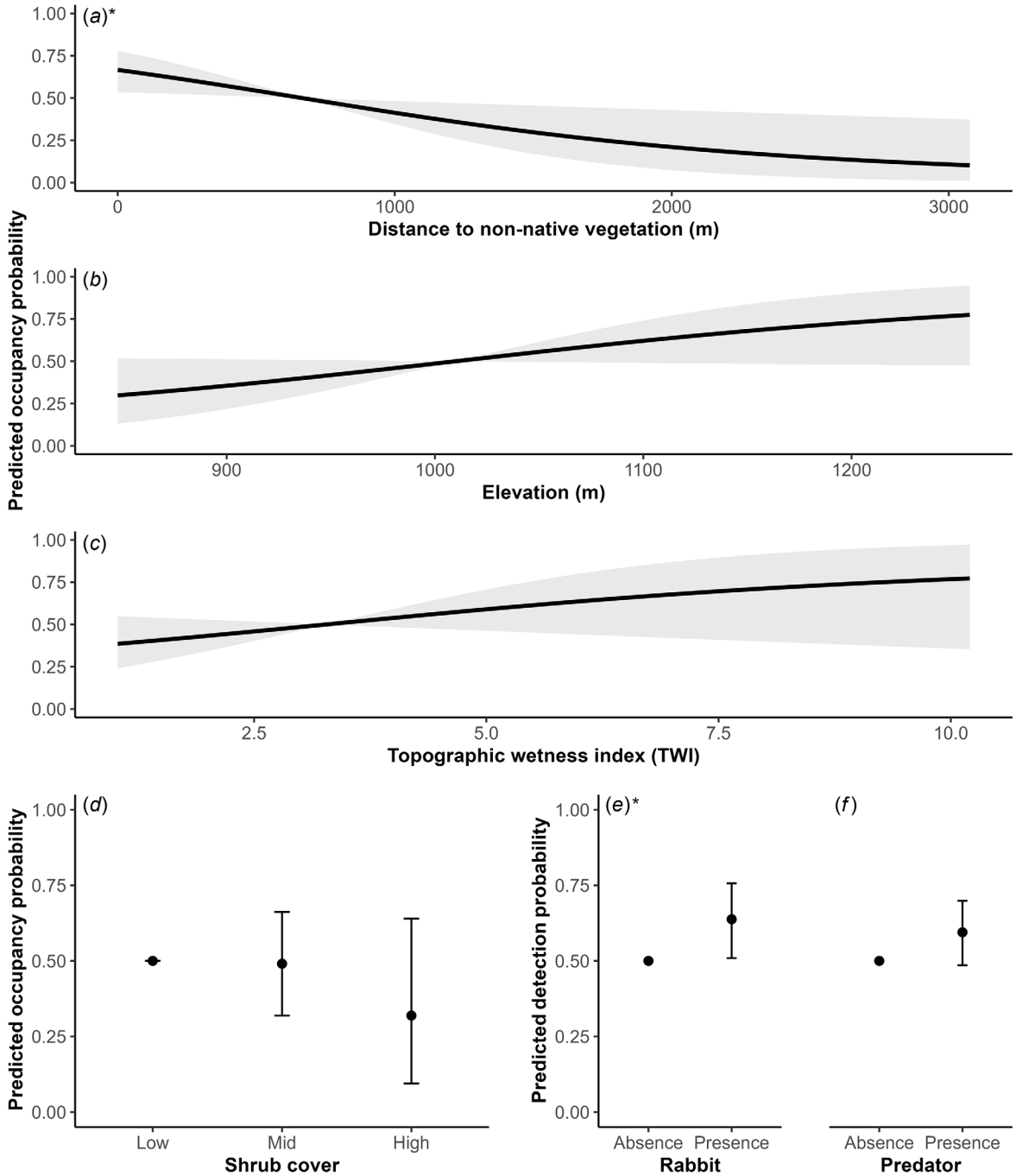

Fig. 1. Predicted occupancy probability of hares with variation in (*a*) distance to non-native vegetation, (*b*) elevation, (*c*) topographic wetness index, (*d*) shrub cover, and predicted detection probability in response to (*e*) rabbit detections and (*f*) predator detections. Predicted occupancy and detection probabilities represent population-level (fixed-effect) relationships, with shaded areas and error bars indicating 95% confidence intervals based on model-averaged uncertainty. Asterisk (*) on the graph indicates the variable had a significant effect ($P < 0.05$).

clearings, which may provide localised foraging opportunities for rabbits without strongly structuring occupancy at the site scale.

Rabbit occupancy also declined with increasing elevation, with higher occurrence at lower elevations. Similar elevational patterns have been reported elsewhere; for example, rabbits in New Zealand were largely restricted to lower elevations compared with other invasive mammals (Foster *et al.* 2022), although the elevational range examined in that study was much broader than in the present study. In our study, rabbits and hares exhibited contrasting elevational associations, with

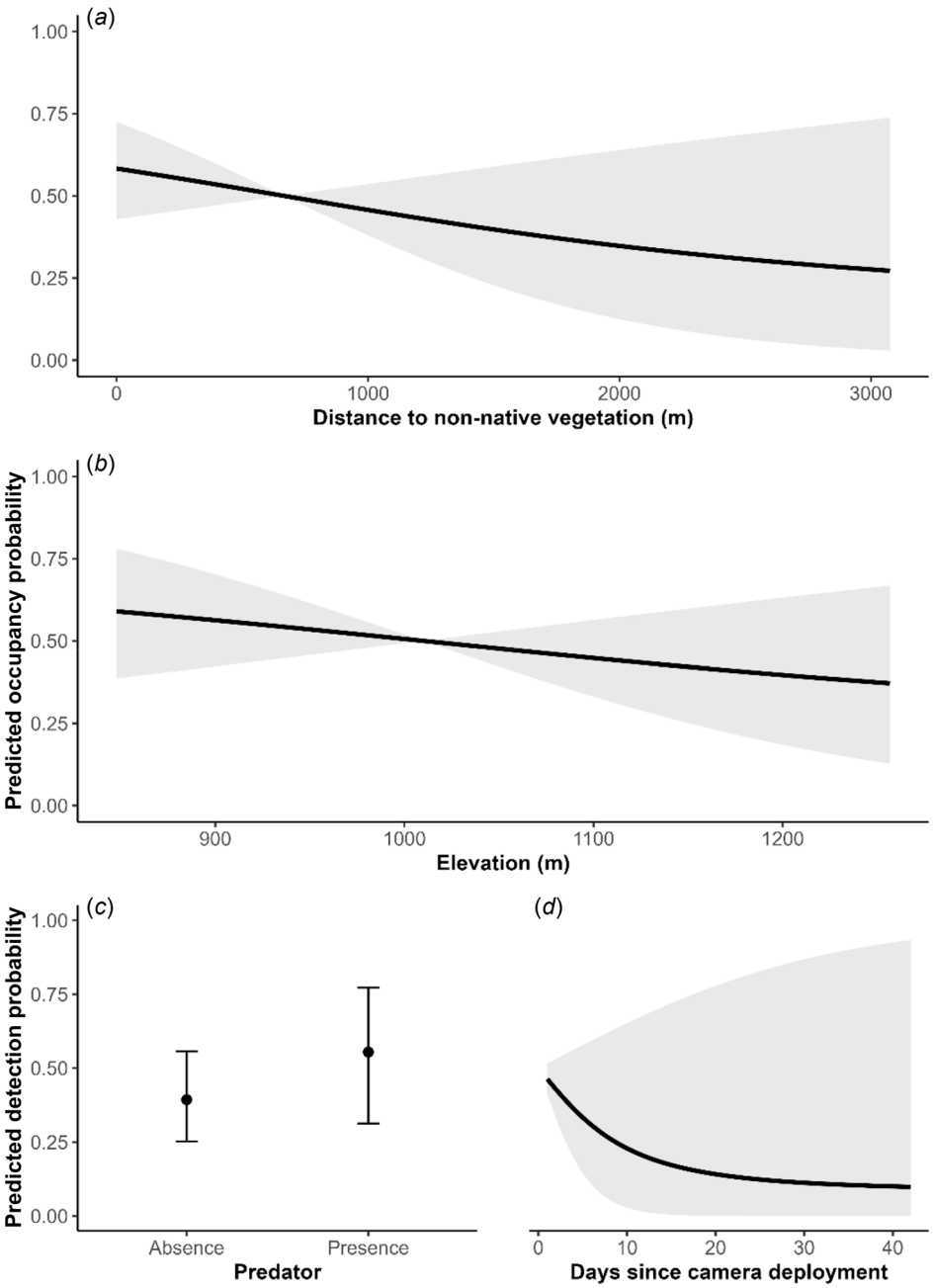

Fig. 2. Predicted occupancy probability of rabbits with variation in (*a*) distance to non-native vegetation, (*b*) elevation, and predicted detection probability in response to (*c*) predator detections and (*d*) days since camera deployment. Predicted occupancy and detection probabilities represent population-level (fixed-effect) relationships, with shaded areas and error bars indicating 95% confidence intervals based on model-averaged uncertainty.

rabbit occupancy greater at lower elevations and hares at higher elevations. This pattern suggests some spatial segregation between the two species along elevational gradients, potentially driven by unmeasured environmental factors such as temperature and rainfall (Elith and Leathwick 2009). Although competitive interactions could contribute to this pattern, our study was not designed to explicitly test interspecific competition, and such mechanisms should therefore be interpreted cautiously.

Soil type was considered as a potential covariate but was excluded from the final models due to limited variability among study sites. The soil types within the Northern Tablelands are clay rich and dominated by Chromosols and basalt-derived Ferrosols, with local Vertosols on alluvial

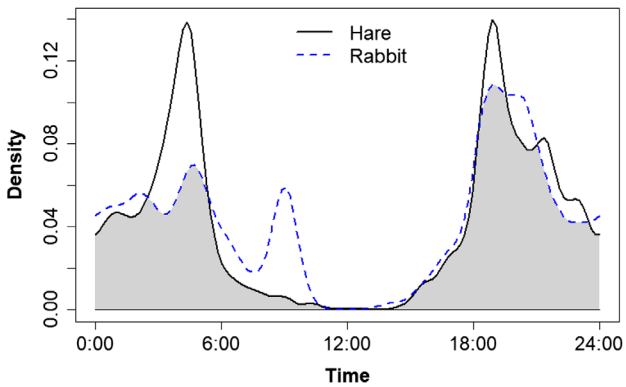

Fig. 3. Temporal overlap between hares and rabbits. The grey shaded area represents the 82.6% overlap between the two species.

flats (King 2009; Murphy and McCormick 2014). Along with the dense vegetation of forested systems, these soil types may limit warren construction (Williams *et al.* 1995) and hinder the success of rabbit populations within our study sites. It is therefore possible that the rabbits present at our study sites are living entirely above ground, particularly given the availability of shelter. Several studies have shown that when adequate aboveground cover is available, rabbits can remain surface dwelling rather than occupy warrens (Wheeler *et al.* 1981; White *et al.* 2003; Moseby *et al.* 2005), which may potentially limit their abundance in forested environments. Similar to hares, habitat variables showed weak and uncertain associations with rabbit occupancy.

Detectability

Hares were detected more readily than rabbits, suggesting possible greater local abundance, greater movement, or larger activity ranges within mesic forest environments. Hare detection probability also increased when rabbits were present, while rabbit detection probability was not influenced by hare presence. Predator detections were positively associated with detectability of both species, although this likely reflects predators selecting areas where prey is already established rather than predators directly increasing prey activity. In light of findings by Henderson *et al.* (2022), highlighting the value of predator-specific surveys over general camera trapping methods, it is worth noting that the camera arrays in this study were not designed specifically for terrestrial predator monitoring. Consequently, we acknowledge the data may have been suboptimal for evaluating the influence of predators on hare and rabbit detectability. Further research into the relationship between predators, hares, and rabbits in forest ecosystems is warranted.

Rabbit detection probability declined through the sampling period, whereas hare detectability did not, suggesting greater sensitivity of rabbits to deployment effects such as lure decay, vegetation changes (e.g. grass re-growth over time), or behavioural habituation. This temporal decline may partially explain the weaker and more uncertain occupancy associations observed for rabbits relative to hares.

Temporal patterns

We found no evidence of temporal partitioning between hares and rabbits. Hares were detected on more cameras than rabbits, which may indicate that hares have a larger home range, greater movement across the landscape or are found at higher densities. Although we did not specifically assess competitive interactions, a previous study has investigated co-occurrence patterns between hares and rabbits in Australia. Stott (2003) reported partial temporal and spatial separation between hares and rabbits at fine spatial scales, largely reflecting differences in habitat use and movement patterns. However, substantial overlap in space use was observed, and avoidance occured only near warrens at dawn and dusk. While that study was confined to a relatively open pasture system, it underscores the need for further research on hare and rabbit interactions within Australian mesic forests, where dense vegetation and limited open spaces may act as a barrier for activity range expansion and movement.

Future research directions

Building on the knowledge gaps identified throughout the Discussion; our results highlight the need for further research on hares and rabbits within forested landscapes. This could include improving our understanding of the factors driving variability in detection probabilities across study sites. Home ranges for lagomorphs in Australia vary, with rabbits occupying relatively small areas (~10 ha), whereas hares can exceed 140 ha in agricultural landscapes (Stott 2003). The smaller home range size of rabbits might mean they are less likely to be detected. Given knowledge gaps in hare and rabbit behaviour within forested systems, understanding both species' movement patterns in structurally complex habitats is needed to clarify how they use these landscapes, including the role of roads or other access routes such as gullies and fire access trails in colonisation, dispersal, and possible movement between resource patches. Habitat differences may impact detection probabilities too, as cleared regions likely form only a part of the utilised area for individuals of each species. Future research could integrate GPS telemetry collars with a refinement in species-specific camera trap monitoring to better understanding habitat use, movement, and predator–prey relationships within these systems.

Conclusion

This study provides insight into the ecology of sympatric hares and rabbits within mesic forest systems of the New England Tablelands in NSW. Occupancy modelling across multiple sites revealed contrasting responses to landscape variables

between the two species. Hare occupancy increased with proximity to non-native vegetation, and showed positive associations with elevation and TWI, suggesting that broader environmental gradients and landscape modification influence their occurrence. Rabbit occupancy also increased closer to non-native vegetation but exhibited weak associations with the covariates assessed, indicating that broad-scale factors alone may have limited explanatory power for rabbit distribution in mesic environments. These contrasting patterns highlight differences in how hares and rabbits utilise forested landscapes and suggest that management strategies may need to account for species-specific responses to environmental gradients and disturbances. Our findings underscore the importance of preserving native vegetation and limiting further landscape modification to reduce the availability of suitable habitat for hares and rabbits within these systems. Furthermore, this research contributes to the broader understanding of the ecological dynamics in this region, emphasising the need for continued monitoring of invasive species to aid managers with tracking changes in populations relative to any future management interventions.

Supplementary material

Supplementary material can be accessed from the article page online.

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Data availability. The data supporting this study will be shared upon reasonable request to the corresponding author.

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