



Semi-naturally managed forests support diverse land snail assemblages in Estonia



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ABSTRACT

Snails are an integral part of most forest ecosystems where their sensitivity to timber harvesting depends on insufficiently understood interactions of multiple factors. Some snail species have been reported to indicate natural forest conditions, and deadwood-rich old growth stands are known to be particularly species rich. Other studies demonstrate rich snail fauna in young forests and hypothesize that clear-cutting is less detrimental on wet soils. We investigated forest management impacts on snail assemblages in hemiboreal Estonian forests. We sampled 100 stands using a balanced design of five site types and four management stages (old growth; mature forest; retention cuts and clear-cuts 4–19 years post harvest). The material comprised ca. 12,500 live individuals and included 52 species of terrestrial shelled snails. Snail assemblages differed mostly among site types, and less among management stages. Dry boreal site type with a thick moss carpet, pine stands and little woody debris had the most distinct, impoverished assemblages. Harvesting-caused assemblage shifts were restricted to nutrient-rich and wet sites, but the assemblages recovered during maturing of the regrowth. We did not detect 'life-boating' function of solitary retention trees on cutover sites. One species, *Vertigo alpestris*, preferred old growth and abundant coarse woody debris appeared to be a reason for that. We conclude that seminatural forest management approach can sustain relatively intact snail assemblages in humid temperate climate and on calcium poor to moderately rich sites. The clearest long-lasting impact is the decline of some wetland species after draining.

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1. Introduction

In order to sustain timber production areas as functional, biologically rich ecosystems, forest managers have to explicitly understand biodiversity impacts of different silvicultural approaches. Land snails belong to the diverse fauna of soil invertebrates, which play an integral role in ecosystem functioning (Fitter et al., 2005). Due to their diverse and efficient digestive enzymes, snails can disintegrate significant parts of forest litter and thus contribute to soil formation and nutrient cycling (Mason, 1974; Gårdenfors, 1987; Coulis et al., 2009). Snails also constitute an important prey for vertebrates and invertebrates, especially as a calcium source (Graveland, 1996; Burton, 1976; Digweed, 1993).

In northern Europe, land snails comprise more than 100 species with shells and, additionally, shell-less slugs. Because most of these species have broadly similar habitat preferences, their assemblages are typically nested (Bengtsson et al., 1994; Hylander et al., 2005). In such case, species richness performs as

a relatively reliable indicator of snail habitat quality (Zellweger et al., 2015). In forests, snail habitat quality is determined mostly by soil and litter conditions – acidity, calcium content, and humidity.

Soil and litter conditions change after disturbances and induce shifts in snail assemblages. Severe wildfire and wind disturbances create harsh open habitat with high evaporation rates and distinct early-successional assemblages (Bloch and Willig, 2006; Santos et al., 2009). The immediate impact of fire can be devastating (Hylander, 2011): it kills the animals and consumes their food resource – dead organic material with its microorganisms (note that wind can increase such food base). However, the snails that survive in sheltered places below boulders and in cryptic refugia (Kiss and Magnin, 2006; Gaines et al., 2011) can initiate population recoveries (Karlin, 1961). Those recoveries are supported by regrowth of pioneer woody plants that produce high-quality litter (Karlin, 1961), the increased pH of burned forest floor, and Ca availability (Simard et al., 2001; Hylander, 2011).

Clear-cutting – a prevailing timber harvesting technique – is an abrupt anthropogenic disturbance that raises the issues of habitat quality, continuity, and connectivity at various scales (Keenan and

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Kimmins, 1993). Its documented impacts on land snails include assemblage shifts, reduced abundance and species richness (Hylander et al., 2004; Foster and Ziegler, 2013). In clear-cuts (as well as in other human-disturbed areas), invasive (alien) species tend to proliferate, and specialist and endemic species to decrease (Schilthuizen et al., 2005; Kappes, 2006). Similarly to natural disturbances, these immediate effects have been attributed to the microclimate – sun exposure and soil drying – and are reversible if the area contains wet patches and downed coarse woody debris (CWD; Shikov, 1984; Moore et al., 2002; Hylander et al., 2004; Müller et al., 2005). Some effects can be mitigated also by live-tree retention, especially in patches (Hylander et al., 2004), and with favorable litter type.

For natural-disturbance-based silviculture, the fundamental question is how harvesting impacts vary depending on forest site type, i.e. on a combination of edaphic and climatic conditions that determine disturbance regimes and successional trajectories. However, the relevant studies remain scarce (Rosenvald and Lõhmus, 2007). In the case of boreal snails, initial clear-cutting impacts may be stronger in upland sites, which are generally drier (Hylander et al., 2004). In contrast, secondary paludification can favor wetland snails in moist cutovers (Remm et al., 2013). It has been also hypothesized that the stress-tolerant species that inhabit acidic coniferous forests may better tolerate harvest (Douglas et al., 2013). It is not known how these patterns are modified during later post-harvest succession.

Long continuity of forest may significantly contribute to snail diversity (Chiba et al., 2009; Moning and Müller, 2009; Juřičková et al., 2013; but see Götmark et al., 2008); yet, it is not clear whether that is caused by specific microhabitats or slow (re)colonization by snails. Snails, especially minute snails and family *Clausiliidae*, can appear as indicators of old growth or of generally high conservation-value forests (Prieditis, 2002; Pilāte, 2003a; Douglas et al., 2013). However, a microhabitat-mediated effect implies that old forests may not be always superior, especially when stand composition changes during the succession. In the temperate zone, most snail species can be more abundant in young secondary forests, because of the favorable litter of early successional trees (Shikov, 1984; Hawkins et al., 1997; Ström et al., 2009). Compared to clear-cutting, partial harvests may promote spruce undergrowth that depletes snail fauna due to the unfavorable litter and effectively intercepted precipitation (Shikov, 1984). Fallen tree trunks provide moist refuges both on clear-cuts (Klüber et al., 2009; Goldin and Hutchinson, 2014) as well as under closed canopies (Ingram, 1942; Caldwell, 1993; Jokić et al., 2004; Utschick and Summerer, 2004). Their benefits for snails are pronounced on acidic soils (Müller et al., 2005) and are caused by soil qualities and litter accumulation near the trunks (Kappes et al., 2007, 2009). Presumably, certain minimum amounts of dead wood are necessary for high snail density and diversity, especially for some species, like hard-substrate specialists of the family *Clausiliidae* (Kappes et al., 2009).

Control over tree species composition is a common aim of silvicultural systems, and the examples above illustrate how it can affect snails through litter quality. Well-documented is the impoverishment of snail fauna after establishing conifers instead of broad-leaved trees (Wäreborn, 1969; Kralka, 1986; Tattersfield et al., 2001; Suominen et al., 2003; Götmark et al., 2008), especially those tree species that contain calcium in an easily assimilating form (Wäreborn, 1969). Fungivorous snails, notably slugs, however, tolerate or even prefer calcium poor and acidic forests with massive fruiting of macrofungi (Beyer and Saari, 1977; Kralka, 1986; Kappes, 2006).

The previous research thus suggests that forest management affects snails (and probably other soil invertebrates) in context-dependent ways. This forms the basis of the broad aims

of the current study: to investigate which snail species, and why, become threatened by timber harvesting, if that is followed by natural regeneration (i.e., in semi-natural forest management). We compare harvesting interventions across a gradient of site types in a generally favorable landscape matrix in Estonia (see Lõhmus and Lõhmus, 2011; Lõhmus and Kull, 2011; Rosenvald et al., 2011). We distinguish the impacts of abrupt intervention (cutovers vs. forests) and long-term development (old growth vs. commercial forests) both at assemblage and species scales, and the role of stand structure. To explore the structural enrichment function of retention trees (Gustafsson et al., 2012), we compare snail assemblages in clear-cuts and retention cuts. We expect that dead-wood amounts and canopy composition mediate forest management impacts, which therefore depend on site type. Combined with our previous analysis of drainage sensitivity of snails (Remm et al., 2013; which includes a subset of the samples used here), this study provides a perspective on integrating snail conservation with sustainable forest management.

2. Methods

2.1. Study sites

The study was carried out in 100 plots (50 forests and 50 cut-over sites; 2 ha each) in the Estonian mainland. Estonia is situated in the European hemiboreal vegetation zone (Ahti et al., 1968). The mean air temperature is 17 °C in July and –6 °C in January and the average precipitation is 600–700 mm/yr. The topography is mostly of glacial origin: flat and undulating moraine plains as well as glaciolacustrine plains with abundant clayey deposits and extensive postglacial paludification. All our study plots were situated <100 m above sea level. The forest management in Estonia combines even-aged silviculture with largely natural regeneration and relatively small areas of cutovers (<5 ha). Such “semi-natural management” approach is maintaining many features of forest structural diversity at near-natural levels (Lõhmus and Kraut, 2010; Lõhmus et al., 2013, in press; Kraut et al., 2016).

Our balanced study setup of five site-types and four management stages has been described in detail by Lõhmus and Kraut (2010) and Lõhmus and Lõhmus (2011). The site-types (site-type groups sensu Lõhmus, 1984) were: (1) dry boreal forests (mostly *Vaccinium*-type) on higher fluvioglacial landforms and till mounds with Podzols (pH_{KCl} 3.5–5.0) where the top layer is periodically dry and ground water deeper than 2 m; (2) meso-eutrophic forests (mostly *Oxalis*-type) on till mounds or rolling plains with Podzols or Stagnic Luvisols (pH_{KCl} 3.2–4.2) where ground water is usually deeper than 2 m; (3) eutrophic boreo-nemoral forests (mostly *Aegopodium*-type) predominantly on undulating sandy till plains with favorably moist (in springtime anaerobic) Gleyic Gambisols or Luvisols (pH_{KCl} 4.7–6.5) and almost no organic horizon; (4) mobile-water swamp forests on thin seasonally flooded Eutric Histosols and Fluvisols, with a peat layer ≥ 30 cm (pH_{KCl} 5.0–6.5) in lowlands and valleys along rivers or around bogs; (5) artificially drained swamp forests (*Oxalis*-type; originating from type (4), see Remm et al., 2013) on well decomposed peat soils (pH_{KCl} 4.0–6.5). The dry boreal stands were dominated by Scots pine (*Pinus sylvestris*); the other sites hosted conifer/deciduous mixtures with Norway spruce (*Picea abies*) or (in some *Oxalis*-type stands) with Scots pine.

The study plots were organized as four-plot blocks, each block including all management stages of a particular site type as close as possible on the landscape (<18 km with two exceptions). There were five replicates of each block, i.e., 25 blocks with 100 plots altogether (Fig. 1). The management stages were: (i) old growth (most trees 100–180 years; coniferous >125 years old; stand ages

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