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Multiple anthropogenic changes cause biodiversity loss through plant invasion

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Abstract

Non-native invasive plants are a widely acknowledged threat to global biodiversity. However, our understanding of the mechanisms underlying plant invasion, and the relative importance of multiple rather than single drivers, remains poor. Here, we provide a case study using time-series data to reconstruct patterns of change, and field experiments to test for causality. We show how, over a 50-year period, a series of unrelated human-induced changes created highly favorable conditions for the non-native tree mallow (*Lavatera arborea*) to turn invasive, causing loss of native vegetation and seabird breeding habitat. The combination of three drivers: human-introduced disease, climate warming and a fisheries-mediated increase in seabird populations, removed major constraints on plant population growth, (i.e. grazer control, climatic control, germination opportunity and nutrient limitation). Collectively, these changes created optimal conditions for the rapid expansion of tree mallow. The resulting dramatic impact on both the native vegetation and breeding seabirds, notably puffins (*Fratercula arctica*), exemplifies how non-native invasive plant species can transform terrestrial ecosystems. While climate change is regarded as a key factor behind plant invasion, we highlight that multiple rather than single factors may be critical to biodiversity loss.

Keywords: climate change, experiment, frost tolerance, island ecosystem, non-native, nutrient subsidies from seabirds, plant invasion, puffin, rabbit grazing, tree mallow

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Introduction

Plant invasions pose a major threat to global biodiversity and are therefore regarded as a significant component of human-induced global environmental change (Vitousek *et al*., 1997; Chapin *et al*., 2000; Sala *et al*., 2000; Weber, 2003). A number of factors, many with anthropogenic links such as the plant trade, land-use change and global warming, have been reported to facilitate plant invasion (D'Antonio *et al*., 1999; Lonsdale, 1999; Walther, 2004; Truscott *et al*., 2006), although conclusive evidence remains scarce. Moreover, it remains unclear whether multiple factors such as the combined effects of natural and anthropogenic disturbance are more common than a single cause accounting for the rapid spread of many non-native plants (Dukes & Mooney, 1999; Byers *et al*., 2002; Callaway & Maron, 2006).

Invasive non-native plant species have been shown to influence native plant species richness (Alvarez & Cushman, 2002; Hulme & Bremner, 2006). However, studies have mostly been correlative with limited evidence of cause and effect (Vitousek, 1990; Hulme, 2003) or of the mechanisms underlying the impacts (Byers *et al*., 2002; Levine *et al*., 2003). Although an increasing number of studies describe how invasive non-native plants influence other trophic levels, studies that quantify these effects remain scarce. Here, we provide a mechanistic reconstruction of a plant invasion and the role played by multiple anthropogenic changes in creating highly favorable conditions for a non-native plant to become invasive and impact native plant and breeding seabird communities.

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A number of coastal islands in the northern and southern hemisphere are currently subject to rapid invasion by a tall (up to 3 m) plant, tree mallow (*Lavatera arborea*), causing marked changes in the plant community and loss of breeding habitat for seabirds. Here, we use time-series data from an island in the Firth of Forth off the east coast of Scotland (56°N, 2°W), to reconstruct the pattern of change. We also conducted field experiments to test predictions that grazing, low temperatures and low soil fertility all reduce tree mallow growth and survival. We discuss how the relaxation of these constraints over a 50-year period due to changes in anthropogenically driven, but unrelated, factors created conditions that allowed tree mallow to expand, thereby replacing native coastal plant species as well as causing a greater than 50% decline in the breeding population of Atlantic puffins (*Fratercula arctica*), an iconic bird species of high conservation and economic value.

Materials and methods

Study species and site

Tree mallow is a tall, biennial Mediterranean–Atlantic herb, whose native distribution in the United Kingdom is limited to the southwest coastal fringe (Cox, 2002). However, the species has long been cultivated in coastal gardens well outside its natural range from where it occasionally spreads into natural and seminatural habitat, including the coastline and offshore islands of southeast Scotland (Firth of Forth; Cox, 2002). Historical details of the plant's status in the Firth of Forth are limited, although it is known to have been introduced to the Bass Rock more than three centuries ago (M'Crie *et al*., 1847). During the first half of the 20th century, it occurred in low abundance on other islands off the southeast coast of Scotland (Beattie, 1966). However, the species has become invasive during the last two decades. The problem is currently most acute on Craigleith (56°N, 2°W), where tree mallow currently covers most of this small 7 ha island. Craigleith has, therefore, been chosen as the focus of our study into the factors that have allowed tree mallow to become invasive.

Pattern of tree mallow expansion

The expansion of tree mallow on Craigleith was reconstructed using aerial photographs of the island taken in April 1952, August 1958, June 1988, August 1999, May 2001 and aerial video footage from September 2006. The images from 1952 and 1958 were vertical black and white stereo-photographs (scale 1 : 10 000) and those from 1988 and 1999 (1 : 24 000) were in color. All these photographs were obtained from the archives of the Royal Commission on the Ancient and Historical Monuments of Scotland. The 2001 image was a high-resolution digital image (25 cm pixel size) purchased from Getmapping Ltd (Hartley Wintney, UK). The 2006 video material was obtained using an ultra-light aircraft flying over the island. All material was inspected carefully either with stereo loupe or on screen, and areas of tree mallow were delineated on maps. The resulting polygons were used to estimate the percentage cover of tree mallow relative to the total vegetated area of the island. Images taken in spring underestimate total plant cover causing minor anomalies, such as an apparent decrease in cover between 1999 (photograph taken in August) and 2001 (May). However, the main conclusion of a major expansion over time (see results below) is clear.

Grazing sensitivity

The tolerance of tree mallow seedlings to rabbit grazing was determined by placing seedlings from Craigleith in early April 2004 into short-cropped grassland at Banchory, Scotland (57°04′N, 2°32′W). Seedlings (8–15 cm height) were individually planted in pots, which were sunk in the ground in sets of four, with 10 cm between plants such that the soil surface in the pots was flush with the grass sward. Ten sets, spaced at least 40 m apart were established and all were unprotected from grazing. Plants were inspected weekly over a 10-week period and any that were dug out or browsed, were transferred to an adjacent area that was inaccessible to rabbits in order to determine whether they recovered. A repeat grazing trial was set up in June 2007 to determine whether seedlings were equally sensitive to grazing later in the year. Eight sets, spaced 20 m apart, with nine seedlings (15 cm height) each and 20 cm between plants were planted in grass-dominated patches of a diverse sward with a wide range of forbs of different height and phenological stage. Plants were inspected every week for 6 weeks and signs of grazing, total removal and potential regrowth was recorded during each visit. For both experiments, there was no need to water the plants because of sufficient natural rainfall. The plant sizes used in both experiments were within the natural range of seedling sizes occurring on Craigleith throughout the growing season.

Frost sensitivity

Frost sensitivity of tree mallow seedlings was determined using seeds collected from Craigleith, initially raised in a 15–20 °C glasshouse and then hardened for 10 days (temperatures ranging between 3 and 12 °C). Eight-week-old seedlings with an average height of

2.8 cm (ranging from 1.5 to 4 cm) were potted out individually and transferred to nine locations in eastern Scotland in early March 2006, selected to create an experimental spring frost gradient. Locations were (ranked from lowest to highest number of frost hours; Fig. 1d): North Berwick (56°03′N, 2°43′W), Cruden Bay (57°25′N, 1°50′W), Golspie (57°58′N, 3°58′W), Elgin (57°39′N, 3°19′W), Banchory-Devenick (57°06′N, 2°09′W), Forvie (57°21′N, 1°56′W), Roseisle Forest (57°40′N, 3°30′W), St Cyrus (56°46′N, 2°24′W), Banchory (57°04′N, 2°32′W). Three batches of eight pots were used per location and protected against grazing and accidental damage by a tall mesh cage. Seedlings were watered during prolonged dry periods. Frost hours (<0 °C) per site were established with high-resolution temperature data loggers (Tinytag *Plus* TG12-0020, Gemini Data Loggers, Chichester, UK) with external sensors (PB4724, 0.2 °C accuracy) that recorded ambient temperature every hour. After 10 weeks, live aboveground plant material was harvested, dried at 65 °C and weighed.

The influence of tree mallow stands on microclimate, in particular the amount of frost hours, was tested using Tinytag *Plus* temperature loggers (see details above) on Craigleith between September 2006 and April 2007. Six loggers were placed in established tree mallow stands and six in adjacent open areas of equivalent aspect and topography. Sensors were placed at ground level on top of the litter layer of tree mallow or grass swards, respectively.

Seed germination

Soil conditions important for tree mallow germination were determined from soil samples (aggregate of three subsamples) taken from entrances to eight puffin burrows and adjacent grass-dominated swards in May 2004. Moisture content was determined as mass of fresh minus dry (103 °C for 18 h) soil divided by mass of dry soil. Total nitrogen content was determined using a Dumas CHN auto-analyzer (NA1500 Elemental Analyser, Carlo Erba, Milan, Italy). Seedling densities were compared between undisturbed and puffin-disturbed habitats in 25 randomly positioned 1 m × 1 m plots in puffin colonies outside mature tree mallow areas.

Consequences of tree mallow invasion

The effect of tree mallow on puffins and understorey vegetation was established in two ways. First, the total number of puffin burrows and cover of all vascular plants were determined in early July 2004 in 24 plots

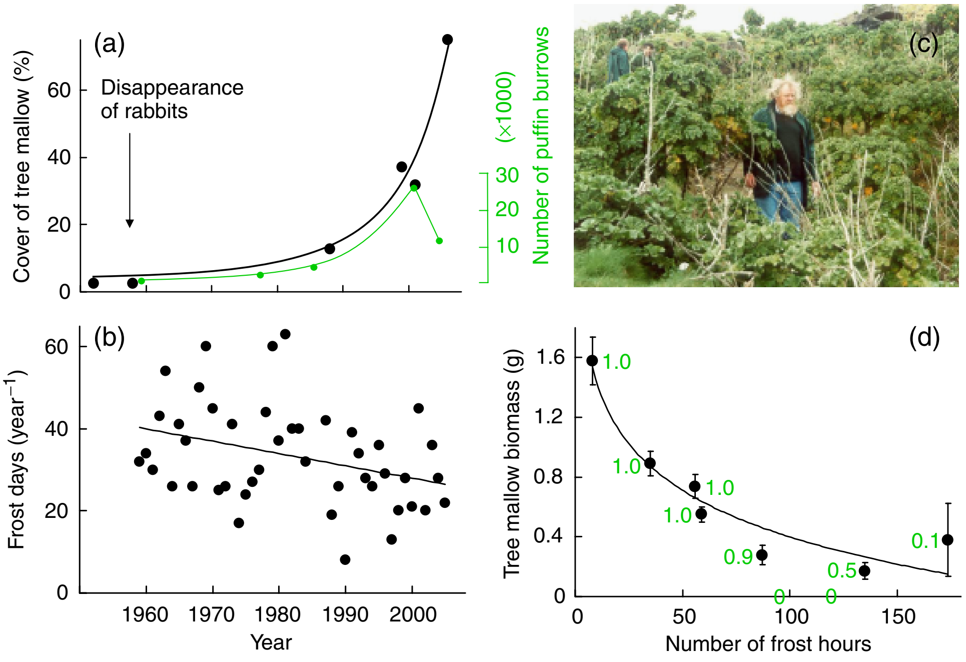

Fig. 1 Pattern and causes of tree mallow expansion. (a) Temporal changes in tree mallow cover (black) and numbers of occupied puffin burrows (green; after Harris *et al.*, 2003) on Craigleith. (b) Number of days with frost at Dunbar, 20 km southeast of Craigleith. (c) Expansion of tree mallow into prime puffin breeding habitat. (d) Performance of tree mallow seedlings at nine locations in eastern Scotland with varying amounts of spring frost. Data points refer to live aboveground plant biomass (mean ± SE of those plants that remained alive) and adjacent numbers (green) are the proportion of plants surviving (out of 24 seedlings per location). Photograph by Stuart Murray.

(3 m × 3 m) that were laid out across the island in suitable puffin breeding habitat as indicated by the presence of current or former burrows, sufficient soil depth (>30 cm) for burrowing, elevated terrain or shallow slopes and suitable landing/take-off sites such as boulders. Six of the 24 plots were in puffin colonies that had not yet been invaded by tree mallow. Plots were at least 30 m apart and located to include the full range of tree mallow cover, aspect and slope present on Craigleith. Plant cover to species level was estimated visually and agreed between two recorders in order to minimize variation in cover estimates among plots. Each burrow was checked for signs of occupancy: digging activity, fresh nest lining, egg or fresh egg shell, chick, downy feathers or feather sheaths, adult on nest, latrine and the presence of a strong smell of ammonia. Second, causality of the relationships between tree mallow and puffin breeding and ground cover was tested by the experimental removal of tree mallow. For this, we used 15 of the 24 plots described above, each which also had an additional (3 m × 3 m) plot located at 5–10 m distance. All of the sets of plots were established at the same time. One plot of each pair was randomly allocated for tree mallow removal through cutting with gardening shears. In addition, tall tree mallow plants were removed from a buffer zone (50–100 cm surrounding a cut plot) where it was needed to facilitate access by puffins. Cut plots were regularly visited during the remainder of 2004, and in 2005 and 2006 to remove any tree mallow emerging from the seed bank. The number of occupied burrows and plant cover were reassessed at the end of May and June 2006, respectively.

Statistical analysis

Statistical analyses were conducted in SAS for WINDOWS V. 9.1. Linear regressions (PROC GLM procedure) were used to detect trends in the number of frost days and minimum winter temperature across years, and to establish relationships between tree mallow cover and puffin burrow density, newly occupied burrows, vascular plant cover and stem litter, individually. General linear models were also used to analyze differences in soil moisture and soil nutrient content between puffin-disturbed and undisturbed habitat. *t*-tests were used to determine differences between cut and intact tree mallow stands in both the cover of ground vegetation and the number of frost hours on Craigleith. The relationships between the number of frost hours across the nine locations in Scotland and seedling survival, as well as their biomass were inspected with generalized linear mixed models (PROC MIXED procedure), for which denominator degrees of freedom were estimated using Satterthwaite's approximation (Littell *et al*., 1996). Within this analytical framework, seedling survival was modeled as a binomial variable and associated logit-link function, frost hours as a continuous fixed variable and location and cage nested within location as random variables. Frost hours were log-transformed in the analysis of seedling biomass and residual variances modeled as constant to the mean.

Differences in seedling density between disturbed and undisturbed habitat were tested for by dividing their log-ratios, the mean/SD which provides a *t*-statistic.

Results and discussion

Before 1960, tree mallow was present on $<5\%$ of Craigleith but has subsequently expanded exponentially to now cover 85% of the area (Fig. 1a). The species forms tall and dense stands of either first or second year plants with large amounts of seeds and plant litter underneath. Seedlings came up from the litter and accumulated biomass with a low root-to-shoot ratio without dying back over winter, growing to full height within two growing seasons. Plants flowered in June/July of their second year, set seed in July/August, died back in September, and were incorporated into the litter layer over the following winter.

Causes of tree mallow expansion

Grazing sensitivity. We suggest that three anthropogenic changes have removed three major constraints on tree mallow population growth and have thereby allowed this non-native plant to become invasive. First, up to the late 1950s, Craigleith had a large population of European rabbits (*Oryctolagus cuniculus*). Apart from humans, the rabbits had no mammalian predators and grazing pressure was likely sufficiently intense to prevent any increase in tree mallow, irrespective of the prevailing climate or nutrient levels (Gilham, 1953). We found that tree mallow seedlings exposed to grazing by rabbits in field trials early in the growing season (April) were all either browsed or dug out, mostly within 12 days. The repeat trial in June when ample alternative forbs were available, confirmed the inability of tree mallow seedlings to withstand grazing, with all plants grazed to the ground within 2 weeks without any sign of recovery. The pan-European outbreak of Myxomatosis, a viral disease introduced by humans in France, reached Craigleith in the late 1950s (Sir Hew Hamilton-Dalrymple, personal communication). As a consequence, the rabbit population rapidly died out thus removing grazing pressure, one of the principal constraints on tree mallow population growth elsewhere (Gilham, 1953).

Frost sensitivity. The second change facilitating expansion of tree mallow was the rise in winter temperature and associated decrease in days of frost that occurred in the area, particularly from the early 1980s onwards (Fig. 1b). The total number of frost days per year declined by 32% ($F_{1,43} = 5.72$, $P < 0.05$) and the average daily minimum winter temperature (October–March) increased by almost 1 °C ($F_{1,43} = 6.79$, $P < 0.05$). The negative impact of low temperature on tree mallow seedlings was demonstrated experimentally in trials across eastern Scotland (Fig. 1d). Both seedling survival ($F_{1,7} = 6.59$, $P < 0.05$) and the performance of survivors ($F_{1,5} = 5.07$, $P < 0.01$) were significantly reduced by prolonged exposure to frost, with very few plants surviving in locations experiencing more than 90 h of spring frost. Plants in North Berwick, 1.5 km south of Craigleith, accumulated by far the greatest biomass, suggesting that the local climate is well suited to tree mallow growth and survival.

Established tree mallow had an extra ameliorating effect on temperature. Underneath tree mallow, a total of 15 h of subzero temperatures were recorded between September and April compared with 53 h in otherwise comparable open grass swards from which tree mallow had been removed ($t_7 = 2.62$, $P < 0.05$). We do not know whether tree mallow seeds germinate during winter but have observed small seedlings throughout the year with particularly high densities occurring in late autumn and early spring, [i.e. periods of the year when frosts occur (R. van der Wal, personal observation)]. Once established, the milder microclimate in stands of tree mallow may well enable the species to retain dominance, even during winters and springs with prolonged periods of frost when establishment in open areas may be prevented.

Nutrient enrichment and disturbance. By the 1990s, grazing and thermal constraints on tree mallow on Craigleith had either been removed or substantially relaxed. The third change that favored tree mallow was an increase in the number of burrow-nesting Atlantic puffins, whose population increased steadily at 10% per annum between the mid-1970s and 1999 (Harris *et al.*, 2003; Fig. 1a). Again, this was thought to have an anthropogenic link, with population increases of puffins and other seabirds attributed to the reduction in stocks of large predatory fish (e.g. cod *Gadus morhua* by human fisheries) resulting in more small fish [e.g. lesser sandeels *Ammodytes marinus* available for seabirds (Furness, 2002; Ratcliffe, 2004)]. Seabirds are major vectors transferring nutrients from sea to land through the deposition of guano, dropped fish and decomposing bodies (Polis & Hurd, 1996; Fukami *et al.*, 2006; Maron *et al.*, 2006). Thus, the dramatic increase in puffin numbers probably increased soil fertility, creating favorable conditions for tree mallow that requires high nutrient levels (Okusanya, 1980; Zed *et al.*, 2006). We lack historical soil data but the comparison between Craigleith (mean soil N content of 1.6 ± 0.4%) and the nearby (35 km away) island of Inchcolm (1.0 ± 0.2% N) with similar bedrock and climatic conditions but where puffin numbers are very low due to the presence of black rats, *Rattus rattus*, may be indicative. While soil enrichment likely played an important role in tree mallow growth, seedling establishment was also enhanced due to disturbance of the ground vegetation and soil caused by puffins excavating burrows, trampling and removing vegetation for nests between March and August each year. Such disturbed ground provided highly favorable germination conditions for tree mallow being competitor free, moist and nutrient enriched (Table 1). Vegetation recording in areas of Craigleith that had not yet been invaded by tree mallow showed that few seedlings became established in the dense grass swards (Table 1). In contrast, seedling density in soil disturbed by puffins was 26 × greater ($t_{24} = 2.62$, $P < 0.01$). Therefore, increased puffin numbers on Craigleith likely played a key role in the expansion of tree mallow through providing favorable germination sites and enhanced nutrient availability for plant growth.

Consequences of tree mallow expansion

Although tree mallow may have benefited from the initial increase of seabirds, the plant invasion eventually

Table 1 Creation of favorable germination sites for tree mallow by puffins

Variable	Undisturbed habitat	Puffin-disturbed habitat	Test results	
Soil moisture content (% of dry soil)	28.7 ± 2.7	114.4 ± 12.1	$F_{1,14} = 47.50$	$P < 0.0001$
Soil nitrogen content (% of dry soil)	1.41 ± 0.11	1.76 ± 0.11	$F_{1,14} = 4.79$	$P < 0.05$
Seedling density (tree mallow m^{-2})	1.5 ± 0.7	39.5 ± 11.9	$t_{24} = 2.62$	$P < 0.01$

Soil moisture, nitrogen content and seedling density for undisturbed and puffin-disturbed habitat. Summary statistical results of tests for differences between the means for the three variables (GLMM or *t*-test) are provided.

had a strong negative effect on the puffin population with the dense growth of tall, woody plants hindering access to burrow entrances and resulting in their abandonment. Thus, while puffin numbers elsewhere in the Firth of Forth continued to increase, numbers on Craigleith declined dramatically from 28 000 burrows in 1999 to only 12 100 in 2003 (Harris *et al*., 2003; Fig. 1a). The density of puffin burrows on Craigleith was strongly and negatively related to the cover of tree mallow (Fig. 2a; $F_{1,21} = 47.82$, $P < 0.0001$). In the absence of tree mallow, burrow density averaged 8.7 burrows $9\,\mathrm{m}^{-2}$ plot compared to only 3.1 burrows under tree mallow; areas with >40% tree mallow cover had particularly few burrows. This relationship was causal because removal of tree mallow allowed puffins to reoccupy existing burrows and excavate new ones, with the greatest increase in newly occupied burrows in areas where tree mallow had previously been densest (Fig. 2b; $F_{1,13} = 9.22$, $P < 0.01$). Population declines of other ground-nesting birds on Craigleith during the last 20 years may also have been due to loss of suitable breeding habitat following tree mallow expansion. For example, the numbers of breeding eider duck (*Somateria mollissima*) declined by >90%, while herring gulls (*Larus argentatus*) and lesser black-backed gulls (*L. fuscus*) combined decreased by >50%, respectively (www.forthseabirdgroup.org.uk).

Tree mallow invasion also altered the island's ground vegetation. The total ground cover of live vascular plants was negatively related to the cover of mature tree mallow (Fig. 2c and d; $F_{1,15} = 12.37$, $P < 0.01$). Perennial grasses, notably *Festuca rubra* and *Holcus lanatus*, were dominant in the few remaining places without tree mallow, reaching a total plant cover of 89 ± 3%, while plant cover under tree mallow was an order of magnitude lower (6 ± 1%) and dominated by the annual forb *Stellaria media* with sparse cover of *F. rubra* and the annual grasses *Poa annua* and *Hordeum murinum*. Instead, large amounts of recalcitrant litter in the form of tree mallow stems and seeds, as well as rapidly decomposing leaf litter and seed heads, made up most of the ground cover under tree mallow. The amount of stem litter was positively related to tree mallow cover ($F_{1,14} = 9.72$, $P < 0.01$). In sheltered parts of the island, a loose layer of primarily tree mallow litter has formed, while on more exposed locations much of

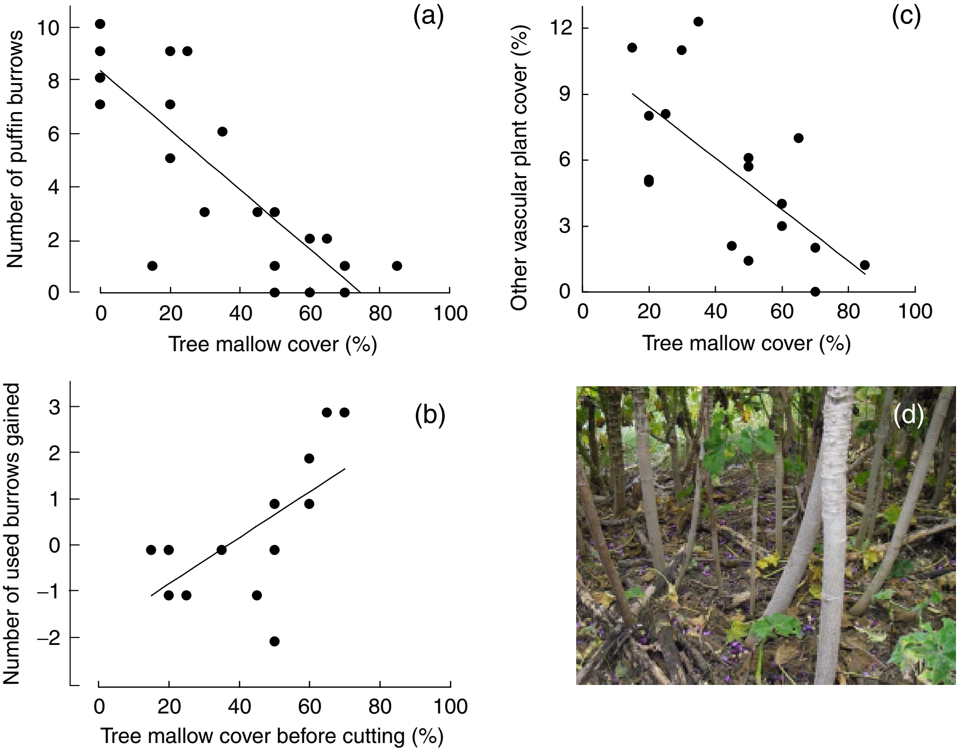

Fig. 2 Impacts of tree mallow on breeding puffins and vegetation. (a) The number of puffin burrows ($9\,\mathrm{m}^{-2}$ plot) and (b) percentage ground cover of understorey vegetation in relation to the cover of the tree mallow canopy. Experimental removal of tree mallow (c) caused an increase in the number of burrows used by puffins for breeding. Changes in (c) are differences between initial (3 months after tree mallow removal) and final assessment 2 years later. (d) Underneath mature tree mallow stands, there is little ground vegetation but predominance of mallow litter and seed heads.

the litter is blown away. Here, the virtual absence of ground vegetation under dense stands has been observed to leave the soil sensitive to erosion during winter when mature tree mallow dies back. Ground vegetation cover increased in 13 out of 15 plots following tree mallow removal and, at a mean cover of 27 ± 6%, was 3 × greater than underneath uncut stands ($t_{14} = -3.37$, $P < 0.01$). This demonstrates that presence of the invasive plants is the cause of sparse ground cover on the island.

Parallel developments in Australia

Equally dramatic suppression of native vegetation and breeding seabirds due to tree mallow invasion has been reported from seabird islands off the coasts of South Australia (Zed *et al.*, 2006) and Western Australia (Rippey *et al.*, 2002). Here, dense mallow stands had no undergrowth and died back in the hot, dry summer, exposing the soil to erosion by strong sea breezes and also rendering it vulnerable to invasion by annual weeds. As on Craigleith, a combination of factors, notably the elimination of rabbits and the arrival of unprecedented numbers of nesting birds depositing guano, were thought to be critical factors that facilitated tree mallow invasion, although no field experiments were carried out to test for causality.

Evaluating the environmental reconstruction

Our study is based on a reconstruction of the temporal and spatial changes in tree mallow abundance and lacks certainty about the historic patterns and underlying causes that have been proposed. Evaluation of alternative interpretations, in particular whether a single rather than multiple factors was behind the invasion, is therefore, appropriate. We identified four potentially important contributory factors: cessation of grazing by rabbits, reduction in days of spring frost, and increased nutrient levels and disturbance of ground vegetation. We are not aware of any island or other location dominated by tree mallow that is grazed. This is in conjunction with our experimental tests demonstrating its great sensitivity to grazing, and suggests that the absence of resident herbivores is a prerequisite for tree mallow invasion. The striking absence of tree mallow on the Isle of May, a relatively large (45 ha), highly fertile but intensively rabbit-grazed seabird island only 13 km from the historic seed source on the Bass Rock, is in line with this notion.

High nutrient status is also likely to be a prerequisite for tree mallow invasion (Okusanya, 1980; Rippey *et al.*, 2002). However, it remains to be seen whether tree mallow will invade islands where only cliff-breeding seabirds are contributing to high soil fertility through atmospheric nitrogen deposition from ammonia volatilized from guano (Wilson *et al.*, 2004). Additionally, our data on seedling establishment indicate that tree mallow expansion is greatly facilitated by disturbance associated with burrowing seabirds. While the burrow-nesting habit is limited to a relatively small number of species (Furness, 1991), physico-chemical impacts of other ground-breeding seabirds such as gulls and terns on the plant–soil system may provide equally suitable germination sites for seedlings (Vidal *et al.*, 2000; Zed *et al.*, 2006). While we doubt that tree mallow could become invasive on islands in the absence of high soil fertility and disturbance, we expect that drivers other than seabirds may generate similar conditions.

Our field experiments demonstrated the great sensitivity of tree mallow seedlings to spring frost, thereby corroborating earlier findings from laboratory studies (Okusanya, 1979). However, the importance of colder springs in the Firth of Forth before the 1980s remains unclear. It may be that milder conditions are responsible for the gradual expansion of tree mallow as is witnessed in the south of the United Kingdom (Cox, 2002), but we cannot exclude the possibility that tree mallow would have become invasive in the Firth for Forth following the removal of grazing, nutrient and germination constraints even in the absence of any climatic amelioration.

It is unknown how many islands in the United Kingdom, Australia or elsewhere are currently invaded by tree mallow. Our knowledge is largely based on islands in the Firth of Forth, Scotland, where tree mallow is invasive on the Bass Rock, Craigleith and Fidra, while individual plants or smaller stands occur on Inchcolm, the Lamb and adjacent mainland coastline. All these islands, except Inchcolm, are within 9 km of the Bass Rock, the likely source (M'Crie *et al.*, 1847) of the whole of the Firth of Forth tree mallow population. Also, in the best documented Australian situation (Rippey *et al.*, 2002), all four tree mallow-dominated islands were within 2.5 km of each other, suggesting that seed dispersal may be a major constraint to range expansion in tree mallow and one of the main reasons why many other islands at greater distance from a continuous and sizeable seed source have not yet been invaded.

Conclusions

Our results indicate that changes in three anthropogenic factors: human-introduced disease (Myxomatosis), climate warming and a fisheries-mediated increase in seabird populations, removed major constraints on plant population growth, [i.e. grazer control (Maron & Crone, 2006), climatic control (Woodward, 1987), germination opportunity (Turnbull *et al*., 2000) and nutrient limitation (Davis *et al*., 2000)]. Collectively, these changes created suitable conditions for the rapid expansion of a non-native species. The dramatic impact on both native vegetation and higher trophic levels, notably breeding seabirds, exemplifies how non-native invasive plant species can transform terrestrial ecosystems. Biological invasions by non-native plants are currently regarded as a great threat to biodiversity (Sala *et al*., 2000). Understanding the often complex processes involved is crucial, particularly where the aim is to develop an effective management strategy in a cost-effective and socially acceptable way (Mack *et al*., 2000; Simberloff, 2003; Fischer & Van der Wal, 2007). In the case of tree mallow on Craigleith, the local community is currently working on a 5-year initiative in partnership with scientists, the first phase of which involves removal of tree mallow by large-scale cutting.

Climate change is currently regarded as one of the most important factors associated with the spread of non-native plants (Dukes & Mooney, 1999). However, as recently suggested by Callaway & Maron (2006), in many cases multiple rather than single factors may be critical to biodiversity loss through plant invasion and our study provides support for this assertion.

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