

How elevation affects ship rat (*Rattus rattus*) capture patterns, Mt Misery, New Zealand

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Abstract: There is a lack of information about how elevation affects the distribution of ship rats in New Zealand. In this study, ship rats (*Rattus rattus*) were captured in traps set along a 2 km elevational transect (455–1585 m a.s.l.) in beech (*Nothofagaceae*) forest and adjacent alpine tussock at Mt Misery, in Nelson Lakes National Park, from 1974 to 1993. A total of 118 rats were captured. In years with beech seed fall, upper range limits corresponded with the red beech forest (*Fuscospora fusca*) limit (~1030 m a.s.l.), with no rats caught above this line in the silver (*Lophozonia menziesii*) and mountain (*F. cliffortioides*) beech forest (1050–1408 m a.s.l.) or alpine zone (1425–1585 m a.s.l.). Binary generalised linear models indicated there is an indirect relationship between ship rat capture and temperature, as well as decreasing elevation, were important predictors of rat capture. There was some evidence to suggest decreasing winter temperature and increasing annual precipitation also influenced ship rat capture and warrants further investigation. Our analyses provide an important insight into the drivers of ship rat elevational distribution, as well as providing a benchmark for comparing both current and future ship rat elevational distributions. Interrogation of more recent rat monitoring data from a range of beech forest types and sites is needed to test hypotheses around how warming temperatures, as predicted with climate change, will both directly and indirectly effect ship rat distribution.

Keywords: alpine; beech forest; climate change; mast seeding; Mt Misery; Nelson Lakes; New Zealand; *Nothofagus*; temperature

Introduction

Ship rats (*Rattus rattus*) are habitat generalists, capable of occupying a wide range of habitats, although they tend to be more abundant in temperate regimes than cold temperate regions (Horskins et al. 1998; Lindsey et al. 1999; Wegmann et al. 2008). Ship rats are present in high elevation forest (1600–2000 m a.s.l.; Sugihara 1997) and shrublands (>2000 m a.s.l.; Cole et al. 2000) in tropical Hawaii, but are also present in colder climates, such as *Poa foliosa* tussock grassland on the high latitude sub-antarctic Maquarie Island (Pye et al. 1999). In New Zealand ship rats occupy a wide range of habitats including exotic pasture (Innes et al. 2010), native forest (e.g. Smith et al. 2009; Christie et al. 2015), as well as sub-alpine and mānuka (*Leptospermum scoparium*) shrubland on Stewart Island (Harper et al. 2005). However, their distribution is far from uniform, with ship rats mostly absent from higher elevation, colder habitats, such as upland mountain beech (*Fuscospora cliffortioides*) forest and above the treeline in the alpine zone, while being more abundant in lowland forests (Studholme 2000; Harper et al. 2005; Christie et al. 2006).

Ascertaining the role of temperature as a driver of ship rat elevational distribution is important. Studholme (2000) suggested ship rat elevational distribution is limited by a mid-winter 2°C approximate mean monthly elevational isotherm. This is unproven, but Christie et al. (2009) noted ship rat capture probability increased in relation to increasing mid-winter minimum temperature along an elevational gradient at a South Island beech forest site. Temperature also indirectly influences food availability in beech forest as beech seed

production and invertebrate activity are both temperature linked (e.g. Wardle 1984; Schaubert et al. 2002; Richardson et al. 2005). Years of high intensity beech seed production, known as a mast, significantly increase the available food for ship rats, resulting in a substantial increase in their numbers (King 1983; King & Moller 1997; Dilks et al. 2003). Establishing whether there is a link between ship rat elevational distribution and temperature is important, because in the next 100 years temperatures are predicted to increase as a result of climate change (Mullan et al. 2016). A temperature-induced increase in ship rat elevational distribution may negatively impact native species that have persisted at higher elevations (Elliott et al. 2010) and are vulnerable to being preyed on by ship rats (Dilks et al. 2003; Innes 2005).

Ascertaining whether a relationship between ship rat presence, elevation and temperature exists, requires datasets with a long temporal extent, collected across an elevational gradient. Information on historical patterns of ship rat distribution is also desirable, so that comparisons with current and future distributions can be made. Very few long-term records of ship rat capture programmes exist, especially prior to 1999. Records from sites such as Cupola Basin (RT, unpubl. data), Craigieburn (King & Moody 1982) and the Orongorongo Valley (Efford et al. 2006), suggest ship rats were rare or non-existent in high elevation silver and mountain beech forest prior to 1999. However, trapping was generally for only short time periods and did not extend into the alpine zone (King & Moody 1982; Efford et al. 2006). A long-term study at Mt Misery (Wilson et al. 1998) summarised changes in the number of mouse and stoat captures across an elevational gradient in relation to beech seed production and season, between

1974 and 1993, but did not include ship rat capture results even though these data were collected. Since 1999, ship rats have been recorded as by-catch in stoat trapping operations in alpine habitats (O'Donnell et al. 2017), and analyses have shown a negative relationship between ship rats and increasing elevation (Christie et al. 2006). This relationship was evident at low elevation sites (i.e. 0–860 m a.s.l.; Christie et al. 2006), as well as high elevation mountainous sites such as the Haast Range (i.e. 20–1470 m a.s.l.; Christie et al. 2009).

The main objective of this paper is to identify the drivers of ship rat capture across an elevational gradient in a South Island beech forest. A second objective is to provide an historical (i.e. pre-1999) baseline for future analyses of the impacts of climate change on ship rat elevational distribution. Although it is worth noting that rat monitoring methods have changed since 1999, so these data are not directly quantitatively comparable with modern records. We summarise the previously unpublished ship rat capture data collected from Mt Misery between 1974 and 1993 by Wilson et al. (1998). We use logistic regression to analyse the influence of elevation, beech seed production, mean winter temperature and precipitation on annual ship rat capture.

Methods

Study area

Mt Misery is located between two glaciated valleys at the head of Lake Rotoroa in Nelson Lakes National Park, in the South Island of New Zealand (41°55'S, 172°39'E). The study site is a truncated spur on the north western side of the peak, encompassing cold-temperate southern beech (*Nothofagaceae*) rain-forest and alpine grasslands, from Lake Rotoroa (455 m a.s.l.) to the top of Mt Misery (1585 m a.s.l.). The climate is cold and wet. At the nearby (~20 km northeast) Lake Rotoiti weather station (620 m a.s.l.) precipitation varied between 1100 and 1900 mm per year. Mean daily maximum temperatures in summer range from 18.7° to 20.9°C, and in winter from 8.3° to 9.7°C. While mean daily minimum temperatures usually range from 7.5° to 8.4°C in summer and -1.9° to -0.6°C in winter (NIWA, unpubl. data). The vegetation along the trap line was classified into seven distinct elevational zones; silver (*Lophozonia menziesii*) / red (*Fuscospora fusca*) beech with podocarps (*Podocarpaceae*) (455–475 m a.s.l.); red / silver beech (485–515 m a.s.l.); red / silver beech with kāmahī (*Weinmannia racemosa*) (525–785 m a.s.l.); red / silver / mountain (*F. cliffortioides*) beech (805–1030 m a.s.l.); silver / mountain beech (1050–1340 m a.s.l.); mountain beech (1360–1410 m a.s.l.); and tussock (*Chionochloa* spp.) (1425–1585 m a.s.l.) (Elliott et al. 2010). Twenty 0.28 m² trays were used to measure annual beech seed production every year except for 1986 and 1987 (Wilson et al. 1998).

Rat trapping

Ship rats were trapped on a single line containing 100 trap sites at 50 m intervals up a truncated spur (455–1585 m a.s.l.; Wilson et al. 1998). At each trap site, one mouse and one rat snap trap were set inside a metal tunnel with an entrance at each end. Traps were baited with a mixture of peanut butter and rolled oats, and set for three consecutive nights at the end of February (summer), May (autumn), August (winter) and November (spring) from May 1974 until February 1984. Between 1984 and 1990, the traps were only set in February

and May 1986. Quarterly trapping resumed from February 1990 until May 1993, but only for the traps below the tree line, with breaks occurring in May and August 1992. At every fourth trap site paired Fenn traps were set (i.e. 200 m spacing, 25 paired sets in total) to trap stoats. These were set at the same time and for the same number of nights as the rat snap traps and also caught rats (Wilson et al. 1998). Because of the low number of captures, ship rat capture data from all three trap types were included in the analysis, even though these traps may vary in their effectiveness.

Statistical analysis

Binary generalised linear models (Logistic Regression; Hosmer & Lemeshow 2000) were used to determine which variables (predictors) best explained probability of ship rat capture at each trap site by austral year (e.g. Aug 1974–May 1975) as a binary variable (response). Only trapping data from below the red beech line (1030 m a.s.l.) were used because no rats were caught above the red beech line so there was no information to model. The analyses were undertaken in R (version 3.2.1; R Development Core Team 2009) using the GLM package to fit the logistic regression models. Akaike's Information Criterion (AIC) was used to determine which model was best supported by the data (Burnham & Anderson 2002). Values (Δ AIC) are reported relative to the AIC of the best model, with models of Δ AIC ≤ 2 having substantial support. Model residuals were examined to determine how well the model fitted the data.

The analysis examined the possible effects of beech seed production, elevation, winter temperature and total annual precipitation on ship rat capture. Candidate models were chosen a priori from a set of available variables which were plausible to consider. These variables were screened to avoid highly correlated weather variables. To determine whether there were any elevation specific beech seed production and weather effects, interactions with elevation were included in the models. Sample effort was also included in the models, because some trapping surveys were not undertaken. This was recorded as the number of sample occasions to occur in an austral year (i.e. 1–4). Beech seed production is summarised as seeds per m² from the preceding austral year, because it is the previous year's seed production which affects the following year's rat abundance (GE, unpubl. data). Elevation is reported as metres above sea level (m a.s.l.) of a trap site. Total precipitation was summarised by austral year (e.g. June 1974–July 1975) to correspond with the response variable. Winter temperatures were calculated as approximate mean monthly temperatures ((mean T_{\min} + mean T_{\max})/2) where T_{\min} is daily minimum and T_{\max} is daily maximum, and averaged across the three winter months of June, July and August at the beginning of each austral year period. Approximate mean monthly temperature is a better measure of enduring daily cold than mean monthly minimum temperature, and may have a greater effect on ship rats foraging for food (Studholme 2000). Temperature and precipitation data were from the Lake Rotoiti weather station (620 m a.s.l.) ~20 km to the northeast of Mt Misery and taken from the New Zealand National Climate Database (National Institute of Water and Atmospheric Research; see <http://cliflo.niwa.co.nz>). The Lake Rotoiti weather station is near enough to Mt Misery to allow conclusions to be drawn about the effects of relative change in temperature and precipitation.

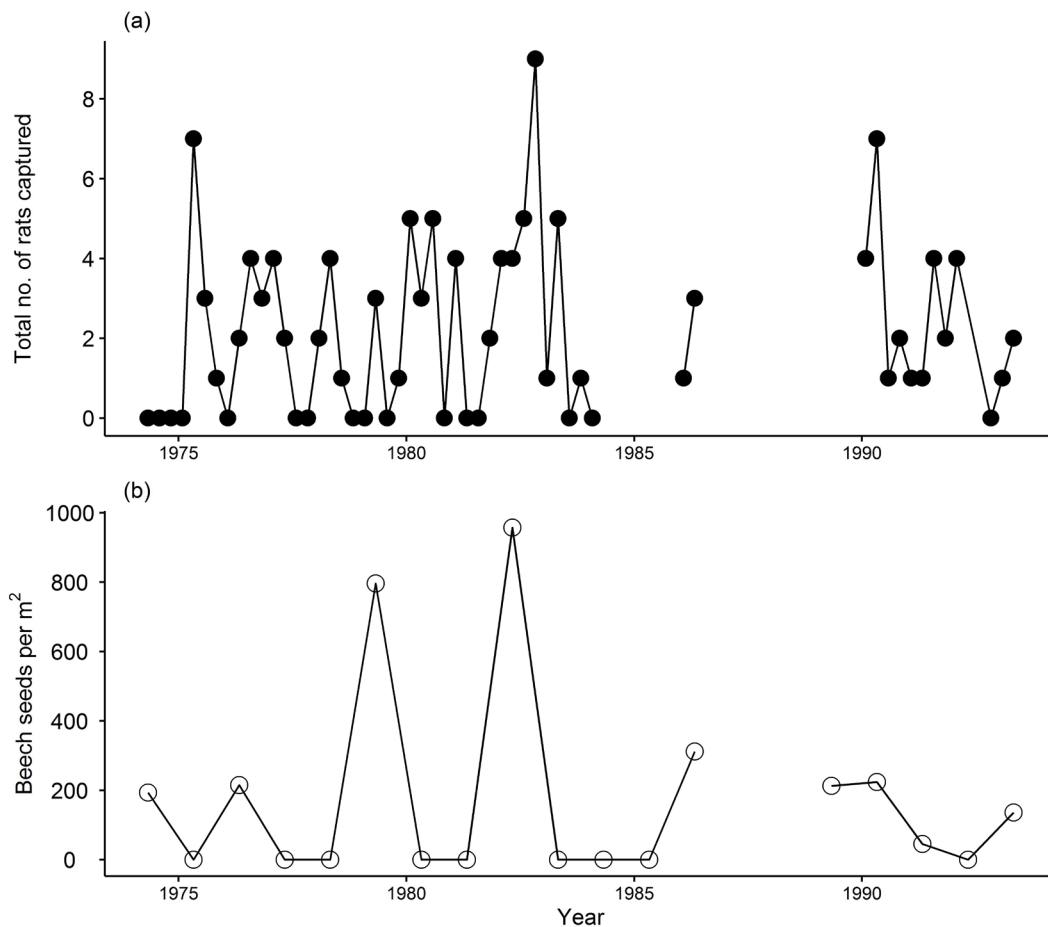


Figure 1. Summary of (a) quarterly totals of ship rats captured and (b) annual beech seed production at Mt Misery from 1974–1993. Missing points on the graphs denote periods when no data were collected.

Results

A total of 118 ship rats were captured between 1974 and 1993. Only small numbers of ship rats were captured each year, and captures varied among years (range = 3–15 rats; Fig. 1a). Annual beech seed production also varied among years (Fig. 1b), with no full masts (>4000 seeds per m²; Wardle 1984) detected in the 18 years of beech seed records. There were only 2 years with partial masts (500–4000 seeds per m²), 7 years with poor masts (<500 seeds per m²), and 9 years with no seed production (Fig. 1b). In the 15 years with both rat capture and beech seed production data, higher numbers of rats were captured in the austral year directly following a year with beech seed (mean = 10.7 ± 4.9 , $n = 7$ years), compared to years where no beech seed was produced in the preceding year (mean = 5.4 ± 3.0 , $n = 8$ years). The elevation of capture also varied according to whether beech seed had been produced, with more ship rats captured and at higher elevations in years with beech seed produced (Fig. 2). No ship rats were captured above the red beech elevational limit (approx. 1030 m a.s.l.; Fig. 2), so they were not detected in the higher elevation mountain and silver beech forest (1050–1410 m a.s.l.), and alpine habitats (1425–1585 m a.s.l.).

Influences on ship rat captures

The two best-supported models for ship rat capture included

beech seed production, elevation, winter temperature and total annual precipitation (Table 1). No evidence was found for an elevational specific effect of beech seed production, winter temperature or total annual precipitation. There was also no evidence for sample effort having an effect on rat capture in the model. According to the best two models (Table 2), rat capture was strongly influenced by the positive effects of beech seed production, as well as the negative effect of increasing elevation. Model 1 also suggests there was some evidence to show that the negative effects of increasing winter temperatures, as well as total annual precipitation, may also influence rat capture. This indicates further investigation into the effects of winter temperatures and precipitation on ship rat capture is warranted. No patterns were evident in the model residuals suggesting that both models fitted the data to an acceptable level.

Discussion

At Mt Misery no ship rats were caught above the red beech tree elevational limit (~1030 m a.s.l.) despite extensive long term trapping. This is consistent with evidence that ship rats are absent from alpine habitats in New Zealand (Studholme 2000; Innes 2005). In a concurrent study at Mt Misery, declines in common bird abundance at low elevations in comparison to

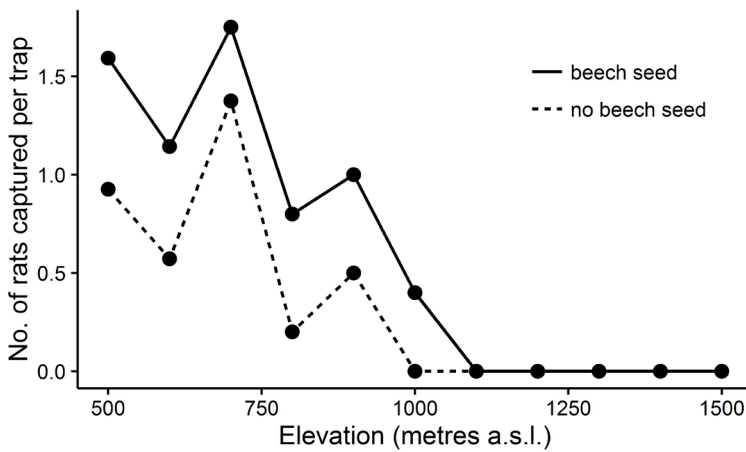


Figure 2. Number of ship rats captured per trap by elevational zone (m a.s.l.) at Mt Misery from 1974–1993 in relation to beech seeding. Number of rat captures per trap are summarised by 100 m elevational zones.

Table 1. Logistic regression models of ship rat capture probability at Mt Misery in relation to sampling effort (effort), annual beech seed (seeds), elevation (m a.s.l.), approximate mean monthly winter temperature (winter temperature) and total annual precipitation (precipitation). In model notation, + indicates an additive effect on the logit scale and × an interaction. *K* is the number of parameters estimated; AIC is the Akaike Information Criterion value of the fitted model; Δ is the AIC value relative to the best model; *w* is the Akaike weight which is a rescaling of model likelihood used as a measure of relative support of the data for the models.

Model	<i>K</i>	AIC	Δ	<i>w</i>
None	1	634.97	24.76	0.00
Effort	2	634.27	24.06	0.00
Seeds	2	620.84	10.63	0.00
Elevation	2	625.70	15.48	0.00
Elevation + seeds	3	611.31	1.10	0.32
Elevation × seeds	4	613.20	2.98	0.12
Elevation × winter temperature	4	625.51	15.30	0.00
Elevation × precipitation	4	629.56	19.34	0.00
Elevation + seeds + winter temperature + precipitation	5	610.21	0.00	0.55

Table 2. Model estimates for the two best logistic regression models for ship rat capture.

Model and variable	Slope	SE	<i>z</i>	<i>P</i>
Model 1				
Intercept	2.673	1.668	1.602	0.109
Elevation	-0.002	0.001	-3.215	0.001
Seeds	0.001	0.000	4.252	<0.001
Winter temperature	-0.479	0.285	-1.683	0.092
Precipitation	-0.001	0.001	-1.752	0.080
Model 2				
Intercept	-0.911	0.414	-2.199	0.028
Elevation	-0.002	0.001	-3.202	0.001
Seeds	0.001	0.000	4.232	<0.001

high elevations were linked to elevational variation in invasive species distribution (Elliott et al. 2010). Ship rats are habitat generalists (e.g. Cox et al. 2000; Harper et al. 2005; Innes et al. 2010), and based on previous records in these types of habitats (e.g. Pye et al. 1999) are capable of occupying high elevation silver and mountain beech forest and alpine tussock. Ship rats live entirely in silver tussock grassland on the sub-antarctic Macquarie Island (Pye et al. 1999) and recent anecdotal evidence from trapping operations suggests they are present in the New Zealand alpine zone at certain sites (O’Donnell et al. 2017) which would be comparable ecologically with Mt Misery. Furthermore, male ship rats have been recorded moving distances of up to 790 m in a night in beech forest (Pryde et al. 2005), so should be capable of living in the forest and commuting into the alpine zone. Overseas, while ship rats tend to be more abundant in temperate locations (Horskins et al. 1998; Lindsey et al. 1999; Wegmann et al. 2008), they are also present in cold climatic zones like Macquarie Island where mean annual temperature is 4.9°C (Australian Government Bureau of Meteorology, unpubl. data). These temperatures are not dissimilar to the New Zealand upper beech forest and alpine habitats where mean annual temperature range between 3.5° to 10.5°C for mountain beech (Leathwick 1998) and 4.7° and 6.4°C at the tree line (Cieraad & McGlone 2014). This suggests either other temperature metrics not captured by this study or factors other than temperature may also influence ship

rat elevational distribution in New Zealand. Below we discuss the effect of beech seeding, elevation, winter temperature and precipitation on ship rat distribution.

There was strong support for an effect of beech seed on ship rat capture. More ship rats were captured in years following beech seed production at Mt Misery, and Wilson et al. (1998) noted corresponding periodic increases in mice and stoats. Beech seed production is episodic, with large seeding events known as masts (Wardle 1984). Between 1974 and 1993 at Mt Misery there were no full masts, only partial and poor masts (Wardle 1984), but a rat response was still evident, suggesting ship rats are able to respond to even small amounts of beech seed production. Furthermore, a full mast was recorded at Mt Misery in 2000 (Department of Conservation, unpubl. data), so the small amounts of seed recorded over the trapping study period were not an artefact of the sampling method. Similar increases in rat abundance after beech seeding have been recorded elsewhere in New Zealand (Blackwell et al. 2001; Dilks et al. 2003), and suggest a strong influence of food supply on ship rat populations.

Elevation was the other important predictor of ship capture, with rat capture decreasing with elevation. Other recent studies have found a similar relationship (Christie et al. 2006, 2009). While there was no evidence for elevation specific effects of beech seed production in our analysis, this may have been because the beech seed production data for Mt Misery were not classified by elevation. However, a relationship between ship rats, beech seed and elevation is not surprising since the frequency and magnitude of beech seed production (Wardle 1984; Richardson et al. 2005), and invertebrate diversity decrease with elevation (Moeed & Meads 1985; Beggs 1991). Beech seed and invertebrates are both important food items for ship rats (Innes 1979; Blackwell et al. 2001; Sweetapple & Nugent 2007; Murphy & Maddigan 2008). Teasing out the proximate drivers of ship rat elevational distribution is difficult because bird abundance (Elliott et al. 2010), temperature (Studholme 2000; Christie et al. 2009) and under-storey diversity (Wardle 1984) all decrease with elevation as well and potentially influence ship rat distribution.

Predictions that ship rats would be limited at higher elevations in beech forest by mid-winter temperatures (Studholme 2000; Christie et al. 2009) were not supported by our models, but this may have been because our model was limited to traps below the red beech elevational limit. Our models showed some support for ship rat capture increasing when temperatures were colder than average, irrespective of the presence of beech seed production. This increase may reflect an increase in probability of capture as temperatures get colder, rather than an increase in rats per se. Similarly, increased ship rat capture with higher rainfall also may reflect increasing probability of capture, rather than abundance. Ship rats are relatively small mammals, with a fast metabolism (Innes 2005), so colder than average winter temperatures or wet conditions may increase their food requirements, and make them more likely to enter a baited trap. Efford et al. (2006) attributed increased winter capture rates to an increase in capture probability of autumn born rats. Alterio et al. (1999) also noted an increase in ship rat capture rates at a beech forest site in late winter followed by a decrease in spring but did not relate this to temperature or probability of capture.

While this study did not find any evidence to support the prediction that winter temperature limits ship rat capture, we speculate that temperature may still have an indirect effect on ship rat distribution. This is because temperature may

indirectly influence ship rat abundance through its effect on invertebrate activity and beech seed production frequency and magnitude. Invertebrate activity increases with warming temperatures (Moeed & Meads 1985, 1986). Invertebrates are a big component of ship rat diet in beech forest especially when beech seed is not available (McQueen & Lawrence 2008). Seasonal peaks in ship rat upper range limits in summer and autumn also coincide with peak invertebrate activity (Moeed & Meads 1985, 1986). Furthermore, beech seed production is an important driver of ship rat capture patterns and is also temperature linked, with warmer temperatures linked to increased beech seed production frequency and volume at higher elevations (Schauber et al. 2002; Richardson et al. 2005).

Our analyses of the historical ship rat data from Mt Misery over the 19-year study provide an insight into which variables might be important for predicting ship rat elevational distribution, as well as providing a benchmark for comparing both current and future ship rat elevational distributions. The results of this study suggest there may be an indirect relationship between ship rat capture and temperature. Strong support for the effects of beech seed production, as well as elevation on ship rat capture, suggests temperature may play an indirect role in ship rat distribution along an elevational gradient. Furthermore, evidence from our models suggest winter temperature, as well as annual rainfall, while less important, may also influence ship rat capture and requires further investigation. Therefore, rising temperatures, as predicted with climate change (Mullan et al. 2016) may result in changes in ship rat elevational distribution, especially if beech seed production increases upslope as the climate warms (Richardson et al. 2005). Rat monitoring data from a range of elevations and associated with different beech forest types and sites, are needed to test hypotheses around how warming temperatures will both directly and indirectly effect ship rat distribution.

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