Human-wildlife competition for Korean pine seeds: vertebrate responses and implications for mixed forests on Changbai Mountain, China

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ORIGINAL PAPER

Human–wildlife competition for Korean pine seeds: vertebrate responses and implications for mixed forests on Changbai Mountain, China

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Abstract

• ***Introduction*** Korean pine (*Pinus koraiensis*) is a dominant tree species in the cold temperate mixed forest zone in eastern Eurasia. Its seeds are food sources for wildlife but have become an important and marketable part of the economy for local communities.

• ***Methods*** We conducted ecological surveys inside and around Changbai Mountain Nature Reserve (CMNR) each year following the legalization of pine seed harvesting in 2000–2005 and restrictions on pine seed harvesting in 2006–2009.

• ***Results*** We found that human harvesting of pine cones was associated with declines in pine seed production and quality, pine regeneration, and populations of Eurasian red squirrel (*Sciurus vulgaris*), sable (*Martes zibellina*), and Siberian weasel (*Mustela sibirica*).

• ***Discussion*** CMNR generally harbored greater wildlife populations than were found outside of its boundaries, but populations inside and outside of CMNR tended to decline in response to unrestricted cone harvesting. Enactment of restrictions on harvesting of cones in 2006 led to rebounds in populations of squirrel, sable, weasel, yellow-throated marten (*Martes flavigula*) and Eurasian jay (*Garrulus glandarius*) in CMNR relative to outside, concurrent with a reduced percent of seed being usurped by humans. However, harvest restrictions failed to diminish damage to trees by humans or seeds by insect pests, and regeneration of pine did not rebound.

• ***Conclusion*** Our findings suggest that wildlife declines are reversible in the short-term, but long-term forest ecosystem stability is likely only if pine seed harvesting is either stopped or dramatically reduced on a permanent basis within CMNR.

Keywords Pine seed harvest · Ecological meltdown · Ecological degradation · Forest conservation · Granivore · Omnivore · Wildlife

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1 Introduction

In many forested ecosystems, the architecture and functional ecology of certain tree species define forest structure, and their species-specific traits control ecosystem dynamics (Ellison et al. 2005). The cool temperate mixed forest ecosystem is distributed in northern parts of the temperate zone, including Northeast China and Far East Russia. Korean pine (*Pinus koraiensis*) is an ecologically and economically important tree species for the cool temperate mixed forest in eastern Eurasia. Hutchins et al. (1996) reported that seeds of Korean pine are an important food source used by at least 22 species of forest wildlife, such as Eurasian red squirrel (*Sciurus vulgaris*) and spotted nutcracker (*Nucifraga caryocatactes*). In turn, these granivores serve as major agents of seed dispersal and seedling establishment by burying and subsequently failing to recover pine seeds (Hutchins et al. 1996; Lee 2002). Therefore, wildlife species are important determinants of the long-term dynamics of Korean pine and, by extension, the mixed forest ecosystem of which it is a vital component.

Humans also are important components of forest ecosystems, including both managed and unmanaged forests. As human populations increase and natural resources decline, many human activities are intensified and can threaten ecosystem structure and functions. Specifically, human activities in managed forests can dramatically alter interspecific interactions and feedback processes and result in impoverished ecological communities. Often, these activities involve over-harvest of wildlife or trees. In Northeast China, nature reserves are important elements of plans to protect natural ecosystems and native biodiversity. Herein, we analyze a 10-year time series to document ecological effects of another type of human over-exploitation, namely, human predation on seeds of Korean pine.

Residents in northeast China have harvested and eaten seeds of Korean pine for decades. Perhaps partly in response to reduced timber harvesting (Zhang et al. 2000), pine seeds have become an increasingly important revenue source for residents of local communities. Because of the integral role of Korean pine in the mixed forest ecosystem, we studied the processes of pine seed harvesting and its ecological consequences inside and outside Changbai Mountain Nature Reserve (CMNR) from 2000–2010. Harvesting of pine seeds inside CMNR was prohibited prior to 2000, although illegal harvesting was inevitable in the 1980s–1990s. Unrestricted harvesting of pine seed was allowed in CMNR from 2000–2005. Enactment of a policy restricting pine seed harvesting in CMNR in 2006 enabled us to quantify responses of wildlife populations to reduced levels of human disturbance. We tested for positive effects of CMNR and restricted seed harvesting on six species of wild vertebrates. We also documented trends in reproduction and regeneration of Korean pine.

2 Study site and methods

Changbai Mountain, on the border of China and North Korea, is the highest mountain in north-eastern Eurasia (Tang et al. 2010). CMNR is located on China's side of Changbai Mountain and is one of the largest nature reserves in China. With an area of 200,000 ha, the geographical range of the reserve is from 127°42′E to 128°17′E, and from 41°43′N to 42°26′N. Between 700 and 2,700 m in elevation, CMNR protects four primary vegetation zones: mixed forest, coniferous forest, mountain birch forest, and tundra. Endemic species have been found in every vegetation zone on the mountain. The mixed forest (42,334 ha) and coniferous forest (94,823 ha) are the dominant forests within CMNR (Shao et al. 1996). Korean pine is a co-dominant tree species throughout the mixed forest zone and in the lower part of the coniferous forest zone. The natural range of Korean pine covers at least 90,000 ha in the reserve.

Five hundred inventory units, or compartments, contained Korean pine trees in CMNR, based on forest inventory data. All of these compartments were contracted to local residents around the reserve for pine seed harvesting in the fall of 2000 due to economic pressure from local communities. The contract was renewed every year until 2006, when the nature reserve became concerned about pine tree recovery from physical damage caused by seed harvesting. Since 2006, the nature reserve has contracted for seed harvesting in one-half of the compartments every year and allowed pine trees in the other compartments 1 year to recover.

Forest inventory data on the number of pine trees within a compartment were used to extrapolate pine seed yield collected from 20 sample compartments covering different slopes and elevations. At each harvesting season, 100 Korean pine trees were selected at random within a sample compartment. The number of cones on each tree was recorded. Ten randomly selected cones were then collected from each sample tree and examined for evidence of infestation by pests. For each cone, counts were made of total seeds produced and available seeds after animals' damage and utilization. Total seed production of seeds per tree was estimated by multiplying average number of seeds per cone with the total number of cones per tree. Animal utilization of seeds per tree was estimated similarly. One thousand seeds were randomly selected from each compartment and used to determine oven-dry weight per 100 seeds.

Korean pine cones grow mainly in the upper canopy, too high to be reached from the ground by humans. Breaking of branches by humans was common while climbing to collect pine cones. After seasonal harvesting by humans, newly broken branches were counted for each sample tree, and bark damage by climbing spurs for each sample tree was recorded. Unfortunately, pine resin made it difficult to recognize every bark wound caused by climbing spurs after the initial damage in 2000. The average pine seed production, weight per 100 seeds, pest infestation rate, and number of broken branches per sample tree were estimated by using records from the sample trees. The total pine seed production within the reserve was then computed by multiplying the average yield per tree with the total number of pine trees.

Indices of population density of Eurasian red squirrel, wild boar (*Sus scrofa*), yellow-throated marten (*Martes flavigula*), sable (*Martes zibellina*), Siberian weasel (*Mustela sibirica*), and Eurasian jay (*Garrulus glandarius*) were estimated along five transects inside the nature reserve and five transects outside the nature reserve every year from 2000–2010.

Located between 750 and 1,000 m in elevation, transects were 3–5 km long and separated by at least 1–2 km. Each transect was visited three to five times each winter ($\bar{x} = 4.7\text{visits/transect/year}$). Animals sighted, animal footprints, and other signs of animal appearances were recorded during each visit. For each transect × species combination, an index of density (counts per kilometer) was computed annually using the average value for the multiple visits during the winter in question.

One-year-old pine seedlings were surveyed with 20×20 m^2 plots that were randomly located along transects. Up to 25 plots were measured, and pine seedlings were examined and counted within each plot every year. The rate of seedling damage by rodents also was computed each year.

We examined responses of wildlife and pine seedling populations to habitat protection and pine seed harvesting using a partitioned random-effects regression. The model estimates the mean counts per kilometer (or counts per hectare for seedlings), *y*, for transect *i* in year *t* as:

$$y_{ijt} = \alpha_{ij} + \beta_{ij}t + \varepsilon_{ijt},$$

where *j* is a binary variable indicating whether transect *i* was outside or inside the reserve. We estimated parameters for the model before and after 2006, which is when pine seed harvesting was restricted in the reserve. By doing so, we were able to test for a reserve effect on populations (pre-2006), as well as an effect of seed harvesting restrictions (2006 onward). Partitioning of transect data according to reserve status and inception of harvest restrictions essentially yielded four regression equations (inside or outside of reserve, before or after inception of harvest restrictions). For each regression, we used a random slopes and intercepts parameterization wherein intercepts, slopes and residual errors were distributed, respectively, as

$$\alpha_{ij} \sim N\left(\mu_{\alpha_j}, \sigma^2_{\alpha}\right), \beta_{ij} \sim N\left(\mu_{\beta_j}, \sigma^2_{\beta}\right), \text{and } \varepsilon_{ijt} \sim N\left(0, \sigma^2_j\right).$$

For regressions occurring within a given time period, we assumed that the variances σ^2_{β} and σ^2_{β} were equal inside and outside of the reserve.

We implemented the general linear mixed model within a Bayesian framework using the software package R 2.9.2 with the add-on package R2WinBUGS (Sturtz et al. 2005), which calls the software package WinBUGS (Spiegelhalter et al. 2003; version 1.4.3). Year *t* was transformed onto the interval [0,1] to aid convergence, i.e., t=(year−2000)/9. Uninformative priors were used to ensure that parameter estimates were based on the observed counts. Flat normal priors centered on zero were used for μ, and uniform [0,10] priors were used for σ^2. An advantage of the Bayesian approach is an ability to construct easily the posterior distributions for derived parameters of interest. In our study, we tested for differences in (1) the mean of initial counts inside and outside of the reserve for the two time periods, (2) the mean rate of change in counts inside and outside of reserves for the two time periods, and (3) the mean rate of change for counts inside the reserve between the two time periods. For each species model, we used five parallel chains each with 26,000 iterations, discarded the first 6,000, and applied a thinning rate of 2. Convergence was assessed using Gelman–Rubin diagnostics (Brooks and Gelman 1998). Posterior predictive checks for model goodness-of-fit were conducted using a sum of squares discrepancy measure (Kéry 2010).

3 Results

The highest pine seed production in the reserve occurred in 2000 and 2001 and the lowest in 2002 (Fig. 1a). Pine seed production increased in 2003–2005 but was still much lower than in 2000 and 2001, and decreased again in 2006–2009. Pine seed price was relatively stable between 2000 and 2005 but increased steadily thereafter (Fig. 1a). Pine seed quality appeared to decline over time, with average seed weight decreasing from 2000 to 2009 (Fig. 1b). On average (±SE), 85±5% of total annual seed production was harvested by humans (Fig. 1c).

The worst branch damage occurred in the first 2 years after legalized pine seed harvesting and again after 2006 (Fig. 1c). On average, 4.1 branches per tree were broken. Of the sampled trees, 69% had five or more broken branches, and 83% had at least one broken branch. Most of the broken branches were from the top of the canopy, where female buds grow. Tree climbers used climbing spurs and caused severe damage to tree boles by punching 80–140 holes through the bark of each tree in 2000.

Pest infestation rate of pine cones sharply increased from less than 5% before 2002 to above 50% after 2005. In addition, the percent of seedlings and saplings damaged by rodents increased 18-fold in the first 5 years, to 41% in 2005 (Fig. 1d). Most rodent damage to pine seedlings and saplings was observed below 1,000 m in elevation (Fig. 1d), in some of the highest quality stands of the mixed forest. One-year-old pine seedlings generally were more abundant inside the reserve throughout the study (Fig. 2). The number of seedlings increased from 2000 to 2002 but declined after 2002 both inside and outside CMNR (Fig. 2). Seedling numbers continued to decline even after restrictions on pine cone harvesting were enacted in 2006 (Fig. 2).

Wild boar exhibited indexes of abundance that were three to six times greater inside of the reserve than outside (Tables 1 and 2, Fig. 3). Wild boar also appeared to increase inside the reserve immediately following implementation of pine seed harvesting restrictions (Fig. 3). However, the

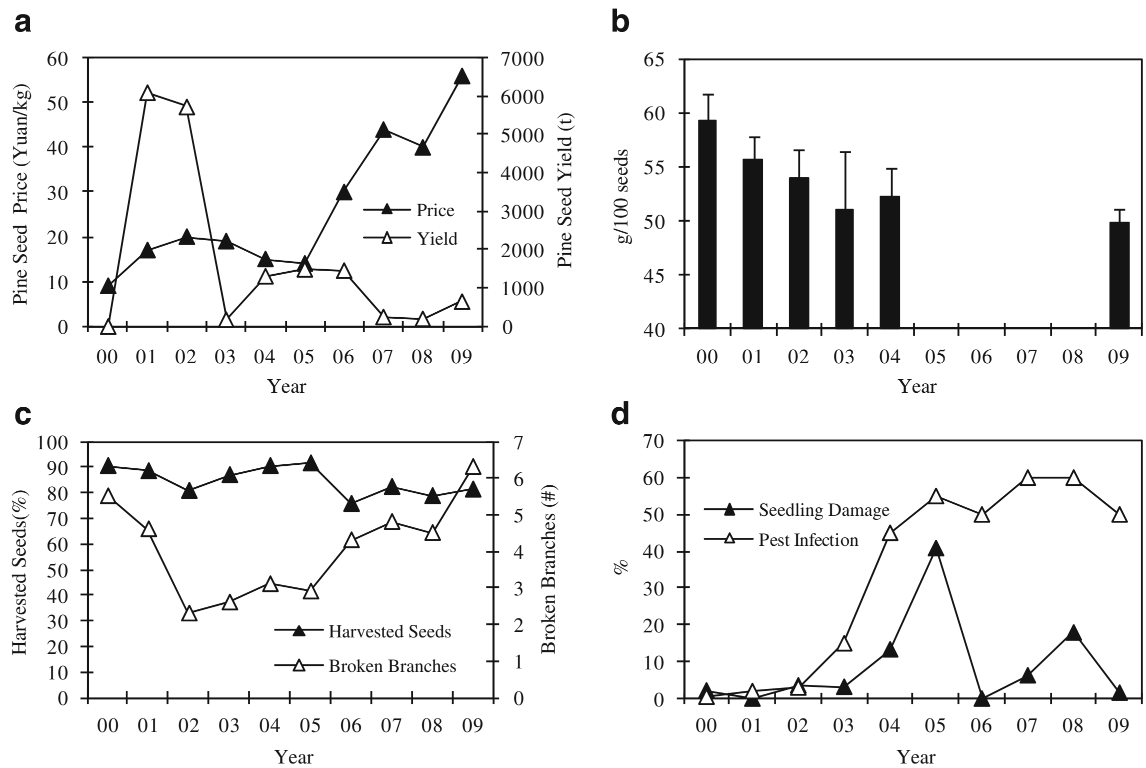

Fig. 1 Temporal changes on Changbai Mountain, China, for pine seed price and yield (**a**), average pine seed weight (**b**),% of harvested pine seeds and number of broken branches per tree (**c**), and pine seedling damage by rodents and pest infestation rate of pine cones (**d**)

overall change in population trajectory following harvest restrictions was opposite what we expected. Specifically, slopes trended from positive before restrictions began to negative afterward (Table 1, Fig. 3). Populations of Eurasian red squirrel exhibited greater mean abundance indexes inside

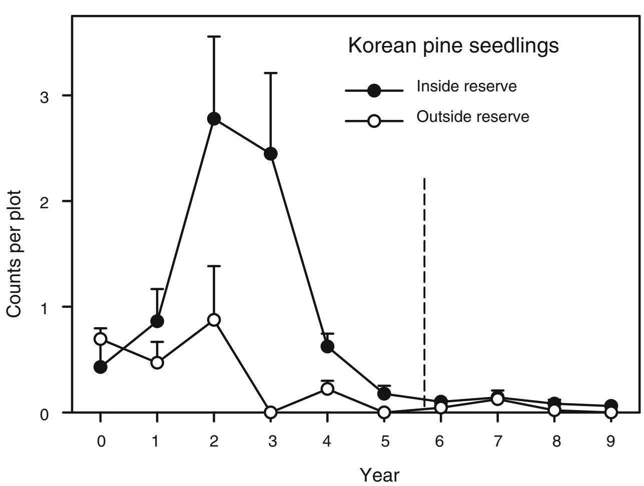

Fig. 2 Mean (±SE) abundance of 1-year-old Korean pine seedling monitored over a 10-year period (2000–2009) inside and outside of Changbai Mountain Nature Reserve, China. Dashed vertical lines depict the beginning of restrictions on harvesting of Korean pine cones within the reserve

of the reserve, declined inside and outside of the reserve during unrestricted pine cone harvesting, and exhibited dramatic reversal to increasing trajectories following enforcement of restrictions on cone harvesting (Tables 1 and 2, Fig. 3). Sable was more abundant inside of the reserve (Table 2) and declined inside and outside of the reserve during unrestricted cone harvesting (Table 1). A positive response to cone harvest restrictions was evident only inside of the reserve (Table 1, Fig. 3). Siberian weasel differed from other species by exhibiting a greater index of mean abundance outside of the reserve than inside during the period of unrestricted cone harvesting (Table 2), even though both populations declined (Table 1). Weasel abundance inside and outside of the reserve reversed their trajectories following cone harvest restrictions, although the effect was most pronounced inside the reserve (Tables 1 and 2, Fig. 3). Yellow-throated marten did not demonstrate protective effects of the reserve during the period of unrestricted cone harvesting, with mean indexes remaining stable. However, mean population indexes inside of the reserve exceeded levels outside the reserve during the period of cone harvest restrictions, when populations declined outside the reserve (Table 1, Fig. 3). Eurasian jay abundance indexes were comparable and stable inside and outside of the reserve during the period of unrestricted cone harvesting. During the period of cone harvest restrictions, there was a slight tendency for divergence of abundance trajectories of

Table 1 Estimated regression coefficients (95% credible intervals) for trends in wildlife density along transects sampled on Changbai Mountain, China. Mixed-effects regressions were conducted before and after implementation of restrictions on Korean pine cone harvesting, as well as inside and outside the nature reserve. For each species and transect, the response variable was the number of animals or sign encountered km^{-1}. Estimates in italics had 95% credible intervals that did not contain zero. If credible interval coverage of zero was small for an estimate, the fraction of the posterior distribution less than zero is referenced with a superscript

Species	Coefficient	No harvest restrictions (2000–05)		Harvest restrictions (2006–09)	
		Inside reserve	Outside reserve	Inside reserve	Outside reserve
Wild boar	α	*0.35* (0.22–0.48)	*0.05* (0.01–0.10)	*1.20* (0.40–1.86)	0.09 (−0.13–0.32)
	β	0.29 (−0.11–0.41)[a]	0.03 (−0.12–0.17)	−0.60 (−1.38–0.35)[b]	−0.06 (−0.34–0.20)
Eurasian red squirrel	α	*0.81* (0.67–0.95)	*0.50* (0.39–0.61)	−1.07 (−1.91–0.19)	−0.23 (−0.48–0.01)
	β	*−1.34* (−1.75—0.92)	*−0.95* (−1.28—0.63)	*1.85* (0.37–2.85)	*0.40* (0.11–0.70)
Sable	α	*0.24* (0.17–0.31)	*0.06* (0.02–0.09)	0.12 (−0.12–0.36)	0.08 (−0.08–0.25)
	β	−0.15 (−0.36–0.06)[c]	−0.10 (−0.20–0.00)[d]	0.16 (−0.12–0.46)[e]	−0.05 (−0.26–0.15)
Siberian weasel	α	*0.21* (0.14–0.27)	*0.34* (0.28–0.41)	0.00 (−0.18–0.18)	0.23 (−0.03–0.46)
	β	−0.18 (−0.38–0.01)[f]	−0.26 (−0.46—0.07)[g]	*0.22* (0.01–0.43)	−0.06 (−0.35–0.24)
Yellow-throated marten	α	*0.24* (0.12–0.37)	*0.17* (0.10–0.25)	*0.49* (0.04–0.94)	*0.45* (0.16–0.77)
	β	−0.16 (−0.53–0.21)[h]	0.03 (−0.19–0.25)	−0.23 (−0.76–0.31)	*−0.41* (−0.79—0.06)
Eurasian jay	α	*0.10* (0.03–0.16)	*0.09* (0.04–0.15)	0.07 (−0.17–0.27)	0.19 (−0.02–0.39)
	β	−0.05 (−0.25–0.14)	−0.07 (−0.23–0.09)	0.03 (−0.19–0.32)	−0.15 (−0.39–0.10)[i]

[a] 0.100
[b] 0.938
[c] 0.922
[d] 0.971
[e] 0.134
[f] 0.969
[g] 0.996
[h] 0.827
[i] 0.919

Table 2 Mean (and 95% credible intervals) differences in regression parameters from Table 1 describing linear trends in abundance for wildlife on Changbai Mountain, China. Mixed-effects regressions were modeled for transects inside and outside the nature reserve, and before (pre-2006) and after (post-2006) implementation of restrictions on harvesting of Korean pine cones by humans. Results in italics represent differences for which 95% credible intervals did not contain zero. If credible interval coverage of zero was small, the fraction of the posterior distribution less than zero is referenced with a superscript

Species	$\alpha_{in,pre}-\alpha_{out,pre}$	$\beta_{in,pre}-\beta_{out,pre}$	$\beta_{in,post}-\beta_{out,post}$	$\beta_{in,post}-\beta_{in,pre}$
Wild boar	*0.30* (0.15–0.44)	0.26 (−0.15–0.68)	–0.54 (−1.38– 0.49)	–0.88 (−1.79–0.17)[a]
Eurasian red squirrel	*0.30* (0.13–0.48)	–0.39 (−0.92–0.15)[b]	*1.45* (0.01–2.48)	*3.19* (1.71–4.25)
Sable	*0.18* (0.11–0.27)	–0.05 (−0.28–0.19)	0.21 (−0.15–0.59)[c]	0.31 (−0.06–0.66)[d]
Siberian weasel	−0.13 (−0.23– −0.04)	0.08 (−0.19–0.35)	0.29 (−0.10–0.63)[e]	*0.41* (0.12–0.69)
Yellow-throated marten	0.07 (−0.07–0.21)	–0.19 (−0.60–0.23)	0.18 (−0.50–0.83)	–0.07 (−0.71–0.57)
Eurasian jay	0.00 (−0.08–0.09)	0.02 (−0.25–0.28)	0.18 (−0.16–0.51)[f]	0.08 (−0.23–0.43)

[a] 0.955
[b] 0.927
[c] 0.115
[d] 0.046
[e] 0.066
[f] 0.147

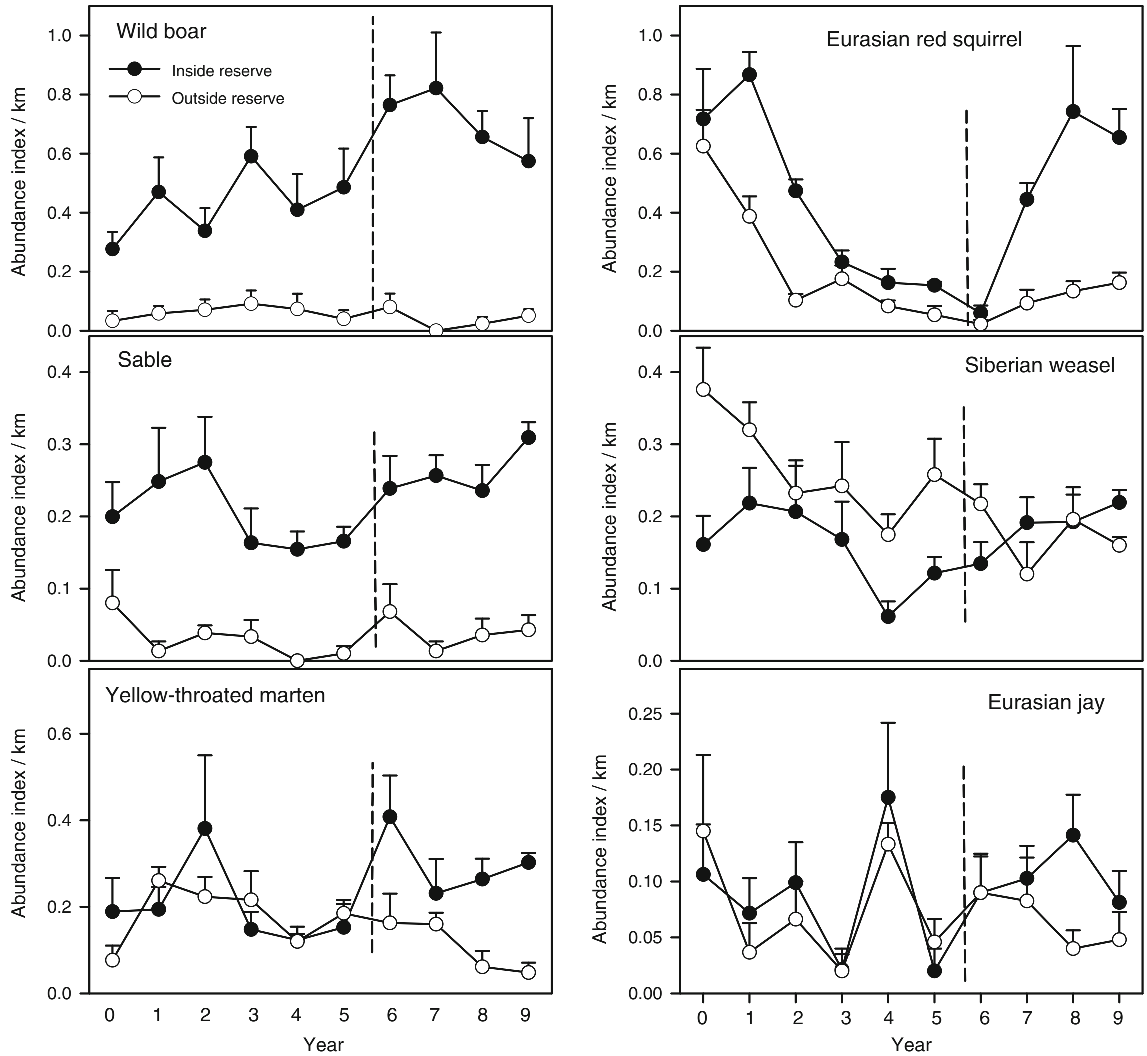

Fig. 3 Mean (±SE) indexes of abundance for six wildlife species monitored over a 10-year period (2000–2009) inside and outside of Changbai Mountain Nature Reserve, China. Dashed vertical lines depict the beginning of restrictions on harvesting of Korean pine cones within the reserve

jays inside and outside the reserve, driven by declines outside (Table 2, Fig. 3).

4 Discussion

Legalizing pine seed harvesting in CMNR has directly harmed natural forest health: pine trees were damaged by breaking of branches and wounds induced by climbing spurs, and injured pine trees produced fewer and smaller seeds. More pine tree branches were broken after 2006, presumably due to increases in illegal harvesting when only one-half of the compartments were contracted out for pine seed harvesting. The continuing declines in pine seed production exacerbated the natural fluctuations of pine seed yield observed in the past (Xu 2001). Tang et al. (2010) suggested that the health of natural forest landscapes has been jeopardized as pine seed harvesting extended to 47% of the primary forest area in CMNR. The sharp increase in pest infestation rates of pine cones provides additional evidence of human-induced forest degradation on Changbai Mountain.

Aside from the direct damage inflicted on Korean pine trees, our data indicate that pine seed harvesting by humans has induced food limitation in vertebrates, with effects on populations of both primary and secondary consumers. By co-opting such a high proportion of the vital pine seed resource, humans who harvest pine cones are functioning as a competitively superior species of granivore with the potential to exclude wild vertebrates from Changbai Mountain. Our results suggest that negative competitive effects can be reversed quickly by imposing restrictions on human harvesting of pine cones, but that effects on Korean pine demography could result in ecological instability on time scales of decades or centuries.

In the period preceding restrictions on pine seed harvesting, greater abundance inside of CMNR was evident for wild boar, sable, and Eurasian red squirrel (Fig. 3). Rhim and Lee (2007) observed greater abundance of wild boar in areas of intact forest. Buskirk et al. (1996a) found that sable prefer a mixture of tree species and dense canopy and concluded that conservation of late successional conifer stands was important to the persistence of this endangered species. Numerous investigators have noted the link between Eurasian red squirrel and expanses of mature coniferous or mixed coniferous-deciduous forest (e.g., Verboom and van Apeldoorn 1990). Thus, habitat conditions favoring all three of these species are evident inside of CMNR. In contrast, Siberian weasels occupy a variety of habitats and can do well in areas of human activity (Fetisoff 1936; Sasaki and Ono 1994), which may explain the greater levels of weasel abundance outside of the reserve from 2000–2006 (Fig. 3).

Before restrictions were imposed on pine seed harvesting, wildlife populations inside and outside of CMNR fluctuated more or less synchronously (Fig. 3). The only exception was the Eurasian red squirrel, which declined more rapidly inside the reserve (Table 2). As the least mobile species and most specialized granivore in the assemblage we studied, a more localized negative response by red squirrels is not surprising. Humans negatively affect activity of red squirrels in Korean pine stands (Hutchins et al. 1996), and red squirrels prefer large, undamaged conifer seed when available (Miyaki 1987). Opening of CMNR to unrestricted pine seed harvesting by humans, coupled with declining seed size, appeared to adversely affect Eurasian red squirrel populations in CMNR. The red squirrel is considered threatened in Europe, apparently owing to forest fragmentation and competitive inferiority to introduced gray squirrels (*Sciurus carolinensis*) in using acorns as food (Verboom and van Apeldoorn 1990; Bertolino and Genovesi 2003). Our results indicate another potential risk factor for red squirrel populations in eastern Eurasia, namely, human competition for pine seed.

After implementation of cone harvesting restrictions, wildlife populations in CMNR grew more rapidly or remained more abundant than populations outside of CMNR for all six species (Fig. 3). Asynchronous dynamics of wildlife inside versus outside of CMNR were common during this period, with positive effects observed for five of the six species monitored (Table 2). Eurasian red squirrel benefited the most, with rapid recovery of the CMNR population (Fig. 3). This is consistent with its aversion to human disturbance and ability to extract Korean pine seeds from cones (Miyaki 1987). Sable prey primarily on rodents (*Myodes*), but pine seeds are present in 6–39% of sable feces (Buskirk et al. 1996b; Dubinin 2010) and apparently serve as an important supplemental food. Siberian weasels in forested habitat are dependent to a large degree on granivorous rodents as prey (Fetisoff 1936; Tatara and Doi 1994). If population trends in Eurasian red squirrels are indicative of trends in other granivorous rodents (e.g., *Apodemus* and *Tamias*), an increase in the rodent prey base likely promoted weasel increases in CMNR after restrictions were imposed on seed harvesting. The response of Eurasian jays is more difficult to interpret, as asynchrony was driven by declines outside of CMNR (Fig. 3). Jays prefer more contiguous forest (Andrén 1992), and their lack of territoriality enables flexible patterns of space use that are dictated principally by food availability (Rolando 1998). We suspect that the divergence in population trajectories of Eurasian jays after 2006 represented a spatial reshuffling of individuals to accommodate a greater proportion inside of CMNR, reflecting the reserve's greater resource availability following restriction of seed harvesting. Indeed, it is possible that spatial redistribution could account for at least some of the increases in counts of sable and Siberian weasel observed in CMNR from 2006–2009, perhaps in response to reduced human activity.

We question whether the short-term positive responses of wildlife to restriction of pine cone harvesting are sustainable. Our concern centers on how long-term cone harvesting will affect regeneration of Korean pine, and the implications of regeneration failure for ecological interactions. Wounding of mature trees may reduce adult survival, and our data suggest that allocation of resources to reproduction declined. As wounding increased, Korean pines reduced seed production and size and exhibited increasing rates of pest infestation on pine cones (Fig. 1). Seed crops of reduced magnitude and quality lessen the likelihood of seed survival, because Eurasian red squirrels are the principal disperser of Korean pine seed in mixed forest ecosystems (Miyaki 1987), they only cache healthy seeds (Miyaki 1987) and rodents in general are less likely to cache seeds when food is limiting (Moore and Swihart 2007). The observation that seedling abundance remained low throughout the period of restricted harvesting (Fig. 2) strongly suggests that any short-term gains exhibited by wildlife populations was achieved at the expense of Korean pine regeneration.

Korean pine seed is high in lipids and capable of long periods of dormancy (Qi et al. 1993), thereby serving as a valuable stored food source for wildlife. In a mixed forest in Japan, Miyaki (1987) estimated that Eurasian red squirrels consumed 22% of Korean pine seed production and scatter hoarded an astounding 74% of production. Hoarded and rejected seeds are available to many other species of wildlife. For instance, wild boar excavate seeds buried by rodents (Focardi et al. 2000), and seeds are dietary components of sable and yellow-throated marten (Zhou et al. 2008). Even if other mast-producing species compensate completely for the loss of Korean pine, they will not be equivalent energetically or in terms of storage. More realistically, regeneration failure of Korean pine likely would lead to increased seed scarcity and interspecific competition among granivores. Omnivores foraging in a frequency-dependent manner may also intensify predation pressure on rodents when seed is scarce (e.g., Wilcox and Van Vuren 2009). Subsequent declines in rodent populations could lead to similar prey-switching by carnivores (Schmidt and Ostfeld 2008). Finally, reduced caches of pine seed essentially would eliminate the ability of rodents to hedge against “bad” years when weather or other food resources are limiting. Without the buffer provided by pine seed, wildlife populations likely would exhibit greater temporal fluctuations, with lagged responses at higher trophic levels (Schmidt and Ostfeld 2008; Dalgleish and Swihart 2011). We recognize that our observations are correlational, and that experimental manipulation of the system will be needed to conclusively demonstrate a causal link between human harvesting of Korean pine seeds and forest ecosystem processes. Collectively, though, the suite of changes we observed strongly suggests that human harvesting is a driving force with substantial implications for pine regeneration and the viability of the mixed forest ecosystem as it is currently configured. Specifically, we believe that pine seed harvesting by humans has produced a chain reaction with the potential for deleterious long-term ecological consequences: (1) unrestricted harvesting reduced pine seed availability, which (2) resulted in declines in the abundance of several wildlife species that either directly or indirectly depend on Korean pine seed; (3) the affected species included important dispersers of pine seed, (4) leading to reduced dispersal and seedling establishment. Even with enactment of restrictions on human harvesting of seed, pine regeneration has been compromised, presumably due to reduced caching of seeds and depletion of seed banks. Low pine seedling counts portend reduced levels of recruitment of pine trees into the canopy layer in the future.

Shao et al. (1994) used a forest dynamic model to simulate the impacts of pine seed harvesting on forest structure and composition. The results suggested that declines in the composition of Korean pine in the canopy layer could not be manifested until 250 years after seed harvesting. This may be an overly optimistic scenario, because the simulations of Shao et al. (1994) failed to adjust mortality rate due to tree damage inflicted by seed harvesting. Our 10 years of observations revealed that the responses of mother trees to human-induced wounding resulted in production of fewer, smaller seeds, presumably with negative consequences for reproductive potential and regeneration. We strongly suspect that the continued seed harvesting and damage to mother trees by humans threatens the long-term survival of the mixed forest ecosystem, with concomitant adverse consequences for wildlife inhabiting the forest on Changbai Mountain.

Our observations on Changbai Mountain provide evidence of another mechanism by which humans can facilitate ecological meltdown (Roy et al. 1999); namely, competition with wildlife for food produced by a foundation tree species. More generally, our observations indicate that human appropriation of net primary production (HANPP) from foundation species (Ellison et al. 2005) such as Korean pine can destabilize interspecific interactions and impoverish ecological communities. The greatest HANPP occurs in Asia and Western Europe (Imhoff et al. 2004), suggesting a potentially greater risk of an exploitation-induced ecological meltdown if key plant species are targeted by human residents in these regions. Care should be taken to monitor ecosystem changes associated with consumptive activities of humans. Continuous efforts are required to achieve the original purposes of establishing protected areas (Primack 2006).

5 Concluding remarks

Harvesting over 85% of the total pine seeds represented a prodigious effort that was economically motivated. Residents around CMNR enjoyed the economic benefits of the forest ecosystem via selling of pine seeds. We doubt that they were aware that the economic benefits they reaped from the forests were simultaneously mortgaging ecological services provided by the forests. Reduction in human harvesting of pine seeds reversed some wildlife declines and suggests sensitivity by those species to the activities of humans and availability of pine seeds on Changbai Mountain. If pine seed harvesting continues, forest health will be weakened further and pine seed production eventually will be diminished to a negligible level. In turn, forest economic benefits will be mostly lost.

Pine seed harvesting is still common outside the reserve and jeopardizes the purpose of the Natural Forest Protection Program on Changbai Mountain (Zhang et al. 2000). The ecological degradation we observed outside CMNR confirms that the Natural Forest Protection Program needs to pay more attention to forest function rather than forest form (big trees) (Tang et al. 2009). The good news is that CMNR still functions as a relatively intact forest ecosystem. To prevent long-term ecological degradation on Changbai Mountain, we recommend complete cessation of pine seed harvesting inside CMNR, or at least substantially stronger restrictions than are currently in place.

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