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REVIEW

Responses of small mammals to clear-cutting in temperate and boreal forests of Europe: a meta-analysis and review

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Abstract We analyzed the responses of small mammals to clear-cutting in temperate and boreal forests in Europe. We conducted a meta-analysis of published research on most often studied small mammal species (the striped field mouse, the yellow-necked mouse, the wood mouse, the field vole, the common vole, the bank vole, the Eurasian harvest mouse, the common shrew and the Eurasian pygmy shrew), comparing their abundance on clear-cuts and in unharvested stands. For four other species (the gray-sided vole, the Siberian flying squirrel, the Eurasian red squirrel and the hazel dormouse), we provide a qualitative review of their responses to forest harvest. Results of the meta-analysis suggest that common species of small mammals usually increase in abundance after clear-cutting or are unaffected by this disturbance. As an exception, the yellow-necked mouse declines after clear-cutting in boreal but not in temperate forest. The qualitative review suggests that the responses of more specialized (e.g., arboreal) species to forest harvest are more varied than the responses of generalist species included in the meta-analysis. For some species of small mammals (e.g., the Siberian flying squirrel), habitat loss resulting from forest harvest is a major threat.

Keywords European forests · Forest management · Logging · Rodents · Shrews

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Introduction

One of the main goals of sustainable modern forestry is maintaining biodiversity in conjunction with ensuring economic services of forests (Bengtsson et al. 2000). To achieve this objective, we need to develop an adequate scientific knowledge on the influence of management practices on forest ecosystems (Simberloff 1999). This will permit the development of effective conservation policies, based on solid scientific evidences (Sutherland et al. 2004). Modern forestry has considerably transformed forests both on the stand and landscape level, and original patterns of those remained only in some remote, mainly mountainous areas (Hansson 1992a). In fact, there are almost no intact forests in Europe (Hannah et al. 1995). For economical reasons, forest harvest is often conducted in the form of clear-cutting, especially in northern parts of Europe (Keenan and Kimmins 1993; Kuuluvainen 2009). Consequently, clear-cutting has replaced fires and wind-throws as the main disturbance in northern part of the continent (Östlund et al. 1997; Kuuluvainen 2009). However, its environmental impact is highly controversial (Keenan and Kimmins 1993; Simberloff 2001; Angelstam and Kuuluvainen 2004; Kuuluvainen 2009). Therefore, there is a need for gathering reliable scientific knowledge on the influence of clear-cutting on different aspects of forest ecosystems.

Small mammals (rodents and shrews) are mostly common and generalist species that play important role in many ecosystems worldwide, including European forests. Small mammals are core components of forest food webs. They can influence tree recruitment through selective foraging on seeds (García et al. 2005; Zwolak et al. 2010) and seedlings (Ostfeld et al. 1997; Gómez et al. 2003). On the other hand, many species of rodents promote forest regeneration by dispersing seeds and caching them in safe sites (den Ouden et al. 2005; Zwolak and Crone 2012). Small mammals also eat and disperse spores of mycorrhizal fungi, thus enhancing functioning of forest trees (Schickmann et al. 2012). Rodents and shrews are important consumers of invertebrates (Drożdż 1966; Churchfield and Rychlik 2006) and may control insect populations (Jones et al. 1998). Small mammals are a crucial part of the diet of numerous species of predators and birds of prey (Jędrzejewska and Jędrzejewski 1998).In addition to their strong trophic interactions, forest small mammals represent important reservoirs of zoonotic pathogens, such as *Borellia* (a cause of Lyme disease) and *Hantavirus*, a pathogen that can cause nephropathia epidemica (NE) in humans (Heyman et al. 2009). There are several studies that summarize the growing body of literature on the influence of forest management in Europe on different taxa of wildlife (e.g., Paillet et al. 2010; Prieto-Benítez and Méndez 2011). However, to the best of our knowledge, there is no such work for small mammals. While in Northern America, there were several reviews on effects of forest management on this important group (Kirkland 1990; Fisher and Wilkinson 2005; Zwolak 2009), similar syntheses on European small mammals are still lacking. In this paper, we aimed to summarize the results of studies investigating the influence of forest harvest on small mammal abundance on the stand level. We focus mainly on clear-cutting because it is one of the most common methods of forest harvest and almost all studies on responses of small mammals to logging in Europe concern this harvest method. For several species of small mammals, relatively large number of published studies of their responses to clear-cutting enabled us to use a meta-analytic approach (Fernandez-Duque and Valeggia 1994). This approach has several advantages over narrative reviews. Most importantly, it is less subjective than traditional reviews and allows improved control of type II statistical error (Arnqvist and Wooster 1995). In a few other cases where we were unable to conduct quantitative analysis, we provided a brief synthesis of the results of published studies conducted both on stand and landscape level.

Materials and methods

Data collection

We searched the Web of Science and Google Scholar online databases for peer-reviewed studies that examined the effects of forest harvest on small mammal abundance. To identify focal publications, we used the following search words: (logging OR clear-cut* OR harvest) AND (rodent OR “small mammal*” OR mice) AND forest. We have also conducted separate search for each species using the Latin and English name of each species instead of phrase “small mammal*” OR mice (e.g., “common shrew” OR “*Sorex araneus*”). We selected only studies that were conducted in Europe. The lists of references from relevant articles were used to find studies that were not found in the first search. We also screened studies that cited focal publications to ensure that we did not miss any article of interest. This searching process was repeated until no further publications could be retrieved. The search was conducted in November 2012.

For the meta-analysis, we selected studies that reported small mammal abundances both in clear-cuts and in unharvested or mature forest. We included only studies conducted up to 20 years post-harvest because studies that reported small mammal abundances on older clear-cuts too rare to provide meaningful inference (5 studies and only 13 out of 169 extracted data points; see Results). We excluded studies that reported data only from harvested sites and studies that did not provide data sufficient to compare abundances in clear-cuts and unharvested stands. To avoid including data points based on accidental captures, we used only studies where at least 10 individuals were captured. Otherwise, we did not use any selection criteria based on quality features of studies because such procedures can lead to potential bias (Englund et al. 1999). If several articles reported the same data, we chose one that provided the most inclusive version. In cases where a single study provided data on abundance of small mammals on several clear-cuts of different age or in different forest types, they were used as independent data points. Otherwise, data were averaged (e.g., several replicates in the same forest type). We did not include studies where abundance of related species was pooled because species within the same genus might react differently to forest disturbance (Sidorovich et al. 2008). Two studies reported data on abundance of small mammals on clearings caused by air pollution (Čepelka et al. 2011; Bryja et al. 2002). As these clearings were the result of cutting and removing trees, they were very similar in structure to commercial clear-cuts (J. Bryja, personal communication) and we decided to include them into our analysis.

Calculation of effect sizes

As evaluating small mammal abundance requires large trapping effort, most of the analyzed studies were not replicated or the number of replicates was too small to calculate variance. Therefore, we were not able to calculate classical effect sizes based on variance (e.g., Gurevitch et al. 1992). Instead, we used the relative abundance index (RAI) developed by Vanderwel et al. (2007):

$$\mathrm{RAI} = \frac{N_{\text{clear-cut}} - N_{\text{forest}}}{N_{\text{clear-cut}} + N_{\text{forest}}}$$

where $N_{\text{clear-cut}}$ is the abundance of focal species in clear-cut and N_{forest} is the abundance of focal species in undisturbed forest. If there was a difference in trapping effort between clear-cut and unharvested stands, we standardized the abundance, e.g., by calculating the number of captures per 100 trap nights. RAI ranges from -1 (when a given species was found only in undisturbed forest) to $+1$ (when it was found only on clear-cuts) and equals zero when a given species is equally abundant in clear-cuts and undisturbed forest. If a study reported data on abundance for each year of the study separately, we averaged abundance for each species across years.

Publication bias

Publication bias in meta-analysis arises when studies with significant results are more likely to be published than those with non-significant results (Murtaugh 2002). We examined funnel plots and conducted linear regression of effect size (RAI) on sample size (the number of captured individuals), as recommended by Egger et al. 1997. We found no relationship between RAI and sample size, and thus, there was no evidence of the publication bias in our set of studies.

Another type of bias can arise from lack of independence among data points if proportionally large number of observations comes from few studies (Gurevitch and Hedges 1999). It was not the case in our analysis because there were no studies providing more than 5 % of data points for a given species (mean = 2.1 data points, SD = 1.4).

Statistical methods

We analyzed species-specific responses of small mammals to clear-cutting using generalized liner models with RAI as the response variable and small mammal species, vegetation zone (boreal or temperate forest) and interaction between these two as explanatory variables. We also explored models that included age and area of clear-cuts, but these variables turned out non-significant (unpublished analyses). Similarly, we also analyzed the data using general mixed models that included correlated random effect of small mammal species over study. However, inclusion of the random effect had negligible influence on results, and thus, we reported results of the less complicated statistical method (as recommended by Zuur et al. 2009). We used model validation graphs and confirmed the assumption of homogeneity (fitted values versus residuals) and normality (QQ plots) in our model. All the statistics were computed in R software (R Development Core Team 2012).

Almost all studies used in the meta-analysis were conducted in coniferous forest. However, the distinction between coniferous, mixed and deciduous forest becomes arbitrary because foresters often cut down one type of forest and plant different one at the same site (e.g., Pedersen et al. 2010). Instead, we run two models: (1) including only data points from coniferous stands and (2) including data points from coniferous, deciduous and mixed stands. The results of both models were almost identical, and thus, we reported results of the more inclusive model. However, since majority of the studies were conducted in coniferous forest, our results are probably more representative of the responses of small mammals to clear-cutting in coniferous than in deciduous forests.

Results

Twenty studies met our criteria (see Table 1 for the list of studies used in the meta-analysis). They were published between 1959 and 2013. Twelve of them were conducted in boreal forests (bringing 61 data points, i.e., species × clear-cut combinations) and eight in temperate forests (95 data points). Out of the 156 data points, 130 were from coniferous stands, 18 were from mixed stands and 8 were from deciduous stands. The data were sufficient to quantify changes in abundance for nine small mammal species: the striped field mouse (*Apodemus agrarius*), the yellow-necked mouse (*Apodemus flavicollis*), the wood mouse (*Apodemus sylvaticus*), the field vole (*Microtus agrestis*), the common vole (*Microtus arvalis*), the bank vole (*Myodes glareolus*), the Eurasian harvest mouse (*Micromys minutus*), the common shrew (*S. araneus*) and the Eurasian pygmy shrew (*Sorex minutus*). The rest of reported small mammal species were reviewed only qualitatively in Discussion. That includes the following species: the gray-sided vole (*Myodes rufucanus*), the Siberian flying squirrel (*Pteromys volans*), the Eurasian red squirrel (*Sciurus vulgaris*) and the hazel dormouse (*Muscardinus avellanarius*).

The striped field mouse increased on clear-cuts in temperate forests of Europe ($t_{15,141} = 2.42$, $P = 0.02$ no studies in boreal forest; Fig. 1). The yellow-necked mouse demonstrated marginally significant increase in response to clear-cutting in temperate forests ($t_{15,141} = 1.76$, $P = 0.08$) and significant decrease in boreal forests ($t_{15,141} = -2.14$, $P = 0.03$). The response differed between the regions ($t_{15,141} = -2.68$, $P = 0.008$). In the case of the wood mouse, there was a marginally significant positive response to clear-cutting in temperate forests

Table 1 Studies used in the meta-analysis on the influence of clear-cutting on small mammal abundance

Reference	Study location (vegetation zone)	Forest type (dominant tree species)	Age of clear-cuts (years)	Small mammal species
Banach et al. 1979	Poland (temperate)	Coniferous (*Pinus sylvestris*)	0.5–15	*A. sylvaticus*, *M. glareolus*
Bryja et al. 2002	Czech Republic (temperate)	Coniferous (*Picea abies*)	0–12	*A. flavicollis*, *M. agrestis*, *M. arvalis*, *M. glareolus*, *S. araneus*, *S. minutus*
Čepelka et al. 2011	Czech Republic (temperate)	Coniferous (*Picea abies*) Mixed (*Fagus sylvatica* and *Abies alba*)	10 1–13	*A. flavicollis*, *M. agrestis*, *M. glareolus*, *S. araneus*
Charles 1981	Great Britain (temperate)	Coniferous (*Pinus sylvestris*)	3–10	*M. agrestis*
Ecke et al. 2002	Sweden (boreal)	Coniferous (*Pinus sylvestris* or *Picea abies*)	0–20	*M. glareolus*
Gorini et al. 2011	Norway (boreal)	Coniferous (*Pinus sylvestris* or *Picea abies*)	5–10	*M. glareolus*
Grodziński 1959	Poland (temperate)	Coniferous (*Picea abies*)	6–13	*A. agrarius*, *A. flavicollis*, *A. sylvaticus*, *M. arvalis*, *M. glareolus*, *S. araneus*
Hanski and Kaikusalo 1989	Finland (boreal)	Coniferous (*Picea abies*)	1–5	Clear-cut: *S. araneus*, *S. minutus*
Hansson 1974	Sweden (boreal)	Coniferous (*Picea abies*)	3–8	*A. flavicollis*, *A. sylvaticus*, *M. agrestis*, *M. glareolus, S. araneus*, *S. minutus*
Hansson 1978	Sweden (boreal)	Coniferous (*Picea abies*)	0–5	*A. flavicollis*, *A. sylvaticus*, *M. agrestis*, *M. glareolu, S. araneus*
Hansson 1992a	Sweden (boreal)	Coniferous (*Picea abies*) Deciduous (*Fagus sylvatica*)	Unknown Unknown	*A. flavicollis*, *A. sylvaticus*, *M. agrestis*, *M. glareolus, S. araneus*, *S. minutus*
Hansson 1994	Sweden (boreal)	Coniferous (*Pinus sylvestirs* and *Picea abies*)	3–14	*M. agrestis*, *M. glareolus, S. araneus*
Henttonen et al. 1977	Finland (boreal)	Coniferous (*Pinus sylvestirs* or *Picea abies*)	Up to 10	*M. agrestis*, *M. glareolus*
Horváth et al. 2005	Hungary (temperate)	Deciduous (*Alnus* spp.)	3–4	*A. agrarius*, *A. flavicollis*, *M. glareolus*, *S. araneus*
Jensen 1984	Denmark (temperate)	Coniferous (*Picea sitchensis* or *Abies grandis*)	10	*A. flavicollis*, *M. agrestis*, *M. glareolus*
Panzacchi et al. 2010	Norway (boreal)	Coniferous (*Pinus sylvestirs* or *Picea abies*)	0–5	*A. sylvaticus*, *M. agrestis*, *M. glareolus*, *S. araneus*
Savola et al. 2013	Finland (boreal)	Coniferous (*Pinus sylvestirs* or *Picea abies*)	3–15	*M. agrestis*, *M. glareolus, S. araneus*
Sidorovich et al. 2008	Belarus (temperate)	Coniferous (*Pinus sylvestirs* or *Picea abies*)	1–12	*A. agrarius*, *A. flavicollis*, *A. sylvaticus*, *M. minutus*, *M. agrestis*, *M. arvalis*, *M. glareolus, S. araneus*, *S. minutus*
Sundell et al. 2012	Finland (boreal)	Coniferous (*Picea abies*)	5	*M. agrestis*, *M. glareolus, S. araneus*
Wołk and Wołk 1982	Poland (temperate)	Coniferous (*Pinus sylvestirs* or *Picea abies*)	1–19	*A. flavicollis*, *M. glareolus, S. araneus*, *S. minutus*

($t_{15,141} = 1.81$, $P = 0.07$), whereas the response in boreal forest was not significant ($t_{15,141} = 1.18$, $P = 0.24$). The field vole strongly increased on clear-cuts both in temperate forests ($t_{15,141} = 4.21$, $P < 0.0001$) and boreal forests ($t_{15,141} = 6.49$, $P < 0.0001$). The same was true for the common vole in temperate forests ($t_{15,141} = 2.32$, $P = 0.02$; no studies in boreal forest). The abundance of bank voles showed no response to clear-cutting (temperate forests: $t_{15,141} = -1.04$, $P = 0.30$; boreal forests: $t_{15,141} = -0.002$, $P = 0.99$). The Eurasian harvest mouse increased in abundance on clear-cuts in temperate forests ($t_{15,141} = 3.01$, $P = 0.003$; no studies in boreal forest). The common shrew increased in response to clear-cut in temperate forests ($t_{15,141} = 2.50$, $P = 0.014$) but not in boreal forests ($t_{15,141} = 1.28$, $P = 0.20$). The Eurasian pygmy shrew showed no response to clear-cutting (temperate forests: $t_{15,141} = 0.14$, $P = 0.89$; boreal forests: $t_{15,141} = 1.10$, $P = 0.27$).

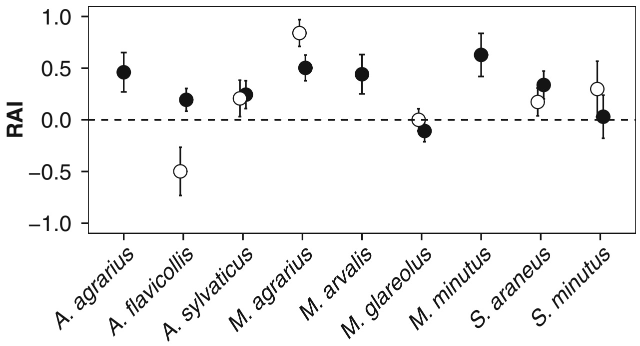

Fig. 1 Relative abundance indexes (RAI) of nine small mammal species in temperate (*filled circles*) and boreal forests (*open circles*) of Europe. RAI indicates relative differences in abundance of a given species between clear-cuts and unharvested forests. RAI might vary from −1 (species present only in unharvested forest) to 1 (species present only on clear-cuts).Whiskers indicate standard errors

Discussion

Responses of small mammals to clear-cutting: a meta-analysis

Our meta-analysis demonstrated a positive influence of clear-cutting on the abundance of most analyzed small mammals. In general, the responses to logging were similar in forests of temperate and boreal vegetation zones. The only species that reacted differently to clear-cutting in these two regions was the yellow-necked mouse, which tended to increase in clear-cuts in temperate zone, but declined in logged boreal forests. The only two species that did not show any change in abundance in response to clear-cutting were bank voles and Eurasian pygmy shrews. The abundance of the rest of the analyzed species increased in clear-cuts to various extends in at least one of the analyzed regions. This result is in line with studies on the effects of clear-cutting on small mammals in North America (Zwolak 2009). Similar as in Europe, many North American small mammal species reach higher densities in harvested than in undisturbed forest. However, while our results suggest that the abundance of bank voles does not change after logging, in North America the red-backed vole (*Myodes gapperi*) strongly decreases in abundance on clear-cuts (Zwolak 2009). This difference is interesting because both *Myodes* species are considered forest specialists (Hansson 1996; Pearce and Venier 2005). The decrease in red-backed voles on clear-cuts could be the result of the strong association of this species with downed wood. As has been recently demonstrated, red-backed voles can be maintained on clear-cuts by providing sufficient amount of coarse woody debris (Sullivan et al. 2011, 2012). It has also been proposed that bank voles are more generalist in food habits than red-backed voles (Gliwicz and Glowacka 2000), and thus, they may be better adapted for colonizing disturbed areas like clear-cuts.

The positive response of most studied mammal species to clear-cuts could be attributed to an increase in forb and grass cover in the harvested areas. Lack of competition with trees in conjunction with better light conditions allows grass and herbs to quickly colonize disturbed areas (Peterken 2008). Abundance and species richness of vascular plants increases on clear-cuts compared to unmanaged stands (Keenan and Kimmins 1993; Paillet et al. 2010), providing small mammals with improved antipredatory cover and enhanced food resources. However, we also note that in the majority of analyzed studies, the reference sites consisted of managed, even-aged coniferous stands, which typically have poorly developed understory and low levels of coarse woody debris. In such situations, clear-cutting might greatly increase the structural complexity of habitats.

The increases in abundance after clear-cutting were most pronounced in species that prefer habitats dominated by graminoids. For example, the striped field mouse is positively influenced by the percentage of grassland in the landscape (Fischer et al. 2011) and reaches highest densities in afforestations and rural habitats (Szacki and Liro 1991). The same is true for the Eurasian harvest mouse, a species that prefers habitats with abundant vegetation cover (Churchfield et al. 1997a; Harris 2008). Strong positive response of the common and the field vole to clear-cutting is also not surprising and most likely results from the strong association of these two species with meadow habitats (Miklos and Ziak 2002; Borowski 2003). Similarly, the slight increase in the abundance of the wood mouse on clear-cuts can be attributed to the association of this species with grassy microhabitats: the wood mouse prefers meadows and windbreaks over closed-canopy habitats of forests (Hoffmeyer 1973; Churchfield et al. 1997a; Heroldová et al. 2007). It is associated with dense, tall vegetation cover and fallen logs (Marsh and Harris 2000). These habitat structures provide shelter and are available in early successional habitats like overgrown clear-cuts. Since distribution of the wood mouse on the stand scale is also correlated with the number of seed-bearing herb and grass species (Angelstam et al. 1987), stronger positive response of the wood mouse in temperate than in boreal forests can be attributed to higher productivity of temperate than boreal habitats. Growing season in the temperate zone is almost two times longer than in the boreal zone, with both precipitation and temperature considerably higher in the temperate zone (Malhi et al. 2002). Therefore, the development of suitable, productive habitat is much faster, and most probably occurs more often after clear-cuts in temperate than in boreal zone.

The same explanation can be applied to the different response of the yellow-necked mouse to clear-cutting in boreal and temperate zones. This species is more strongly associated with forest habitats than the wood mouse (Montgomery 2008), although both grassland and forest habitats are considered suitable for this species (Hoffmeyer 1973). Therefore, the decline in abundance after clear-cutting in boreal zone can be attributed to more permanent loss of habitat in boreal forests: while in the temperate zone, forest can be replaced with equally suitable grassland, in the boreal zone this process is slower and less likely to occur. Moreover, in boreal forests, tree seeds that are lost after clear-cutting may represent more important food source for the yellow-necked mouse then in relatively food-rich temperate forests. However, we did not find a relationship between RAI and age of clear-cut in boreal or temperate forest (unpublished analyses). Such association would be expected if habitat productivity played a role in described differences in species responses. One can expect that potential differences in abundance between clear-cuts and unharvested forest would diminish with time since disturbance and in more productive temperate habitats this process should occur faster. Nevertheless, the absence of relationship with time most likely reflects lack of power caused by small sample size or is related to the relatively narrow time window of analyzed responses (up to 20 years after disturbance). It is reasonable to assume that in the long term, the effects of disturbance on species abundance will taper off and finally disappear as was the case in North America (Zwolak 2009).

Both analyzed species of shrews are considered habitat generalists (Churchfield et al. 1997a), but the Eurasian pygmy shrew has wider niche breadth (Rychlik 2000) and is less dependent on habitat productivity than the common shrew (Hanski and Kaikusalo 1989; Churchfield et al. 1997b). Therefore, lack of response of the Eurasian pygmy shrew to habitat change in both zones may be attributed to opportunistic traits of this species. On the other hand, increase in the common shrew after logging in the temperate region could be associated with the increase in plant cover on clear-cuts, which provides shelter from predators. Birds of prey are the most important predators of shrews (Korpimäki and Norrdahl 1989), and the common shrew is preferred as prey over the smaller Eurasian pygmy shrew (Korpimäki and Norrdahl 1989). Hence, the common shrew could benefit more from the increased availability of cover on clear-cuts than the Eurasian pygmy shrew.

Another reason for the observed differences in shrews' response to clear-cutting could lie in their differing moisture requirements. The Eurasian pygmy shrew is more strongly associated with wet habitats than the common shrew (Rychlik 2000). Therefore, clear-cuts, which are generally drier than closed forest (Hansson 1992b), could be less suitable for *S. minutus* than for *S. araneus*.

Influence of forest management practices on small mammal species: a review

The meta-analysis was necessarily limited to the most widespread and common species of small mammals. Such species could be expected to have wide ecological tolerance and to be less affected by clear-cutting. Are the reactions of commonly studied small mammals representative of all small mammal species? The qualitative review provided below suggests that the effects of forest harvest on more specialized small mammal species (summarized in Table 2) are more varied than the generally positive effects on the most common small mammals.

Gray-sided vole

A long-term decline in numbers of the gray-sided vole observed in Fennoscandia is a subject of a wide debate (Hörnfeldt 2004; Christensen et al. 2008; Ims et al. 2008; Ecke et al. 2010). It is possible that the decline is caused by the global warming and thus warmer winters, affecting not only the gray-sided vole, but also *Microtus* species (Hörnfeldt 2004; Bierman et al. 2006; Ims et al. 2008). Increased temperatures in winter negatively affect the

Table 2 Main threats resulting from forest harvest posed to gray-sided vole (*M. rufucanus*), Siberian flying squirrel (*P. volans*), red squirrel (*S. vulgaris*) and hazel dormouse (*M. avellanarius*)

Species	Threat	Threat level
Gray-sided vole	Fragmentation (Christensen and Hörnfeldt 2006; Christensen et al. 2008; Ecke et al. 2010).	Moderate: forest harvest contributes to population decline caused primarily by climate change.
Siberian flying squirrel	Fragmentation (Mönkkönen et al. 1997), habitat loss (Lampila et al. 2009; Santangeli et al. 2013b), change in tree species composition (Reunanen et al. 2001).	Severe: forest harvest is considered the main cause of population decline.
Red squirrel	Habitat loss (Mortelliti et al. 2011).	Minor: remain viable in fragmented landscapes but rely on mature trees for food.
Hazel dormouse	Fragmentation (Bright and Morris 2008; Mortelliti et al. 2011).	Moderate: prone to isolation in forest fragments, but extensively use mid-successional clear-cuts.

depth of snow cover and the occurrence of subnivean space, both of which provide voles with protection against predators and adverse climatic conditions (Kausrud et al. 2008). In addition, more frequent melting–freezing events and winter rains encapsulate the vegetation in ice and decrease the availability of winter food for voles (Hansen et al. 2013). Forest harvest acts as a contributing factor, acting through habitat destruction and fragmentation. Occurrence of the gray-sided vole at the landscape level depends on the availability of high-quality, large patches of coniferous forests with low degree of fragmentation (Ecke et al. 2010). Clear-cuts seem to be avoided by *C. rufucanus* (Christensen and Hörnfeldt 2006), which suggests that increased amount of clear-cuts can make the dispersal of this species difficult and hence confine it to large forest patches (Christensen et al. 2008). As the long-term decline takes place also in areas where forestry is absent, the changes in landscape due to forest management could not be treated as the main cause of the decline (Ecke et al. 2010). However, while populations of the gray-sided vole in remote mountain areas have a chance to rebuild under favorable weather conditions, they will most likely not have this opportunity in fragmented lowland landscapes (Ecke et al. 2010).

Siberian flying squirrel

Siberian flying squirrel is an arboreal rodent that underwent severe decline in numbers in Europe and was even recognized regionally extinct in Finland (Hokkanen et al. 1982). Since then, the flying squirrel became a focal species in sustainable forest management in Finland and its persistence in managed forests is considered vital. Recently, it has been suggested that the flying squirrel could serve as an umbrella species for organisms depending on dead wood and old-growth forests (Hurme et al. 2008). Large-scale habitat changes due to modern forestry are suggested as the main cause of its decline (Hokkanen et al. 1982; Selonen et al. 2001; Reunanen et al. 2002b). The occurrence of this species is positively related to the cover of mature spruce forest with deciduous mixture, mainly aspen *Populus tremula*, birch *Betula* spp. and alder *Alnus incana* (Hanski 1998; Selonen et al. 2001; Reunanen et al. 2002b; Hurme et al. 2005; Hurme et al. 2007; Santangeli et al. 2013a). Old trees provide cavities for shelter or roosting, and deciduous trees are the main source of food as the flying squirrel forage on their leaves in summer and on catkins of alder and birch in winter (Hanski et al. 2000). Unfortunately, spruce trees were often replaced with pines in commercial forests, and the deciduous component of forest has been reduced or eliminated due to its low economic value (Reunanen et al. 2002a). Moreover, deciduous forest patches in boreal zone disappear during natural forest succession if not maintained by recurrent disturbances (Pickett 1985). Therefore, maintaining the deciduous mixture, particularly in spruce-dominated forest, should be of the primary importance in conservation policy of that species (Reunanen et al. 2001). In addition, the amount of mature spruce-dominated forest area in the landscape should not drop below 12–16 % (Reunanen et al. 2004). The connectivity of suitable forest patches was also recognized as an important landscape feature (Reunanen et al. 2001; Reunanen et al. 2002c). Habitat fragmentation, the proportion of pine trees within the forest patch and open habitats such as clear-cuts negatively influence the habitat suitability for flying squirrels (Reunanen et al. 2002b; Mönkkönen et al. 2006; Santangeli et al. 2013a). On the stand scale, clear-cutting decreases survival and population growth of flying squirrels (Lampila et al. 2009) and causes strong reduction in site occupancy (Santangeli et al. 2013b). Thus, forest management practices that are changing landscape prosperities, species composition of forest stands and clear-cutting in particular are most probably the main threat for Siberian flying squirrels populations.

Eurasian red squirrel

The Eurasian red squirrel is strongly declining in Great Britain, and this decline has been linked to the displacement by the introduced gray squirrel (*Sciurus carolinensis*). Because there are some established populations of gray squirrels in Italy that in nearest future may spread over continental Europe the problem is not limited to British Isles (Bertolino et al. 2008). Moderately intense forest harvest is not considered to be a threat because populations of red squirrels often remain viable in fragmented landscapes (Andrén and Delin 1994; Delin and Andrén 1999; Verbeylen et al. 2003). Red squirrels are able to travel relatively long distances on open ground, thus are not as strongly affected by fragmentation as are other arboreal species (Wauters et al. 2010; Mortelliti et al. 2011). However, the amount of forest cover in the landscape is an important factor related to squirrels' presence (Mortelliti et al. 2011) and red squirrels avoid clear-cuts (Hansson 1994). Indirect evidence (changes in the diet of avian predators) suggests that red squirrels are declining in numbers in Fennoscandia where gray squirrels do not occur (Selonen et al. 2010). This decline might be caused by forest harvest and resulting habitat loss (Selonen et al. 2010). Red squirrels strongly rely on tree cones for food; therefore, young stands created by large-scale clear-cutting cannot support populations of squirrels until trees mature and produce seeds (Lurz et al. 2003).

On the other hand, forest management can be used to ensure viability of the red squirrel populations. Gray squirrels gain competitive advantage over red squirrels in conifer forests with oaks mixture (Lurz et al. 1995), but have lower survival in pure conifer stands (Kenward and Holm 1993; Kenward et al. 1998). Therefore, not planting oak species in large pine patches has been proposed as a part of conservation policy for red squirrels (Lurz et al. 2003).

Hazel dormouse

Hazel dormouse is red-listed in many European countries (Juškaitis 2007). As a strictly arboreal rodent, it is particularly vulnerable to habitat fragmentation and loss of patch connectivity (Bright and Morris 2008; Mortelliti et al. 2011). Although this species is able to move through open field when forced to do so (Bright 1998; Mortelliti et al. 2012), enhancing connectivity of patches in landscape by hedgerow planting greatly increases the probability of occurrence of hazel dormouse (Mortelliti et al. 2011). Moreover, this species lives in unusually low densities compared to other rodents (Bright and Morris 2008). Therefore, small isolated patches maintain low numbers of individuals that can easily go extinct due to demographic stochasticity (Bright and Morris 2008). On the other hand, clear-cutting per se is not a serious threat for the hazel dormouse as the decrease in abundance after this management practice is ephemeral and clear-cuts are usually recolonized within 5 years after disturbance (Juškaitis 2008; Troutet et al. 2012). Mid-successional sites with structurally heterogeneous young shrubs are known as the most suitable habitats for this species (Berg 1996). Such habitats are often found in young clear-cuts (Berg 1996). Thus, it appears that small-scale clear-cutting is does not pose a danger to this species. However, large-scale harvesting (thinning or clear-cuts) resulting in fragmentation and isolation of forest patches or destruction of winter hibernation nests might be detrimental for the hazel dormouse (Trout et al. 2012).

Management implications

Because species differ in their responses to forest harvest, there is no one-size-fits-all management solution. However, harvesting methods that produce less intense disturbances, such as removing single trees or small groups of trees, might be preferable over stand-replacing harvest when the goal is to minimize negative effects on wildlife. In addition, because of the importance of unharvested refugia, sometimes it might be better to conduct small-scale clear-cutting than large-scale lower-intensity disturbance such as thinning (Trout et al. 2012). Forest harvest that results in changed species composition of stands, particularly when the endpoint are large-scale monocultures, is more likely to be detrimental to small mammals than harvest that does not result in tree species conversion (Pedersen et al. 2010). Leaving more coarse woody debris in harvested stand is highly recommended and has been recognized as a crucial practice for maintaining populations of small mammals and other wildlife (Siitonen 2001). Finally, longer harvest rotations would result in higher proportion of old forest, which ensures food resources for animals dependent on cones and fruits produced by mature trees.

Many of these recommendations are common sense solutions, and their effectiveness in specific situations should be validated with research (Simberloff 1999). In particular, studies on responses of European small mammals to methods of forest harvest other than clear-cutting are rare. Furthermore, studies on species that are rare or ecologically specialized are particularly needed because such species are potentially threatened by forest harvest.

Conclusions

The results of our meta-analysis and the literature review suggest that small mammal vulnerability to forest management is species-specific. Commonly studied species included in the meta-analysis tended to increase in abundance in clear-cuts, and thus, this form of forest harvest is unlikely to pose a threat to widespread small mammal species. Open areas created by clear-cutting create suitable habitats for these species, and it is unlikely that resulting forest fragmentation will harm their populations. All of them are ground-dwelling species that take advantage of increased vegetation cover on clear-cuts. On the other hand, arboreal rodents like the Siberian flying squirrel, the Eurasian red squirrel and the hazel dormouse are more affected by forest discontinuity and therefore might be threatened by forest harvest, although to a different extent. This is not surprising since these species rely on the three-dimensional space created by tree and shrub branches that is destroyed by felling. Moreover, even-aged stands often created by forest management decrease the structural heterogeneity of the arboreal habitat. However, responsible forest management policy that takes into account species-specific habitat requirements could considerably reduce the negative impact of forest harvest on most small mammal species.

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