Indirect effects of invasive species removal devastate World Heritage Island

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Summary

1. Owing to the detrimental impacts of invasive alien species, their control is often a priority for conservation management. Whereas the potential for unforeseen consequences of management is recognized, their associated complexity and costs are less widely appreciated.

2. We demonstrate that theoretically plausible trophic cascades associated with invasive species removal not only take place in reality, but can also result in rapid and drastic landscape-wide changes to ecosystems.

3. Using a combination of population data from of an invasive herbivore, plot-scale vegetation analyses, and satellite imagery, we show how a management intervention to eradicate a mesopredator has inadvertently and rapidly precipitated landscape-wide change on sub-Antarctic Macquarie Island. This happened despite the eradication being positioned within an integrated pest management framework. Following eradication of cats *Felis catus* in 2001, rabbit *Oryctolagus cuniculus* numbers increased substantially although a control action was in place (*Myxoma* virus), resulting in island-wide ecosystem effects.

4. *Synthesis and applications*. Our results highlight an important lesson for conservation agencies working to eradicate invasive species globally; that is, risk assessment of management interventions must explicitly consider and plan for their indirect effects, or face substantial subsequent costs. On Macquarie Island, the cost of further conservation action will exceed AU$24 million.

Key-words: invasive species, cats, rabbits, sub-Antarctic, trophic cascade

Introduction

Biological invasions can lead to large-scale alterations in ecosystem functioning. On oceanic islands, these impacts may extend from species extinctions (Blackburn *et al*. 2004) to more complex outcomes such as a switch from competition to predation-dominated systems (Roemer, Donlan & Courchamp 2002), and in extreme cases to 'meltdown' of ecosystems (O'Dowd, Green & Lake 2003). Where island systems rely on marine-derived nutrient subsidies via seabirds, as is often the case, the effects of invasive predators may also propagate to the base of food webs, altering soil nutrient content, plant and soil faunal species composition, and community characteristics. Impacts of this kind have been recorded in a range of systems including the Aleutians following the introduction of both

Arctic foxes *Alopex lagopus* (Croll *et al*. 2005; Maron *et al*. 2006) and rats *Rattus norvegicus* (Kurle, Croll & Tershy 2008), the offshore islands of New Zealand owing to *R. norvegicus* and *R. rattus* invasions (Fukami *et al*. 2006), and the sub-Antarctic islands owing to the introduction of cats (e.g. Crafford & Scholtz 1987). Invasions of rats (Jones *et al*. 2008) and cats (Nogales *et al*. 2004) on many islands have had similar impacts due to their detrimental effects on seabird populations (Courchamp, Chapuis & Pascal 2003).

Consequently, control or eradication of invasive alien species is widely undertaken and recommended (Courchamp *et al*. 2003; Nogales *et al*. 2004). The preferred outcome of such interventions is the recovery of indigenous species or ecosystems following the removal of an alien transformer. However, management action may have other unintended consequences. Removal of top predators may cause mesopredator release, resulting in significant, often inadvertent

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consequences (Courchamp, Langlais & Sugihara 1999; Courchamp *et al.* 2003), which can only be remedied by further control of the mesopredator. For example, on New Zealand's Little Barrier Island, removal of cats resulted in reduced breeding success of Cook's petrel *Pterodroma cookii*, which only increased following rat eradication (Rayner *et al.* 2007). Other impacts might also include the release of invasive plants from herbivores (D'Antonio & Vitousek 1992). Trophic cascades, or the extension of effects of changes in one species' abundance across multiple links in the food web, are being increasingly recognized as a consequence of the effects of eradication (Zavaleta, Hobbs & Mooney 2001; Duffy *et al.* 2007). Although the potential for such indirect effects following management interventions is now recognized (Zavaleta 2002; Blackburn *et al.* 2004) and has been modelled in several contexts (e.g. Courchamp *et al.* 1999; Tompkins & Veltman 2006), real-world examples remain relatively uncommon. Moreover, even where the potential for such effects is recognized by managers, the way in which these might play out may be unexpected, given simultaneous management interventions for several invasive species in an area and variation among sites in the area being managed (e.g. Rayner *et al.* 2007). Theory emphasizes the significance of indirect effects in governing ecosystem dynamics, and the sensitivity of these dynamics to species interactions, the initial conditions of the system, and the ways in which ongoing changes interact to affect the state of the system (Chase 2007; Jordán *et al.* 2008). Moreover, it also recognizes that the complexity of the outcomes is such that predictive ability may often be low (Montoya, Pimm & Solé 2006). Clearly, the unexpected consequences of management interventions are one aspect of this lack of predictability and need to form part of the risk assessment process for all management interventions.

Here, we combine population data on invasive herbivorous rabbits *Oryctolagus cuniculus* (L.), plot-scale vegetation analyses, climate analysis and landscape change detection techniques using satellite imagery, to show how a local management intervention, the eradication of feral cats *Felis catus* L., has precipitated a trophic cascade leading to rapid, landscape-wide ecosystem changes on sub-Antarctic Macquarie Island. Specifically, we first review evidence demonstrating that cats consumed substantial numbers of rabbits prior to their eradication. Next, we show that since the eradication of cats, rabbit numbers on the island have increased significantly. We then provide evidence of impacts of rabbits on vegetation via grazing, at both plot and landscape scale between 2000 and 2007, which cannot be attributed to other causes, such as climate change or seasonal variation. In combination, these data demonstrate that the removal of cats has resulted in an increase in rabbit abundance, which has led to substantial local and landscape-scale changes in vegetation. Although this trophic cascade was predictable given the history of rabbit impacts on both this and other islands (Costin & Moore 1960; Flux & Fullagar 1992; Courchamp *et al.* 2003), and was not entirely unexpected (Brothers & Copson 1988), its extent was not fully anticipated. Indeed, management reviews predicted ongoing restoration of the vegetation following the introduction of *Myxoma* virus. We discuss why this trophic cascade was not fully anticipated and what steps might be taken to prevent a similar situation as further rabbit control (to eradication) is implemented.

Materials and methods

STUDY SITE AND HISTORY

World Heritage Macquarie Island (54°30′S, 158°57′E) is an oceanic island in the sub-Antarctic region (Bergstrom & Chown 1999). Low-lying, 34 km long and with a cool, maritime climate (Pendlebury & Barnes-Keoghan 2007), it is covered in tundra-like vegetation, featuring tussock grasses, megaherbs and bryophytes (Selkirk, Seppelt & Selkirk 1990).

Rabbits were introduced to the island in 1878 by sealing gangs. They initially reached very high numbers and became the main prey of cats, which had been introduced 60 years previously (Cumpston 1968; Jones 1977; Flux & Fullagar 1992; Copson & Whinam 2001). Hyperpredation probably resulted in the extinction of two flightless bird species (an endemic parakeet and endemic rail, Taylor 1979). Extensive grazing by rabbits was documented at least by the early 1950s (Taylor 1955) and by 1960, the effects were catastrophic, with a prediction that the, '... grassland vegetation on Macquarie Island is doomed to destruction' (Costin & Moore 1960). Management of rabbits commenced in 1968 with the introduction of the European rabbit flea *Spilopsyllus cuniculi* (vector of the *Myxoma* virus), but it took 10 years for the flea to become widespread. The rabbit population peaked at 130 000 in 1978 (Copson & Whinam 2001), the year when *Myxoma* virus was introduced. Unfavourable environmental conditions required annual releases of the virus (Brothers & Copson 1988), but eventually rabbit numbers dropped to less than 20 000. Island vegetation had recovered substantially 8–10 years after virus release (Copson & Whinam 1998), and management reviews predicted the return of several highly palatable plant species (Copson & Whinam 2001). *Myxoma* virus spreading ceased in October 2006, due to technical reasons.

By the mid-1980s, it had become clear that prey-switching by cats, given decreases in rabbit availability, was detrimentally affecting seabird populations (Copson & Whinam 2001). A cat eradication programme commenced in 1985 and was expanded in 1998. Between 1985 and 1995, approximately 124 cats were killed per year and it was estimated that the recruitment rate matched the kill rate (Copson 2002). The eradication rate increased to *c.* 220 cats per year for the next 3 years, dropping to 99 cat kills in 1999, and a single cat (the last cat) shot in 2000. Rabbit numbers then increased rapidly, and in a little more than 5 years, they have substantially altered large areas of the island (Scott & Kirkpatrick 2008), making its future conservation significance questionable in the absence of further action (Miller 2007).

CAT PREDATION AND RABBIT POPULATION ESTIMATES

Using the methods of Jones (1977), estimates of the consumption by cats of rabbits, rats and mice were calculated for 1997, based on estimated cat daily food intake and the proportion of food items reported for the gut content of 49 cats examined from the 157 shot in that year (consumption data reported in Copson & Whinam 2001; see Supporting Methods in Supporting Information). Estimates of annual rabbit population size were supplied by Parks and Wildlife Service, Tasmania (PWS). Their estimates are based on monthly

mean rabbit densities from eight rabbit count areas, established in different vegetation types which were then combined with planimetric estimates of the area spanned by each vegetation type across the island to calculate total rabbit population for the island (data calculated by this technique hereafter referred to as PWS Model 1). For 2004 to 2006, PWS supplied two additional estimates for each year, based on different models used to estimate rabbit abundance. PWS Model 2 used the established method but included seven more rabbit count areas (RCAs). PWS Model 3 also used the monthly counts for each of 15 RCAs and extrapolated upwards using more accurate vegetation type area measurements calculated from a 5 m Digital Elevation Model (DEM) overlaid with vegetation type (see Supporting Methods in Supporting Information).

RABBIT POPULATION CHANGE

Our primary hypothesis is that the eradication of cats led to an increase in rabbit abundance. However, both *Myxoma* virus and variation in climate among years may have also affected abundance. To investigate the influence of these factors, generalized linear models (assuming a normal distribution and using an identity link function) were constructed using the $\log_{10}$ rabbit abundance data as the dependent variable, and presence/absence of *Myxoma* virus as a categorical independent variable and seasonal mean temperature and precipitation data (1974–2006, see Supporting Methods) as continuous independent variables. PWS Models 1 and 3 of rabbit abundance were used as they represent the lower and upper range of abundance estimates. The Akaike Information Criterion (AIC) and Akaike weights were used to select the best-fit model from the suite of models available. Years with missing rabbit abundance data were excluded from the analysis (1977, 1981–1983). Following these analyses, the years before the introduction of *Myxoma* virus (1974–1977) were also excluded from the analyses. The models were then applied to $\log_{10}$ rabbit abundance data, with cat presence or absence as a categorical variable and the major climatic variables identified as important in the previous models (autumn, spring and summer precipitation and autumn temperature) as the continuous variables.

VEGETATION CHANGE

Between November 2000 and March 2001 (hereafter 2001), 45 ecological research sites across the range of vegetation types were established to investigate long-term vegetation change and its likely causes. Plots (5×5 m) were positioned within areas with high visual homogeneity of the vegetation. In April 2007, 18 of these plots, close to the research station were revisited during the brief, annual resupply voyage to examine their status (limited time precluded additional sampling). Sites were chosen in advance of fieldwork to represent a range of vegetation types (i.e. prior knowledge of the likelihood of rabbit impact did not play a role in site selection).

In each of the plots, both in 2001 and 2007, individual plant species cover as a percentage was visually calculated within five, randomly selected, 1 m^2 quadrats and mean values were determined. We examined our data matrix (consisting of 18 sites, 34 taxa and two sample times (2001 and 2007)) using PATN, a software package for identifying and displaying patterns in multivariate data (Belbin 1993). A cubed-root transformation was used to reduce the influence of species with high cover values. A Bray–Curtis (Bray & Curtis 1957) association matrix was generated between all pairs of the 18 sites. This matrix was then used for hierarchical classification (flexible UPGMA, beta = −0·1) and ordination using semi-strong hybrid multidimensional scaling (Belbin 1991). The structure of the 18 sites in

the classification dendrogram and their distribution in the 3-dimensional ordination plot were both used to select eight vegetation groups (see Supporting Methods for details). These groups summarized the variations among the sites.

Analysis of similarity (ANOSIM) (Clarke & Green 1988) was used to test for significant differences between a priori groups defined by sample time (2001 and 2007; see Supporting Methods). The probability that the 2001 and 2007 time groups for the complete data set could have been formed at random was 12%. ANOSIM was repeated on the data set after three sites that had showed no loss or gain of species between 2001 and 2007 had been removed [two fell-field sites and a *Stilbocarpa polaris* (Hombr. Et Jacquinot ex Hook. F. A. Gray) herbfield] and the probability decreased to < 0·01%. Species richness and turnover between 2001 and 2007 for each site and evidence of rabbit activity in 2007 is recorded in Supporting Information, Table S1.

USE OF REMOTE SENSING IMAGERY

Information on changes in vegetation communities was examined at a whole-island level using satellite imagery. We used Landsat ETM+ imagery acquired on 12 December 2000 and Quickbird imagery acquired on 15 March 2007 to detect changes in vegetation cover on Macquarie Island. Due to improvement in technology, the Quickbird image had a greater resolution than the Landsat image. In consequence, the pixel values and spectral resolution in the Quickbird image were resampled to match the resolution of the Landsat image (see Supporting Methods). The images were orthorectified to correct terrain and geometric distortions. Radiometric, illumination, and atmospheric differences were also corrected. These corrections are crucial for change detection algorithms as false changes are often introduced by geometric offsets and shadowing effects (Coppin, Bauer & Marvin 2004).

Two methods of change detection were used. Change Vector Analysis (CVA) (Lambin & Strahler 1994) quantifies the difference in pixel intensity (spectral reflectance) of all multispectral bands between two images. Figure 1 shows the magnitude (amount) of change for each pixel. The change magnitude values range between 0–100% and were classified into five classes. A value of 100% indicates a spectral change from complete absorption to complete reflection (or the opposite) in all image bands. The threshold for the no-change class was set at 17%, which included the change magnitude values that were observed in geo-referenced field sites for gravel (no change), water (no change), and vegetation which was known to show seasonal change. This approach ensured that the changes depicted by the change classes highlighted significant changes in vegetation as opposed to sensor differences or seasonal spectral variation (see Supporting Methods).

The second change detection method, Normalized Difference Vegetation Index (NDVI), quantified the direction of change to determine locations of vegetation loss (see Lyon *et al.* 1998) by applying a normalized difference ratio of the highest absorption and reflectance wavelengths of chlorophyll (red and near-infrared, respectively). Subtraction of the 2000 NDVI image from the 2007 NDVI image resulted in negative and positive change values for each image pixel.

Quantification of change in pixel intensity in CVA and chlorophyll loss and gain for NDVI were calculated and expressed as percentages of total pixels for each of the change categories. Strong chlorophyll gain was observed in west-coast shadow areas; thus, a component of the positive NDVI difference values was an artefact. Accordingly, we present only chlorophyll loss data.
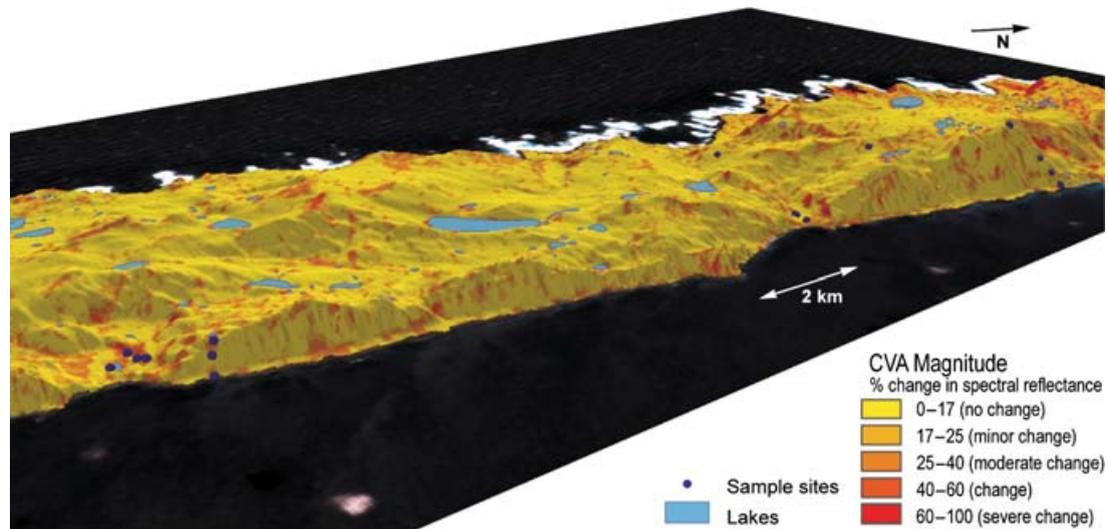
Fig. 1. Change Vector Analysis (CVA) 2000–2007, for two-thirds of Macquarie Island. Orange to red areas indicates a scale of moderate to severe change (see Supporting Information, Table S2 for values). Coastal flats and slopes, and inland valleys show substantial rabbit-induced vegetation change.

Table 1. Best-fit generalized linear models (those with the lowest Akaike Information Criterion (AIC) values and largest Akaike weights (w_i)) of the relationship between $\log_{10}$ rabbit abundance and several predictors. The model outcomes are for each of six separate analyses (a–f) using slightly different data sets. For each analysis, only models with the two, highest w_i are shown (the other models had w_i either substantially lower than the models shown or w_i less than 0·1). The analyses are of: rabbit abundances estimated using (a) PWS Model 1 and (b) PWS Model 3 (see text for details) for the period 1974 to 2006, and for rabbit abundances estimated using (c) PWS Model 1 and (d) PWS Model 3 (see text for details) for the period 1978 to 2006, that is after *Myxoma* virus had been introduced. The latter models were also re-run including only summer and autumn precipitation and cat presence/absence (models e and f). The models assumed a normal distribution and used an identity link function. The 'Variables' column indicates the variable, its sign, and whether or not it entered the model significantly (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, n.s. not significant)

Model	Variables	AIC	w_i (a)
(a) $\log_{10}$ rabbit abundance	–autumn precipitation[n.s.], –*Myxoma**	21·6	0·082
PWS Model 1974–2006	+summer precipitation[n.s.], –autumn precipitation[n.s.], –*Myxoma**	22·0	0·067
(b) $\log_{10}$ rabbit abundance	–autumn temperature[n.s.], +summer precipitation[n.s.],	31·0	0·064
PWS Model 3 1974–2006	+spring precipitation[n.s.], –*Myxoma**		
	–autumn precipitation[n.s.], –*Myxoma**	31·2	0·058
(c) $\log_{10}$ rabbit abundance	–autumn precipitation*, +cat absence*	16·7	0·19
PWS Model 1, 1978–2006	+summer precipitation[n.s.], –autumn precipitation*, +cat absence*	17·1	0·16
(d) $\log_{10}$ rabbit abundance	+summer precipitation[n.s.], –autumn precipitation[n.s.], +cat absence**	21·4	0·9
PWS Model 3, 1978–2006	–autumn precipitation[n.s.], +cat absence**	21·6	0·18
(e) $\log_{10}$ rabbit abundance	–autumn precipitation**, +cat absence*	16·7	0·42
PWS Model 1, 1978–2006	+summer precipitation[n.s.], –autumn precipitation**, +cat absence*	17·1	0·35
(f) $\log_{10}$ rabbit abundance	+summer precipitation[n.s.], –autumn precipitation**, +cat absence***	21·4	0·47
PWS Model 3, 1978–2006	–autumn precipitation**, +cat absence***	21·6	0·43

Change in vegetation could be a consequence not only of rabbit influences, but also changing climates that are typical of both the island (Pendlebury & Barnes-Keoghan 2007) and the region (Bergstrom & Chown 1999). To determine whether annual and seasonal temperature and precipitation have changed over the period since cats have been eradicated (2000–2006), linear regressions were used to examine the relationship between year and annual mean temperature and precipitation, and year and each of the seasonal temperature and precipitation parameters (see above).

Results

The generalized linear models indicated that between 1974 and 2006 *Myxoma* virus presence and precipitation, either in autumn (PWS Model 1 abundance data) or in autumn, summer and spring (PWS Model 3 abundance data) were retained in the models with the lowest AIC and highest Akaike weights (Table 1). *Myxoma* virus and autumn precipitation presence both had negative effects on rabbit abundance and other precipitation values had small positive effects. None of the precipitation values were significant following a Type III assessment, but were retained in the best fit models (Table 1). Nonetheless, the models were weak in both cases, with low Akaike weights.

When using data from the 1978 to 2006 period (i.e. when *Myxoma* virus was present), both cat presence and autumn precipitation had significant negative effects on rabbit
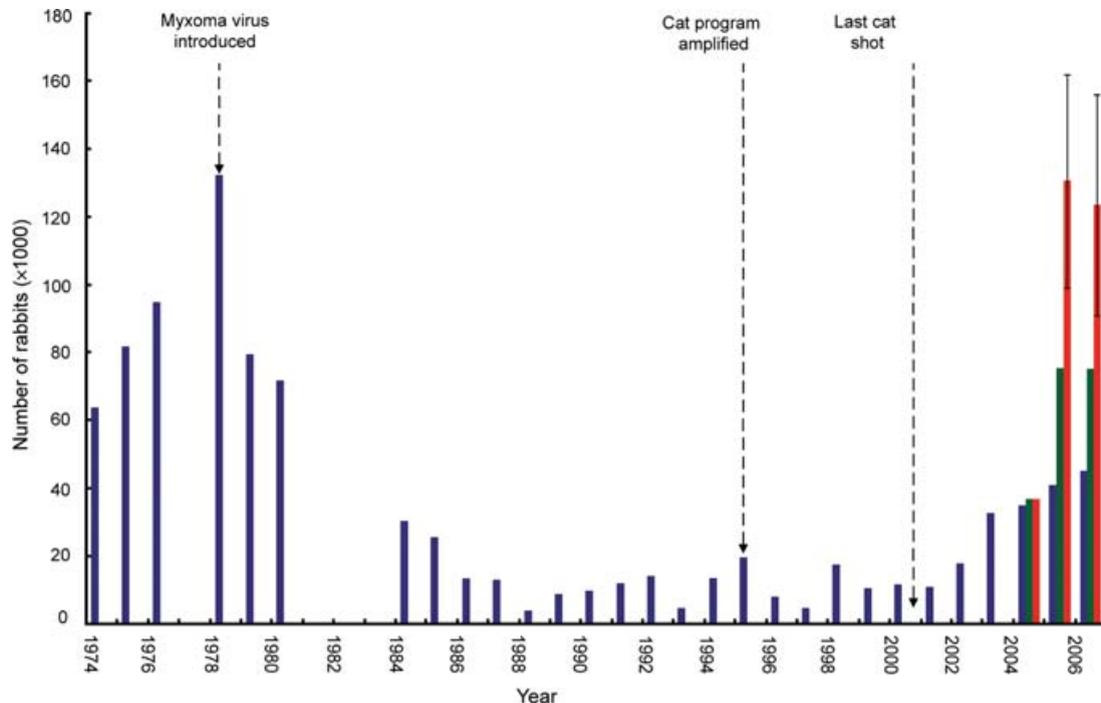
Fig. 2. Rabbit population estimates from 1993 to 2007 using PWS Model 1 (blue). Two additional scaling-up models are include for the later 3 years (Model 2, green; Model 3, red). There are no data points for 1977, 1981–1983.

abundance for the PWS Model 1 data, but only cat presence had a significant negative effect for PWS Model 3 data (Table 1). The generalized linear model outcomes for both PWS Model 1 and PWS Model 3 had high Akaike weights. Thus, the increase in rabbit numbers following the eradication of cats in 2000 (Fig. 2) is clearly attributable to the removal of cats. By 2006, rabbit numbers had reached *c.* 130 000 individuals (Fig. 2), despite ongoing release of *Myxoma* virus.

Diet data provide additional support for these results. We conservatively estimate that the 157 adult cats shot in 1997 were consuming at least 4000 adult-sized rabbits per year (and *c.* 103 000 mice and 36 600 rats). If rabbit kittens were a component of the cats' diet, the total number of rabbits consumed could have been substantially higher (consumption estimate based on rabbit kittens only = 13 700, i.e. greater than the estimated rabbit population size).

Analysis of 18 vegetation plots sampled in 2001 and again in 2007, identified substantial change at most sites. Impacts of rabbits, such as grazing, burrows and scats, were typical of many sites (Supporting Information, Table S1). Fifteen sites had changed substantially (ANOSIM; $P < 0.01$), mainly through loss of species cover and gain of new taxa (Fig. 3; Supporting Information, Table S1). Three coastal vegetation sites and two *Polystichum vestitum* (G. Forst.) C. Presl fernbrake sites showed significant change from tall complex vegetation to short grazing lawns (Figs 3, 4a–b), with gaps colonized by small herbs, thallose liverworts and the invasive alien grass *Poa annua* L. Such taxa were either previously interstitial or were new colonizers to the site (Supporting Information, Table S1). For example, in 2001 *P. annua* was present at four of the 18 sites, but by 2007 had colonized a further seven sites.

Other megaherb-dominated sites photographed in 2001 and 2007, but not sampled, show similar rabbit-induced change (Fig. 4c–d and Supporting Information, Figs S3–S4).

Satellite image comparisons (December 2000 – Landsat 7 ETM+; March 2007 – Quickbird) revealed substantial island-wide rabbit-induced vegetation change (Fig. 1). By 2007, impacts on some protected valleys and coastal slopes and flats had become acute (see Supporting Information, Fig. S2). We estimate that 36·4% of total island area had changed, with 17·5% having moderate to severe change. Examining only the coastal slopes (< 1500 m from coastline, slope > 25°), 50% had changed, with 31·9% showing moderate to severe change (see Supporting Information, Table S2). NDVI values corroborate this observation. Negative changes in the coastal NDVI values, indicated replacement of vegetation by bare ground at many localities (Supporting Information, Figs S1 and S2) with 22·4% of the island and 25·2% of coastal slopes having lost chlorophyll between sampling events (Supporting Information, Table S3).

It seems unlikely that climate change so typical of the sub-Antarctic region is the cause of the vegetation change we observed. Despite increasing temperatures and precipitation over the 56-year climate record for Macquarie Island (Pendlebury & Barnes-Keoghan 2007), no significant trends in annual climate variables were found for the period 2000 to 2006 (linear regression, mean annual temperature $r^2 = 0.06$, d.f. = 5, $P > 0.5$; mean annual precipitation $r^2 = 0.002$, d.f. = 5, $P > 0.9$). However, a significant positive seasonal trend was found for autumn mean air temperature (2000–2006, linear regression $r^2 = 0.50$, d.f. = 5, $P < 0.05$, Table S4 Supporting Information). Since 2001, the long-term, mean autumn air
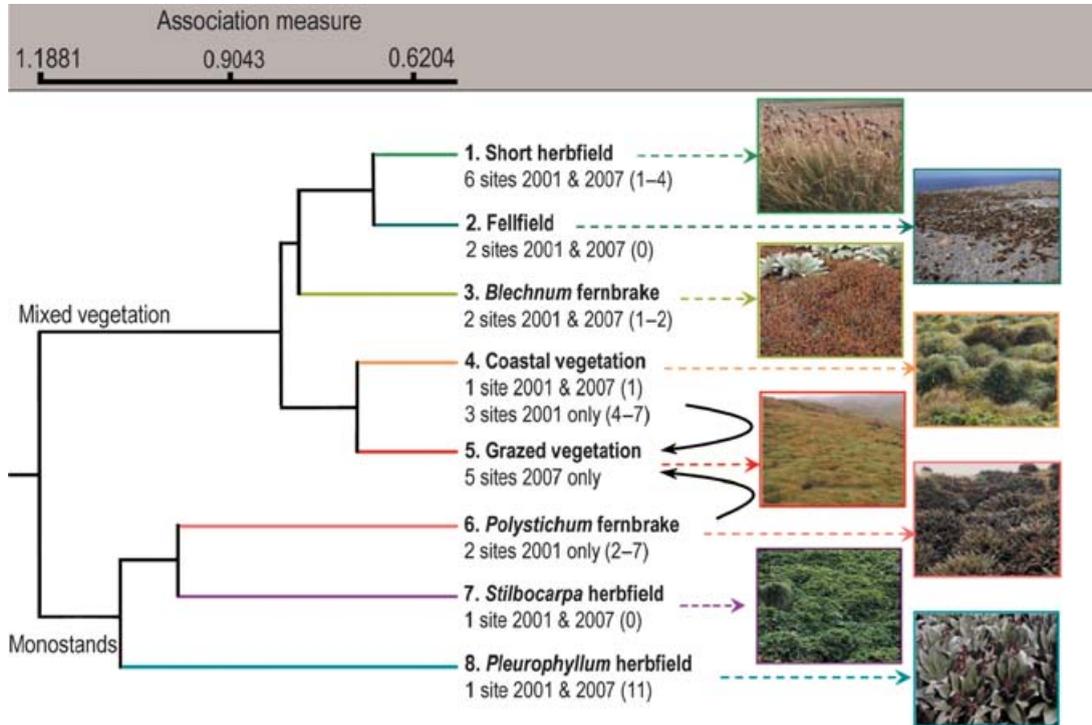
Fig. 3. Classification dendrogram of the 18 sites depicting the eight vegetation groups. Five sites from two vegetation groups (tall coastal vegetation or *Polystichum* fernbrake) had undergone extensive change to grazing lawns between 2001 and 2007, as indicated by the recurved black arrows. In addition 10 sites had also changed, although remained in their original (2001) vegetation group. Change is indicated by the range of new taxa found within sites in 2007 compared with 2001 for each group (within brackets).
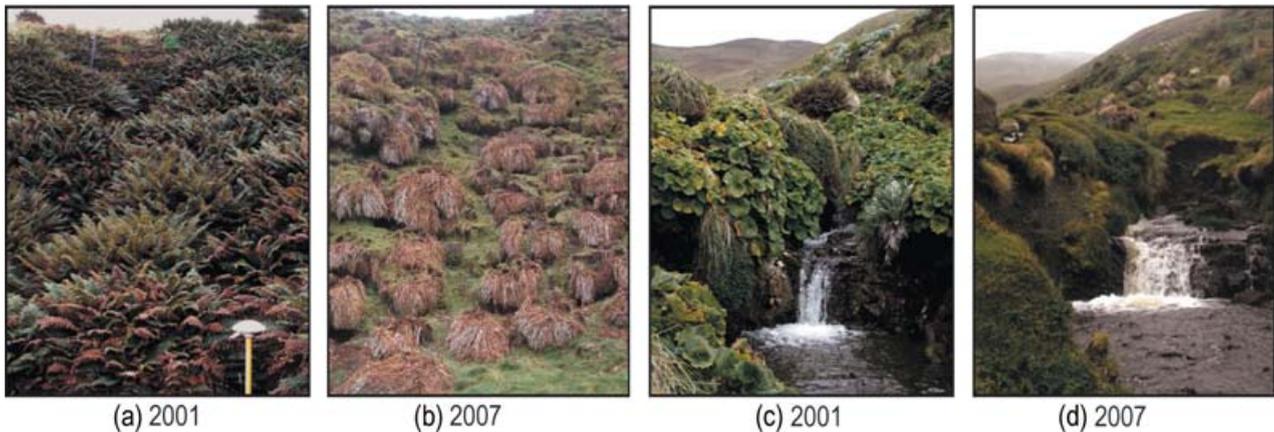

Fig. 4. Vegetation at a *Polystichum* fernbrake site in 2001 (a) and 2007 (b) in Green Gorge and herbfield around Finch Creek in 2001 (c) and 2007 (d). The large shield ferns (a) were completely grazed by rabbits leaving dead remnant bases which were colonized by small unpalatable species (b). The large megaherbs and tussock grasses (c) have been grazed and replaced with other species including *Poa annua* (d).

temperature (5·27 °C, SD = 1·82 °C) has been exceeded in 4 of the last 6 years.

Discussion

Rabbit numbers on Macquarie Island have returned to pre-control levels (Fig. 2) and this can be clearly ascribed to the removal of cats. The eradication of cats was positioned in a commendable, integrated pest management framework (see Copson & Whinam 2001), but the unintended consequences have been dire. We estimate that at least 4000 rabbits per year (as well as many mice and rats) initially entered the ecosystem after the last cat kill. Rabbit natality on Macquarie Island, has been observed to be as high as 19 kittens per breeding female (Skira 1978), with up to 57% of all females pregnant in a season. Our models also suggest that wetter springs and summers, possibly reflecting greater food availability and drier autumns (possible reduction in kitten drownings from

flooded burrows, see Skira, Brothers & Copson 1983) also contribute to higher rabbit numbers. Although temperature did not enter the generalized linear models as significant terms, autumn air temperature (the one climate variable that has significantly changed in the last 6 years) was often included in the best-fit models. Higher autumn temperatures may have improved rabbit kitten survivorship up to the winter months.

Increased rabbit herbivory has caused substantial damage at both local and landscape scales including changes from complex vegetation communities, to short, grazed lawns or bare ground. In support of these findings, Scott & Kirkpatrick (2008) reported light or moderate grazing on 15 steep, coastal, mainly southern tussock slopes in 2003, with photographic evidence indicating severe grazing by 2007. Although natural successional change may have been responsible for some of the vegetation differences we detected, such change typically operates on a much longer timeframe in the sub-Antarctic than the period investigated (Scott & Kirkpatrick 2008). Other physical disturbances such as landslips or disturbance by birds and seals are all more local in effect (Selkirk *et al.* 1990).

Our plot-scale changes match previously documented rabbit impacts before rabbit control, including selective grazing of palatable, high biomass species such as the large tussock grass, *Poa foliosa* (Hook. f.) Hook. f. and the regionally endemic fern *Polystichum vestitum*, and megaherbs, *Stilbocarpa polaris* and *Pleurophyllum hookeri* Buchanan (Costin & Moore 1960; Copson 1984; Copson & Whinam 1998, 2001). Further impacts, such as changes to soil structure and nutrient cycling are also anticipated. Additionally in 2007, we observed rabbit tunnelling destroying petrel burrows, with petrel wings lying at the base of a slope, indicating attack by skuas *Catharacta longbergii* Matthews, the local predatory bird species.

Impacts by rabbits on vegetation (see Scott 1988) and their likely secondary consequences for breeding seabirds led to initiation last century of efforts to control rabbits. Substantial recovery of the vegetation on the island followed in the 1990s, with the expectation that the rabbit control programme would continue to deliver conservation benefits and would require comparatively little effort to sustain (Brothers & Copson 1988; Copson & Whinam 2001). Recovery of plant species and communities, as observed on Macquarie Island (Copson & Whinam 1998; Scott & Kirkpatrick 2008), has also been documented for other islands, both in the region (Chapuis, Frenot & Lebouvier 2004) and elsewhere (Courchamp *et al.* 2003). What makes this case unusual is that the efforts towards management action to control rabbits, which began in 1968 has been reversed in only 6 years. The pace and spatial extent of the inadvertent trophic cascade precipitated by what appeared to be a sensible and much-needed management intervention are remarkable and herald a warning for other eradication programmes.

With the luxury of the wisdom of hindsight, we can suggest that the current situation arose as a consequence of inadequate recognition of top–down control of rabbits by a population of only 160 adult cats. A long-held assumption was that continued use of the *Myxoma* virus as a control measure would keep rabbit abundance low (see Brothers & Copson 1988; Scott 1996). Such a view is understandable; even the present analyses have demonstrated that the release of *Myxoma* virus had a significant impact on rabbit abundance. Indeed, despite the cessation of virus spreading by rangers in October 2006, the impact of *Myxoma* virus was still evident in April 2007, with numerous rabbit carcasses present at the base of coastal slopes despite some speculation of reduced efficacy of the virus (Scott & Kirkpatrick 2008).

Implications for management

Our assessment of Macquarie Island has several significant implications for management. This study is one of only a handful which demonstrate that theoretically plausible trophic cascades associated with invasive species removal (see Zavaleta *et al.* 2001), not only do take place, but can also result in rapid and detrimental changes to ecosystems, thus negating the direct benefits of the removal of the target species (as theoretically demonstrated by Tompkins & Veltman 2006). It also demonstrates that whilst the need to make management decisions within a comprehensive assessment framework is widely recognized (Zavaleta *et al.* 2001), even a structured, management framework can result in unanticipated outcomes. Formal techniques for assessing ecological risks and the most appropriate conservation actions are becoming widely available (Zavaleta 2002; Marcot 2006). Their use, in conjunction with sound information on the biology of the target species, interspecific interactions including trophic interactions (see Duffy *et al.* 2007) and the creation of models of likely changes (see Tompkins & Veltman 2006; Caut *et al.* 2007), could go a long way to reducing the risks of unanticipated outcomes of invasive species management interventions.

Unanticipated management outcomes not only can lead to new substantial problems, but can also render past efforts less valuable than they otherwise might have been, thus risking disinvestment by political decision-makers. Twenty years into the vertebrate management process on Macquarie Island, Brothers & Copson (1988) recognized the need for continued conservation funding and the significant risk of a substantial loss of investment (at that time estimated to be 15·5 human years) if funding were to cease. If the rate of conservation investment on the island had continued at that same rate, then current human investment would be *c.* 37 human years (but in fact the investment was increased with the cat eradication programme, making this figure exceptionally conservative). In many ways, this effort has now largely been lost. Indeed, it appears that Costin & Moore's (1960) prediction that the 'vegetation on Macquarie Island is doomed to destruction' is rapidly being realized.

The nature of conservation funding often limits agencies to restricted, step-by-step eradication programmes rather than more comprehensive ones. Rabbit population control on Macquarie Island was followed by cat control/eradication. Rabbit and rodent eradication was identified as the next logical steps in management (Parks and Wildlife Service 2006) although funding for these steps had not been secured

at the time of writing the management plan. The scenario on Macquarie Island suggests that funding of larger but more holistic conservation measures, as opposed to smaller, stepwise measures may, in the long run have been more successful and cost-effective. Our work has focused only on the impact of rabbits on the Macquarie Island ecosystem, but it is likely that a pulse of at least 103 000 mice and 36 600 rats have also entered the ecosystem since cat eradication. It is probable that rats have impacted on at least four trophic levels (mice, plants, birds and invertebrates) and mice on the latter three levels.

The substantial changes to the Macquarie Island ecosystem caused by the increase in rabbits has raised considerable alarm in the conservation community (Springer 2006), especially considering the conservation value of the island (Chown *et al.* 2001). In response, Federal and State governments in Australia have committed A$24 million for an integrated rabbit, rat and mouse eradication programme (Parks and Wildlife Service 2007) in recognition of the potential for inadvertent interactions among these species. Our findings suggest that a full risk assessment of the planned eradication programme and species modelling of potential impact of the remaining alien species on the Island may assist in maximizing the effectiveness of this conservation measure. Macquarie Island is the largest island on which an eradication programme has ever been attempted (Parks and Wildlife Service 2007). If Parks and Wildlife Tasmania manage to eradicate the target species, it should be a great conservation success, but if they fail, risk assessment and modelling should assist in the development of contingency plans, such as a targeted mice control programme in key habitats to maximize outcomes. Furthermore, establishment of measures of success beyond the level of eradication of targeted alien species may contribute to greater clarity of purpose.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Supporting methods (extended methods description).

Fig. S1. Normalized Difference Vegetation Index (NDVI) for Macquarie Island.

Fig. S2. Changes in spectral reflectance at Finch Creek.

Figs S3–S4. Comparative photographs (2001 and 2007).

Table S1. Major vegetation changes at each of the 18 field sites.

Table S2. Percentage area for CVA magnitude change classes.

Table S3. Percentage area for NDVI change classes.

Table S4. Trends in climate indices for 1949–2006 and 2000–2007.

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