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Disease-induced decline of an apex predator drives invasive dominated states and threatens biodiversity

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Running title: Apex predator loss promotes invasive communities

ABSTRACT

Apex predators are important in protecting biodiversity through top-down influence on food webs. Their loss is linked with competitive release of invasive mesopredators and species extinctions. The Tasmanian devil (*Sarcophilus harrisii*) has experienced severe declines over a 15 year period as a novel transmissible cancer has spread across its current geographic range. We surveyed the mammalian community, using hair traps, across the spatial extent of the devil's progressive population decline. We found increased activity of alien invasive species (feral cats, black rats), and reduced small and medium-sized native prey species in response to the timing of the decline. In areas of long-term devil decline invasive species comprised a significantly larger proportion of the community. The results provide evidence that the devil plays a keystone role in Tasmania's ecosystem with their decline linked to a shift towards an invasive state and biodiversity loss in one of Australia's most intact faunal communities.

KEYWORDS: Tasmanian devil; trophic cascades; mesopredator release; DFTD; apex predator; mammals; invasive species; hair traps; feral cat; community composition

INTRODUCTION

Severe declines of apex predators are occurring in ecosystems worldwide (Ripple et al. 2014), leading to more homogenised (Estes et al. 2011) and invaded (Wallach et al. 2010) ecosystem states. Larger predators are especially vulnerable to environmental and anthropogenic stressors, such as habitat fragmentation, emerging diseases and persecution (Purvis et al. 2001, Pedersen et al. 2007). Large carnivores provide a buffer to biodiversity loss (Letnic et al. 2012); their decline is associated with changes in community composition (Terborgh et al. 2001), competitive release of mesopredators (e.g. Prugh et al. 2009) and concomitant extinction of species at lower trophic levels (Crooks and Soulé 1999, Johnson et al. 2007). Nearly 50% of all mammal extinctions worldwide over the past two centuries have occurred in Australia (Short and Smith 1994), where widespread mammal declines continue (Ceballos and Ehrlich 2002). The majority of these extinctions are in the prey size range of common alien mesopredators, the red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*) (Johnson et al. 2007), and where an apex predator, the dingo *(Canis lupus dingo*) is present, declines are less severe (Letnic et al. 2012).

Environmental perturbations are often associated with ecosystem state-shifts and changes in species dominance (Scheffer et al. 2001), and provide opportunities for invasive alien species while non-invasive native species might be constrained by the same processes (MacDougall and Turkington 2005). Invasive species are listed as causal factors in extinctions for more than half of species on the IUCN list (Clavero and García-Berthou 2005). Alien predators may have more severe effects on native prey species than native predators because of prey naïveté and lack of specific avoidance behaviours (Salo et al. 2007).

"Natural experiments" offer opportunities to investigate the influence of apex predators on ecosystems. Manipulative experiments on predators are logistically and ethically challenging

(Trewby et al. 2008). Some of the best evidence for trophic cascades comes from research on the ecosystem effects following the extirpation (e.g. Crooks and Soulé 1999) or reintroduction (e.g. Ripple and Beschta 2007) of apex predators. A natural experiment on the trophic influence of apex predator loss on an intact mammal community is unfolding in the island state of Tasmania, Australia. An apex predator, the Tasmanian devil (*Sarcophilus harrisii*), is in severe decline with the emergence in the mid-1990s of a consistently fatal transmissible cancer, devil facial tumour disease (DFTD) (McCallum et al. 2009). Population decline of devils is rapid and severe following DFTD outbreak (McCallum et al. 2007, McCallum et al. 2009). Localised declines in early-diseased areas exceed 90% and the disease has spread to more than 84% of the devil's range (STTDP 2012), with no indication of population recovery, although devils still persist in diseased regions at low densities (Hollings et al. 2014).

In contrast to the mainland of Australia, Tasmania retains an almost intact community of native marsupial and avian carnivores (less the 20th century extinction of the thylacine *Thylacinus cynocephalus*), and all native mammalian prey species are extant. The size-structured native carnivore guild comprises the Tasmanian devil (weight: males=~12kg, females =~7kg), the effective apex mammalian predator following extinction of the thylacine (25-35kg), the spotted-tailed quoll (*Dasyurus maculatus*; males=~4kg, females=~2kg) and eastern quoll (*D. viverrinus*; males=~1.5kg, females=~1.0kg). Alien mammal species include two predators (feral cat, ~3-5kg; red fox, ~3-10kg) and three rodents (black rats *Rattus rattus*, brown rats *R. norvegicus*, house mouse *Mus musculus*). Feral cats have been in Tasmania since European settlement (Abbott 2002) but, in contrast to mainland Australia, have not caused any native mammal extinctions. Competition is likely between cats and spotted-tailed quolls due to similarities in body size and prey composition, comprising small- and medium-sized animals (Dickman 1996, Jones and Barmuta 1998). Since 1998 and until recently there has been evidence of a very low population of red foxes (Sarre et al. 2012) but they have disappeared or remain at densities too low to have measurable impacts..

We investigate how mammal community composition and abundance varies with the time since disease outbreak and the corresponding severe and ongoing decline of the apex predator. We ask: 1) is abundance or activity of alien invasive mammal species higher and is species diversity lower with increasing time since disease outbreak? 2) do ecologically similar native and alien species respond differently to apex predator decline? 3) is there evidence for mesopredator release of native or alien mesopredators in response to devil decline? 4) does the presence of certain predator species affect the abundance of their prey species? We address these specific community and species responses by conducting rapid snapshot surveys across Tasmania in a space-for-time framework that encompasses the full range of DFTD-arrival times, representing a proxy for devil population decline over time.

METHODS

Site selection

We partitioned the island of Tasmania into three regions based on the timing of DFTD outbreak (Figure 1). North-east Tasmania was defined as the "early-disease region", where DFTD outbreak occurred between 1996 and 1999, 10-14 years prior to the study, and where devil population decline was more than 90%. The "midterm-disease region" was the central part of the island where disease outbreak occurred between 2003 and 2007, 3-7 years prior to the study, and where devil populations declined by 50-70% (Lachish et al. 2007, McCallum et al. 2009). The "disease-free region" of north-west Tasmania retained high devil densities at the time of the study. We estimated the number of years sites had been diseased by combining extrapolations of confirmed disease from surrounding regions with expected patterns of disease spread (McCallum et al. 2007, STTDP 2012).

We selected 48 field sites with equal numbers in each DFTD outbreak region, using ArcGIS (Version 9.2). Predefined criteria were established to ensure sites were as environmentally comparable as possible: altitude below 650m, mean annual rainfall between 1100 and 1600mm (Australian Bureau of Meteorology data) and where possible located in northern Tasmania to limit variation from a north-south temperature gradient (Figure 1). Environmental gradients exist across the island, which affect species distributions; however site selection to match environmental parameters should prevent any confounding effects. Within each of the three DFTD-outbreak regions, we selected four replicate sites for four vegetation types: mature wet eucalypt forest (~15% of total forest area in Tasmania); mature dry eucalypt forest (~38% of total forest area); regenerating wet eucalypt forest (~10% of total forest area); and coastal heath and scrubby woodland (~6% of total land area) (TasVeg GIS layer; Forestry Tasmania State of the Forest 2012) (Figure 1). Each site comprised a 2km unsealed track accessible by four-wheel drive, which was never or infrequently used by the public. All but one site was located on public land (State Forest or National Park).

Data collection

We conducted rapid site surveys using a total of 5,760 hair traps to obtain a relative index of abundance or activity for devils, mesopredators and mesopredator prey species. Each site was surveyed for three consecutive nights during three field seasons: April-December 2009, March-June 2010 and September-December 2010. The survey order of the 48 sites was randomised within each field season, with eight sites in each region surveyed in a two week block, subject to weather and bushfire conditions. Hair trapping has been regularly used to detect forest mammals in Australia (Mills et al. 2002), with effectiveness of different types known to vary among species (Lindenmayer et al. 1999, Mills et al. 2002). Accordingly, at each site we deployed two different hair trap types: 20 hair tubes, consisting of a PVC pipe with ~10cm strips of double-sided adhesive tape within both ends, and 20 commercially produced hair funnels (Faunatech, Australia). Half the traps of each type were baited to attract herbivores (rolled oats, peanut butter and walnut oil) and half were baited for carnivores (dried liver soaked in muttonbird oil). We secured at ground level one herbivore and one carnivore hair trap every 100m on alternate sides of the track, at least 20m from the track and a minimum of 10m from each other, alternating combinations of trap and bait type. Hair samples were identified to species using colour, and cross-sectional shape and pattern of the cortex and medulla (Triggs et al. 2002). Almost a quarter of hair samples collected (~600) were sent to an independent expert (B. Triggs) for analysis; these included samples that contained only a few hairs and samples for verification of our identifications. Hair samples which could not be identified to species were removed from the dataset. To further verify the accuracy of hair identifications, species detected in hair traps were compared to those detected with four baited remote infra-red motion-activated cameras (Model: Scoutguard 550), four of which were deployed at 500m intervals at each site during the hair trap surveys. Cameras were set 10-30cm above the ground in vegetation at least 20m from the track and were set to record 1 minute of video when activated.

Data handling

We treated the site records of species presence at each hair trap as indices of activity for medium- and large-bodied mammals because they could visit multiple hair traps spaced 100m apart. For small mammals site records represent an index of relative abundance because of the short deployment time and small home range size relative to trap spacing (e.g. 45m radius for the swamp rat (*Rattus lutreolus*) (Taylor and Calaby 1988)). Individuals of species were not identified and therefore the maximum number of detections for any one species at a site was limited by trap number, a maximum never reached.

We classed the hair-trap data for small mammals into "native" and "alien". Of five native rodent species and three carnivorous marsupials that occur in Tasmania, we identified hair from the long-tailed mouse (*Pseudomys higginsi)* and the swamp rat. Black rats were the only alien rodent species included in the analysis. We excluded house mice because they underwent a population irruption in 2010 in the early and mid-DFTD regions, associated with environmental conditions ideal for breeding (Figure 4). Brown rats were not detected in any samples. We combined data in a "medium mammal" category (weight 600-1200g) for three native marsupials: the southern brown bandicoot (*Isoodon obesulus),* eastern-barred bandicoot (*Perameles gunnii),* and long-nosed potoroo (*Potorous tridactylis*). Tasmanian bettong (*Bettongia gaimardi*) and eastern quoll samples were excluded from analyses as they have restricted geographic distributions (Figure 4).

Statistical analysis

Community composition

To assess whether species composition and degree of homogeneity of mammal communities varied with DFTD region, we applied nonmetric multidimensional scaling (nMDS) with the Bray-Curtis dissimilarity matrix (library 'vegan' in R 2.11.0). Species composition data were derived from the number of positive hair traps for each species for each of the three replicate surveys from all field sites. Data were standardised by applying a log (x + 1) transformation to reduce the influence of the most abundant species and to increase emphasis on the rarer species (Legendre and Legendre 1998). Species composition was analysed separately for the four vegetation types as habitat value will vary for each species.

We conducted a permutational multivariate analysis of variance (Anderson 2001) on the composition data for the four vegetation types with the Bray-Curtis dissimilarity matrix as the response variable and the number of years a site had been diseased as the predictor variable. We restricted the permutations to within field seasons to account for the randomization of the repeated measures from the three repeat surveys of field sites.

Invasive species community composition

We assessed whether alien species of different trophic levels (cats and black rats), comprised a greater proportion of the overall community composition in response to declining apex predator populations. Hair traps positive for devils were excluded from the community composition data. First, we plotted the proportion of hair traps positive for alien species within each DFTD-arrival region. Second, we modelled the proportion of positive hair trap records for all alien species, with the number of years a site had been diseased and vegetation type as predictor variables. We used generalized linear mixed models (GLMMs) with a binomial error structure and logit link function (library 'lme4' in R version 2.11.0). These models included random effects of sites and field season to account for the repeated site surveys across three field seasons. To assess the support for the four alternative models, including the null, we used the weights (w_i) derived from small sample corrected Akaike Information Criterion (AICc) (Burnham and Anderson 2002).

Mesopredator activity and relative abundance of prey

We assessed whether there were discernible differences in the activity or abundance index of each species in relation to 1) length and extent of devil population decline, and 2) occurrence/abundance of competitively dominant species, predators or prey. For all species except cats, the response variable was the proportion of hair traps deployed that were positive for the species of interest, for each individual survey of a site. For cats we used presence/absence data as only two sites had more than one trap positive for cat hair.

For all models, the predictor variables were the number of years since DFTD arrival, vegetation type, and other species which may have a direct effect on the species of interest (depending on the species this was measured as either occurrence (presence-absence), abundance or activity). Correlations between predictor variables were assessed prior to analyses using Spearman's rank correlation coefficient. The only predictor variables that were strongly correlated (inversely) were devil activity measured from hair traps and years since DFTD arrival (Spearman's rank correlation coefficient = -0.69). We used years since DFTD arrival as the predictor variable in all analyses to represent devil abundance. This variable is a better proxy for extent of devil decline on a regional scale, whereas the activity measure is a more localised and potentially 'noisier' index of devil activity. To reduce over-fitting, we limited the number of species used as predictor variables to two, using those predators or prey species the authors considered likely to have the most influence on the species being analysed, based on relevant literature of mesopredators' diet (e.g. Dickman 1996, Jones and Barmuta 1998, Glen and Dickman 2008). No species were used as predictor variables for devils. For mesopredators, the cat and the spotted-tailed quoll, we used native and alien small mammals as predictors. These mesopredator species were used as the predictor variables for their prey species, the medium mammals and the native and alien small mammals.

We tested for zero inflation (using 'glmmADMB' package in R) for each species by fitting zero-inflated GLMMs with random effects to the null models. The fit of the zero-inflated binomial model against a binomial GLMM was assessed using AICc. There was no evidence for zero-inflation for any species and all species that had many zeros in the data had low mean:variance ratios.

We used GLMMs with a binomial error distribution and logit-link function to fit the models with random effects of site and field season as for previous analyses. A set of alternative models was fitted to species data, with the most parsimonious model selected on its AICc. All combinations of models were tested using the four predictor variables for each species. The relative importance of each explanatory variable was quantified by summing the weights of all models containing the variable (Burnham and Anderson 2002, Rhodes et al. 2006).

RESULTS

Community composition

Non-metric multidimensional scaling indicated that a large proportion of sites within the early-diseased region were closely related and therefore clustered together in three of the four vegetation types (Figure 2). The signal was strongest in the dry eucalypt forest sites and coastal woodland scrub but absent in the wet eucalypt regeneration forest. No pattern was evident for either the midterm or the disease-free sites. Permutational multivariate analysis of variance corroborated the findings from the nMDS, indicating that community composition was significantly associated with the number of years the site had been diseased in three vegetation types, with the strongest effects in dry eucalypt and coastal vegetation (Figure 2). The tighter clustering of early-diseased sites, relative to disease-free sites, may represent a tendency towards more homogenised mammal communities. There was no evidence of clustering or association with the number of years diseased in wet eucalypt regeneration sites.

Invasive species community composition

Some of the differences in community composition between DFTD-arrival regions may arise from an increased dominance of alien species in the early-diseased region, particularly in dry eucalypt forest (Figure 3). The predictors of number of years since disease outbreak and vegetation type were important in explaining the proportion of positive hair traps for alien species, with the best supported model (w_i =66%) containing both variables (Table 1). The second best model, containing only years since disease outbreak, was not significantly different from the best supported model (ΔAICc < two) and accounted for 32% of the weight within the candidate model set (Table 1).

Mesopredator activity and relative abundance of prey

The activity of devils showed clear and significant declines associated with the number of years since disease outbreak (Figure 4). Only two models had substantial (w_i>1%) weight in the candidate model set: the model with the years since disease outbreak as the single predictor variable (w_i = 62%) and the model with years since disease outbreak and vegetation type as predictors (w_i = 38%) (Table 2a). This result provides strong support for the use of years since disease outbreak as a predictor variable to represent the extent of devil population decline, and the use of hair trap rates as a proxy for species activity.

The activity index for cats was strongly and positively linked with the time sites had been diseased (Figure 4). The GLMM model with the number of years diseased as a single predictor variable had the highest weight (w_i = 39%) and the relative importance of this variable (the weight of all models containing it as a predictor) was 93% (Table 2a). Cat activity was also positively associated with the presence of both native and alien rodent species (models within ΔAICc of two), although the relative importance of these predictor variables carried lower weight at 33% and 28%, respectively (Table 2a).

The native spotted-tailed quoll was positively associated with populations of alien small mammals. The model containing this single predictor carried the highest weight (w_i =25%) and models containing this variable comprised a relative importance of 81% (Table 2a). Vegetation type also had some importance for spotted-tailed quolls populations (w_i =19%; relative importance 41%). The highest detections of spotted-tailed quolls for all vegetation types occurred in the midterm-diseased region (Figure 4). Lowest recorded activities were in the early-diseased region for all vegetation types except wet eucalypt regeneration forest. Neither years since disease outbreak nor the abundance of native rodents had a strong influence on the spotted-tailed quoll activity index with relative importance in the candidate model set of 25% and 27%, respectively.

The relative abundance of mesopredator prey species reflected secondary effects from devil decline and increased cat activity, but the nature of the effects varied between native and introduced species (Table 2b). Native medium mammals were negatively associated with the activity index of the spotted-tailed quoll (relative importance 51%), followed by that of the cat (relative importance 42%) (Table 2b). The model with spotted-tailed quolls as a single predictor variable had the highest model weight ($w_i = 0.16$), however this was not substantially different from five other models, including the null model ($w_i = 0.15$). The lowest recorded number of positive hair traps of native medium mammals for all vegetation types was in the midterm-disease region (Figure 4).

Small native mammals were strongly negatively affected by the number of years since disease outbreak; the relative importance of this variable was 96% (Figure 4, Table 2b). Vegetation type was also important for these species with relative importance of 98%. The model containing both these predictors was the only model in the final set and held 52% of the weight in the candidate model set. The highest hair trap rates were in mature wet eucalypt forest (Figure 4) – this was substantially higher than wet regeneration forest for all regions.

The abundance of black rats was positively associated with the number of years a site had been diseased and the activity index of cats and spotted-tailed quolls. These three variables were included in the final set of three models that were within an AICc of two (Table 2b). The relative importance for the spotted-tailed quoll as a predictor of black rats was the highest at 80%, followed by a less substantial influence of cats at 34%. Vegetation type was not important in explaining black rat populations.

For all models in this study which used species predictor variables, there is a measurement error which causes a bias towards the null model. Only medium mammals had the null model falling within the candidate model set (i.e. ΔAIC < 2). Whilst at some sites and times, cameras detected species that hair tubes did not, and vice versa, detections by hair tube and camera in each region were congruent for each species (see Table S1 in supplementary materials). Small mammals were not identified due to the very large number of videos, and difficulties in identification of some species due to image quality and distance from the camera

DISCUSSION

Tasmania's mammal community is shifting towards dominance by alien species following the disease-induced decline of the Tasmanian devil, supporting the hypothesis of top-down keystone function in the largest extant mammalian predator. In three of the four vegetation communities, mammalian species composition changed with increasing time since DFTD arrival and thus with decline of devil populations. There was a greater proportion of invasive species (cats and black rats) and a reduced proportion of all native prey species following disease arrival, likely mediated by the greater activity of cats. These patterns were less evident in wet regeneration forest, possibly because positive hair traps for native species were generally lower in wet regeneration forest relative to wet mature forest.

Our results provide strong support for mesopredator release of cats, with increasing activity correlated with increasing number of years since DFTD arrival. This space-for-time study corroborates our previous findings from analysis of long-term spotlighting surveys of an increase in cat observations in some ecosystem types following devil decline (Hollings et al. 2014). That two independent analyses, each with their own advantages and limitations, have reached the same conclusion greatly increases confidence that this is a real phenomenon. Our conclusion that devils have a strong competitive effect on cats is supported by findings of two camera studies conducted at sites with very low devil densities. Lazenby and Dickman (2013) found that cats avoided devils at camera stations placed to the sides of unsealed vehicular tracks, as in this study. This result is remarkable because of the low to very low devil densities at all three surveyed sites due to habitat and bioclimatic unsuitability for devils, or population reductions following DFTD outbreak 5-7 years prior to the study. A second camera study, done in 2012, also shows that at extremely low devil densities 8 - 10 years after disease outbreak (midterm-diseased region), cats strongly modified their time of activity to avoid devils, a pattern that was less evident 13 – 15 years after disease outbreak (early-diseased region) (Fancourt et al. 2015). Devil populations undergo rapid and severe decline following disease outbreak, to 90% decline after about five years (Lachish et al. 2007, McCallum et al. 2007). All studies concur that devils are able to effect spatial and temporal avoidance behaviour in cats for a decade after disease arrival and severe population decline, although this effect may diminish after an extended period of very low population densities. This provides strong support that there is likely to have been competitive release of cats following catastrophic decline of the devil across its range.

Some of the increased activity recorded by hair traps and spotlighting surveys could be related to changes in the behaviour of cats following devil decline. Devils may be differentially attracted to roads to scavenge for roadkill, and to tracks and ecotones between grassland and forest to hunt, place latrines, disperse and otherwise travel; behaviours that could displace cats at high devil densities. Hair traps in this study were placed in bush away from disused or rarely used tracks, with little chance of roadkill and a reduced focus of devil activity and so are more likely to record a population increase in cats rather than behavioural change. Our results have parallels with the situation on mainland Australia, where reduction in the population of a different apex predator, the dingo, can permit feral cats to relax spatial and temporal partitioning behaviours by which they avoid dingoes and thus take greater advantage of prey availability (Brook et al. 2012). Following apex predator loss, behavioural changes, such as increased activity, altered activity times and changes in habitat use may occur rapidly. As these behaviours are linked to fitness they can translate over time to changes in population vital rates (survival, growth and reproduction) and population size (Morris et al. 2009).

Evidence for mesopredator release in the spotted-tailed quoll is less clear. Competitive release could be expected following devil decline on the basis of diet overlap (Jones and Barmuta 1998), but this may be countered by competition from an increasing cat population; cats and quolls are similar in body size, diet and space use (Dickman 1996, Glen and Dickman 2008). The results suggest suppression of quoll activity by cats. Activity indices of spotted-tailed quolls were lowest in the early-diseased region where devil populations are lowest and cat activity is highest, and highest in the midterm-diseased region where devils declined recently and cat activity is lower than in the early-diseased region. These cat activity patterns across the DFTD regions in this study are from sites matched for habitat type; the patterns in Hollings et al. (2014), which showed contrasting top-down and bottom-up influences in forest and farmland habitats, respectively, reflect aggregations of sites across DFTD regions which were not ecologically equivalent. In contrast to the response of cats to devil decline, the activity index of the spotted-tailed quoll was closely related with the abundance of prey species, both native and alien. It is also possible the mammalian responses are blurred by competing avian species: highly mobile raptors and/or corvids may respond to beneficial circumstances more rapidly than mammals. Increases in carrion are expected as devils are a major scavenger. Avian scavengers are known to respond positively to increased carrion as a result of changing predator dynamics (Wilmers et al. 2003a), and their mobility and ability to communicate about resources allows them to derive a greater advantage from carrion in some circumstances (Wilmers et al. 2003b) .

Increasing mesopredator populations will increase predation pressure on their prey, potentially causing population declines and extinctions in native species (Crooks and Soulé 1999, Johnson et al. 2007). In this study, the relative abundance of all mesopredator prey species studied correlates with either the time since commencement of devil decline, or mesopredator activity, in particular of the feral cat, although the direction of the response for native and alien species varies. Small native mammals in particular appear to be facing substantial population declines, with the greatest magnitude of response of all prey species, although causes and correlates of decline cannot be disentangled with this dataset. The abundance of black rats, in contrast, has increased with the occurrence of cats and years since DFTD arrival. There are two plausible explanations for the difference in the response of native and alien prey species. First, native species are often naïve to alien predators, making them considerably more vulnerable to predation by alien than by native predators (Salo et al. 2007). This naiveté has been demonstrated in two native Tasmanian mammals: eastern quolls and swamp rats (Jones et al. 2004, McEvoy et al. 2008). Second, “invasional meltdown” may occur (Simberloff and Von Holle 1999), whereby high numbers of cats facilitate the establishment and high abundance of alien invasive prey (rabbits and rodents), which in turn support high cat densities. In the Tasmanian context, the mechanism could be that increased predation on both native small mammals and alien rodents may favour residency of black rats, which have a higher intrinsic reproductive rate (Yom-Tov 1985). They may then gain a priority effect over the re-establishment of native small mammals which have previously been able to resist invasion (Stokes et al. 2009). Either way, the varied responses of prey species are suggestive of alien invasive species driving community structure in areas of long-term devil decline. Increased predation and competition by introduced cats and rodents could place all small native mammal species in Tasmania at risk of local declines or extinction.

Environmental variables can influence the magnitude of responses to apex predator loss (Elmhagen and Rushton 2007, Hollings et al. 2014). Vegetation type differentially affected the response of native species to devil decline, with the strongest effects in native small mammals, followed by the spotted-tailed quoll. In contrast, there was almost no vegetation effect on alien species, either rats or cats. These results support theoretical predictions that successful invasive species are frequently habitat generalists, an attribute that contributes to their invasion success (Marvier et al. 2004). Native rodents are more sensitive to vegetation type and may be more vulnerable than introduced species to ecosystem disruption, including habitat loss and degradation.

Wallach et al. (2010) indicated that mainland Australian ecosystems, now dominated by alien placental carnivores, the red fox and the cat, have undergone a state-shift from which ecosystem recovery is difficult. We believe that we are the first to document a mammal community in transition to an invasive state. Extinction is obviously irreversible, but broad-scale predator-induced declines of species are extremely difficult to rectify because of the difficulty of controlling foxes and cats. We have already seen the dramatic and sustained decline in eastern quolls, which is correlated with devil decline (Hollings et al. 2014); and possibly the extinction of the Tasmanian subspecies of the New Holland mouse (*Pseudomys novaehollandiae*), which has not been detected in the wild for 10 years (Billie Lazenby, *pers. comm.*). To different degrees, both are vulnerable to predation by cats.

Invasive alien species have successfully colonised and now dominate landscapes in most parts of the world, resulting from both the intentional and accidental release of species (Kolar and Lodge 2001, Didham et al. 2005). As devils continue to decline and competitive and predatory suppression is further lifted, invasive species, which often have greater adaptability to changing anthropogenic influences (Didham et al. 2005), may extend their ecological dominance, potentially becoming the dominant force in driving community structures (Croll et al. 2005). The loss of an ecologically functional apex predator leading to a more invasive state has been demonstrated previously (Wallach et al. 2010) and may be a common consequence of apex predator loss (Estes et al. 2011). Common generalists such as the indigenous forest raven *(Corvus tasmanica)* and alien rodents may also be optimally placed to take advantage of new resources freed by diminished competition (Marvier et al. 2004).

This study is a dramatic example of an emerging infectious disease causing not only large-scale population decline in an apex predator but far-reaching and possibly irreversible effects on ecological communities. This research helps provide answers on the role of rising invasive mesopredator populations on the resilience and persistence of native fauna. The risk that disease-induced decline of an apex predator may have substantial, detrimental effects on ecological communities is unlikely to be restricted to Tasmania. Carnivores are one of two mammalian orders (the other artiodactyls) most commonly reported in the Red List as being threatened by parasites and pathogens (26% of canids and 8.3% of felids) (Pedersen et al. 2007). Apex predators globally have been lost from large tracts of their historical ranges. Their preservation and restoration as keystone species may be critical for protecting biodiversity and promoting ecosystem resilience.

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SUPPLEMENTARY MATERIALS

Supplementary Table S1: Small-sample corrected *AIC* (AIC_c) values for generalised linear mixed models comparing detection of mammals in hair trap samples and camera traps.

TABLES

TABLE 1: *GLMM model outputs testing the assertion that alien species comprise a greater proportion of the community with increasing time since DFTD arrival with ΔAICc, k = number of parameters, model weight (w_i) and model coefficient estimates with ±1 SE. Dashed lines highlight the most heavily weighted models from the candidate model set within ΔAICc of two. Relative importance of variables represents the weight of all models which contain that variable. Vege type parameters are against coastal scrub, W = Wet mature eucalypt forest, D = Dry eucalypt forest, WR = Wet eucalypt regeneration forest.*

Model rank	***k***	**ΔAICc**	**w_i**	**Parameter estimates**		
				Intercept	**Years diseased**	**Vegetation**
1	4	0.00	**0.66**	-2.19±0.47	0.14±0.04	D:1.00±0.53 W:-0.62±0.52 WR:-0.07±0.53
2	7	1.48	**0.32**	-2.14±0.39	0.12±0.04	
3 (Null)	3	7.67	**0.01**	-1.45±0.31		
4	6	8.88	**0.01**	-1.55±0.45		D:0.87±0.58 W:-0.47±0.56 WR:0.26±0.56
Relative importance of variable (%)					**98**	**33**

TABLE 2*: Most parsimonious GLMM models and parameter estimates for a) top order carnivores and, b) mesopredator prey species for hair trap data analysis. k = parameters, model weight (w_i) and model coefficient estimates with ±1 SE. Models from the candidate model set within ΔAICc of two of best model are shown, together with the null model. Relative importance*

of variables sums the weight of all models in the candidate set which contain that variable. Vege type parameters are against coastal scrub, W = Wet mature eucalypt forest, D = Dry eucalypt forest, WR = Wet eucalypt regeneration forest. NA = Not assessed for that species.

a) *Top order carnivores*								
				Parameter estimates				
Model rank	***k***	**ΔAICc**	w_i	**Intercept**	**Years diseased**	**Vege Type**	**Small mammal introduced**	**Small mammal native**
Tasmanian devil								
1	4	0.00	**0.62**	-1.69±0.21	-0.23±0.03		NA	NA
2	5	1.24	**0.38**	-1.22±0.29	-0.22±0.03	D:-0.50±0.37 W:-0.75±0.37 WR:-0.76±0.38		
3 (Null)	3	43.11	**0.00**	-3.09±0.22				
4	4	44.57	**0.00**	X		X		
Relative weight of variable (%)					**100**	**38**		
Feral cat								
1	4	0.00	**0.39**	-2.64±0.46	0.13±0.05			
2	5	1.41	**0.19**	-2.88±0.56	0.14±0.05			0.11±0.13
3	5	1.93	**0.15**	-2.70±0.49	0.13±0.05		0.10±0.21	
4	6	3.32	**0.07**	X	X		X	X
5	5	3.87	**0.06**	X	X	X		
6	6	4.79	**0.04**	X	X	X		X

7 (Null)	3	4.97	**0.03**	X				
Relative weight of variable (%)					**93**	**14**	**28**	**33**
Spotted-tail quoll								
1	4	0.00	**0.25**	-4.54±0.27			0.17±0.08	
2	5	0.56	**0.19**	-3.96±0.41		D:-1.24±0.55 W:-0.32±0.53 WR:-0.73±0.53	0.18±0.08	
3	5	1.91	**0.10**	-4.59±0.28			0.03±0.07	0.17±0.08
4	5	2.04	**0.09**	X	X		X	
5	6	2.72	**0.06**	X		X	X	X
6 (Null)	3	2.81	**0.06**	X				
7	6	3.14	**0.05**	X	X	X	X	
8	4	3.59	**0.04**	X			X	
Relative weight of variable (%)					**25**	**41**	**81**	**27**

b) Mesopredator prey species

Model rank	***k***	**ΔAICc**	w_i	**Parameter estimates**				
				Intercept	**Years diseased**	**Vege Type**	**Feral cat**	**Spotted quoll**
Medium mammals								
1	4	0.00	**0.16**	-5.11±0.30				-0.18±0.14
2 (Null)	3	0.04	**0.15**	-5.23±0.26				

3	5	0.49	**0.12**	-5.02±0.30			-0.74±0.65	-0.18±0.14
4	4	0.56	**0.12**	-5.13±0.26			-0.73±065	
5	4	1.42	**0.08**	-4.92±0.35	-0.03±0.04			-0.18±0.14
6	6	1.53	**0.07**	-5.05±0.33	-0.03±0.04			
7	5	2.30	**0.05**	X	X		X	X
8	6	2.41	**0.05**	X	X		X	
9	5	2.74	**0.04**	X		X		X
Relative weight of variable (%)					**31**	**20**	**42**	**51**
Native small mammals								
1	5	**0.00**	**0.52**	-3.44±0.37	-0.10±0.03	D:-0.98±0.51 W:0.87±0.44 WR: 0.04±0.46		
2	6	2.07	**0.19**	X	X	X	-0.09±0.26	
3	6	2.16	**0.18**	X	X	X		0.01±0.05
4	7	4.26	**0.06**	X	X	X	X	X
Null	12	13.85	**0.00**	X				
Relative weight of variable (%)					96	98	26	25
Introduced small mammals								
1	4	0.00	**0.35**	-5.08±0.23				0.13±0.06
2	5	1.09	**0.20**	-5.16±0.25			0.39±0.38	0.14±0.06
3	5	2.00	**0.13**		0.02±0.04			0.14±0.06

4 (Null)	3	2.43	**0.10**	X				
5	6	3.22	**0.07**	X	X		X	X
6	4	4.14	**0.04**	X			X	
7	4	4.49	**0.04**	X	X			
Relative weight of variable (%)					**25**	**7**	**34**	**80**

FIGURE LEGENDS

FIGURE 1: *Field sites in Tasmania, categorised into vegetation type and arranged into three disease arrival regions: early DFTD presence (1996-1999); midterm DFTD presence (2003-2007); and DFTD absent (disease-free).*

FIGURE 2: *Non-metric multidimensional plot for species compositions across the three DFTD regions of early-disease, midterm-disease and regions which are currently disease-free. Plots display all repeat surveys from each field site. Grey lines are "spider plots" connecting each point to the centroid of its group. Results for the permutational multi variate analysis are shown inside the plot for each vegetation type.*

FIGURE 3: *The proportion of positive hair traps which were identified as an alien species, based on mesopredators and their prey species in regions that vary in the time since DFTD outbreak, representing a proxy for the extent of devil population decline. Error bars represent the 95% binomial confidence intervals.*

FIGURE 4: *Number of positive hair traps as a measure of activity index or relative abundance of species in different habitat types, across the range of DFTD arrival times. Medium mammals = southern brown bandicoot, eastern barred bandicoot and long-nosed potoroo; Native mammals = swamp rat and long-tail mouse.*

FIGURES

FIGURE 1:

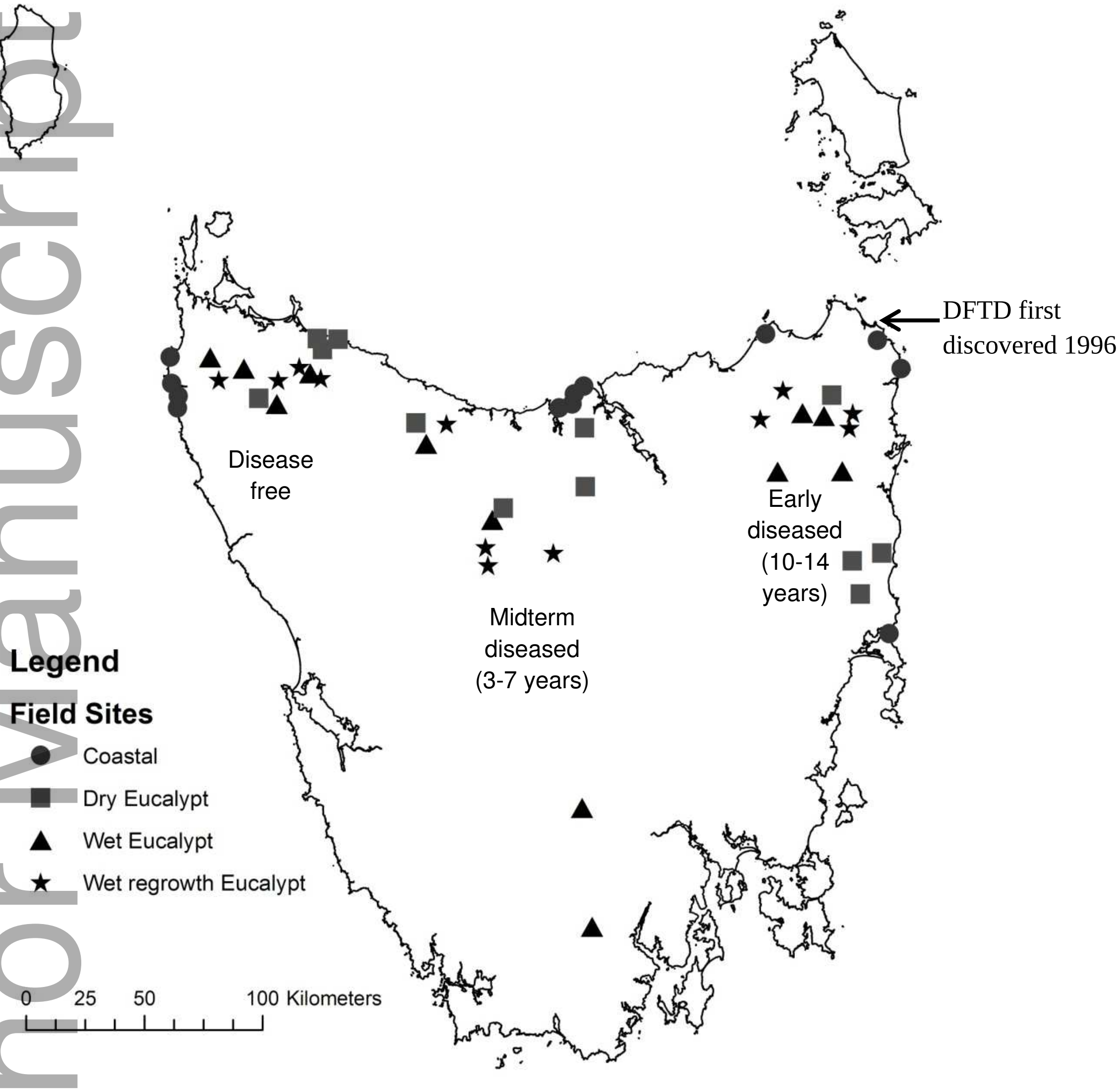
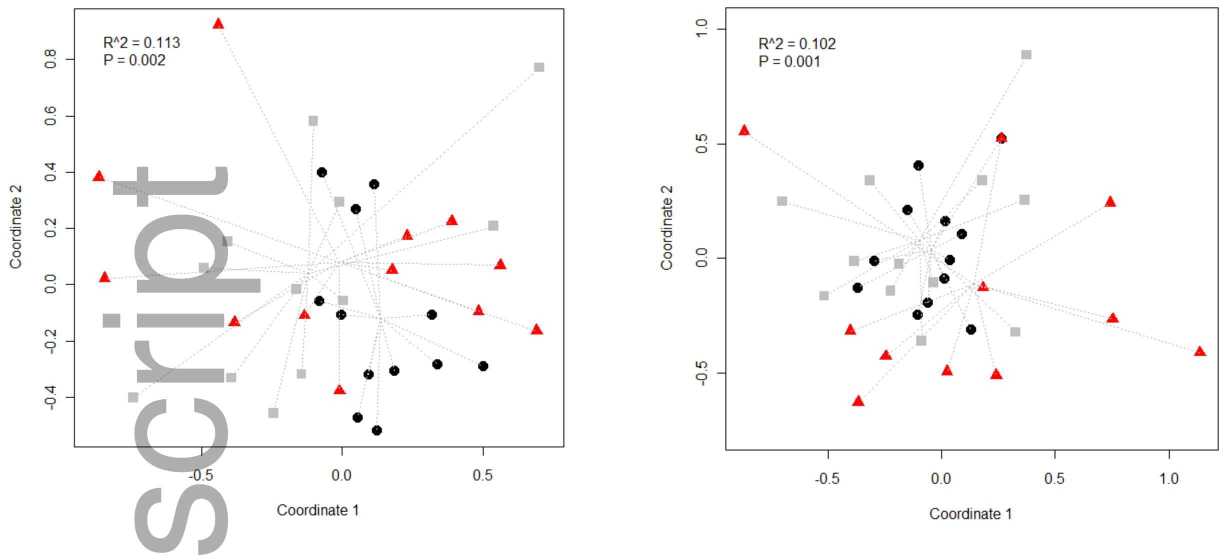


FIGURE 2:

Coastal scrub and woody vegetation **Dry eucalypt forest**



Wet eucalypt regeneration forest **Wet eucalypt mature forest**

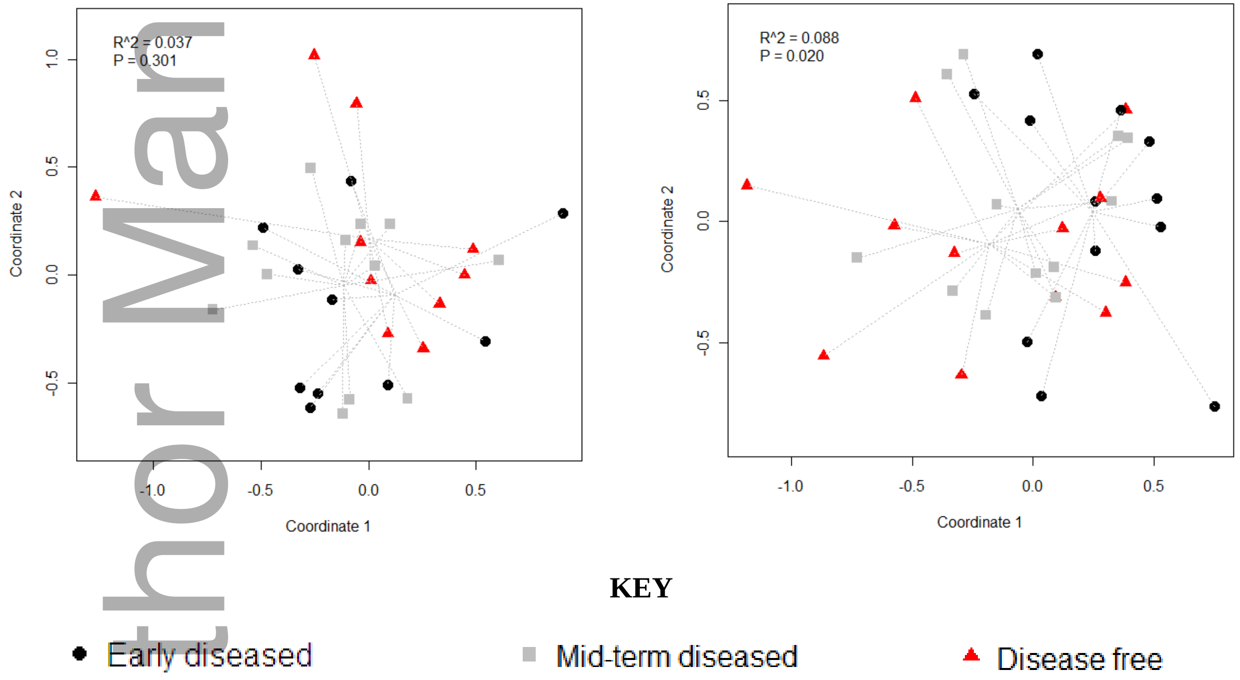


FIGURE 3:

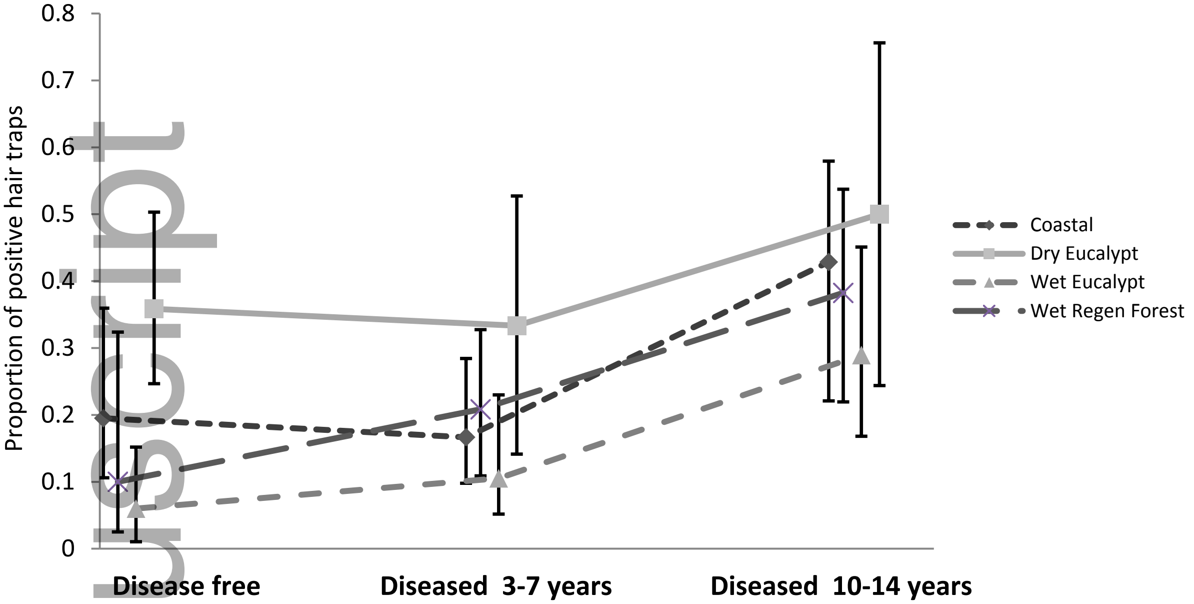
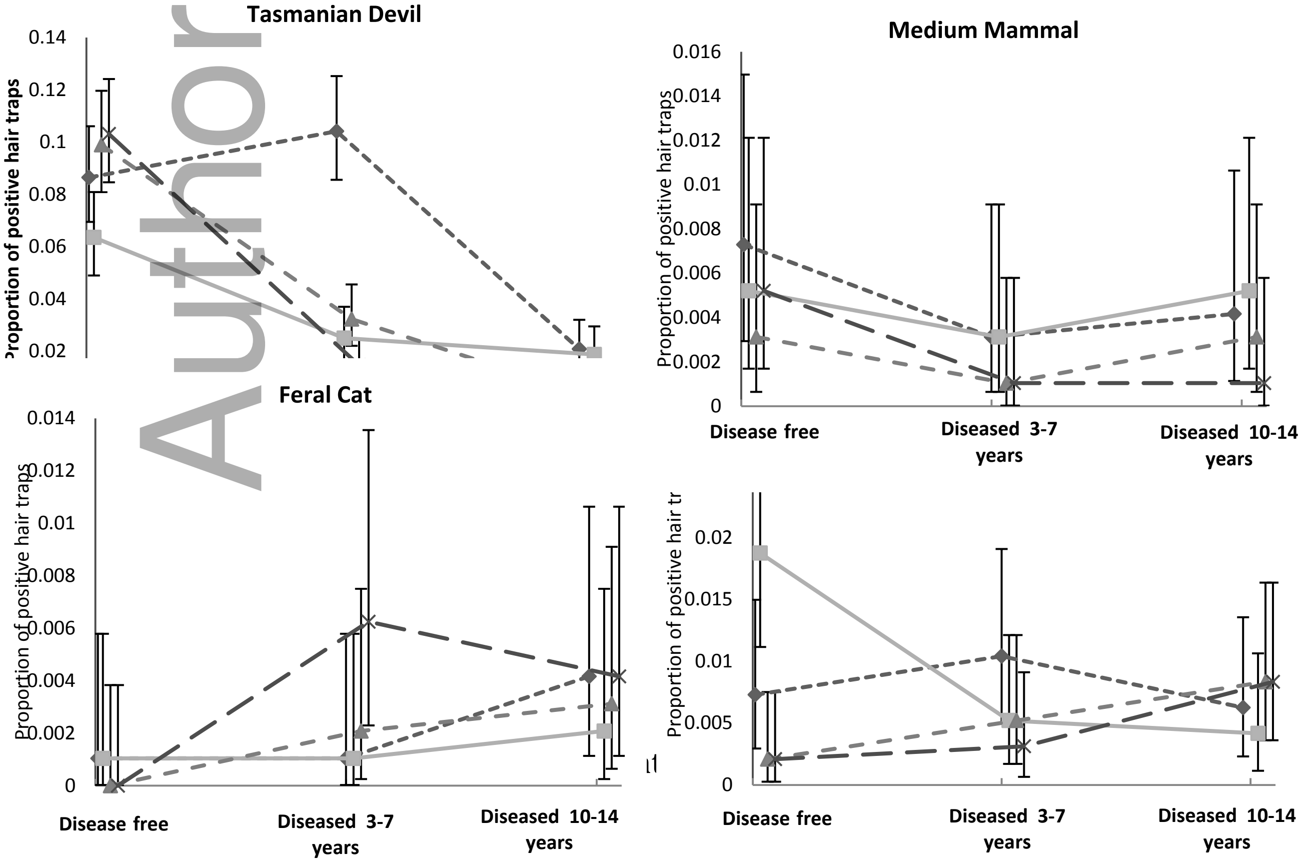
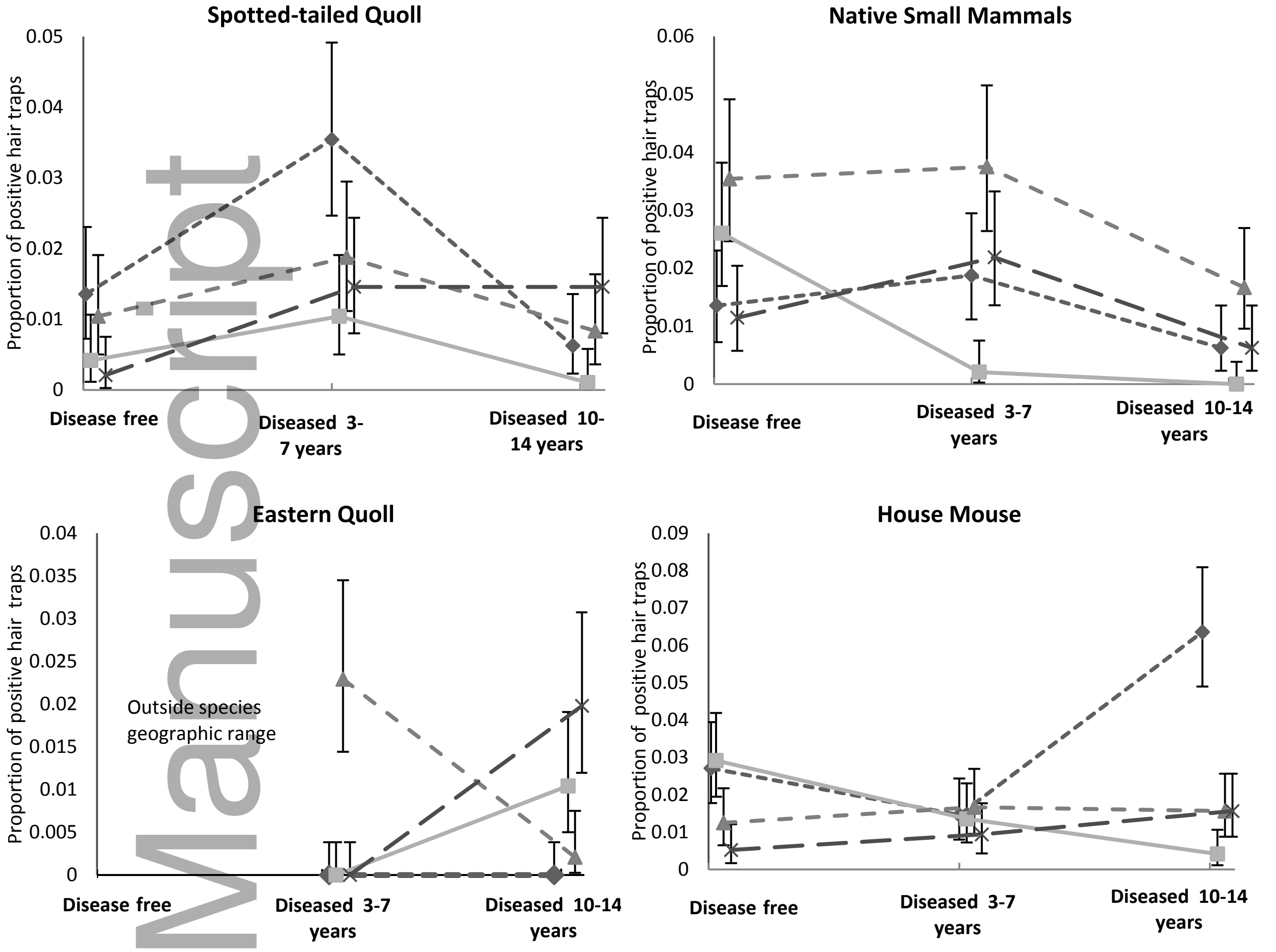

0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Proportion of positive hair traps
Disease free
Diseased 3-7 years
Diseased 10-14 years
Coastal
Dry Eucalypt
Wet Eucalypt
Wet Regen Forest

FIGURE 4:


Tasmanian Devil
0.14
0.12
0.1
0.08
0.06
0.04
0.02
Proportion of positive hair traps
Medium Mammal
0.016
0.014
0.012
0.01
0.008
0.006
0.004
0.002
0
Proportion of positive hair traps
Disease free
Diseased 3-7 years
Diseased 10-14 years
Feral Cat
0.014
0.012
0.01
0.008
0.006
0.004
0.002
0
Proportion of positive hair traps
Disease free
Diseased 3-7 years
Diseased 10-14 years
0.02
0.015
0.01
0.005
0
Proportion of positive hair tr
Disease free
Diseased 3-7 years
Diseased 10-14 years



KEY

--◆-- Coastal woodland scrub —■— Dry eucalypt – ▲ – Wet eucalypt —×— Wet Regeneration forest