Small rodent population cycles and plants – after 70 years, where do we go?

Eeva M. Soininen[1,*] and Magne Neby[2]

[1]*Department of Arctic and Marine Biology, UiT-The Arctic University of Norway, Postboks 6050 Langnes, Tromsø 9037, Norway*
[2]*Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Høyvangvegen 40, Ridabu 2322, Norway*

ABSTRACT

Small rodent population cycles characterise northern ecosystems, and the cause of these cycles has been a long-lasting central topic in ecology, with trophic interactions currently considered the most plausible cause. While some researchers have rejected plant–herbivore interactions as a cause of rodent cycles, others have continued to research their potential roles. Here, we present an overview of whether plants can cause rodent population cycles, dividing this idea into four different hypotheses with different pathways of plant impacts and related assumptions. Our systematic review of the existing literature identified 238 studies from 150 publications. This evidence base covered studies from the temperate biome to the tundra, but the studies were scattered across study systems and only a few specific topics were addressed in a replicated manner. Quantitative effects of rodents on vegetation was the best studied topic, and our evidence base suggests such that such effects may be most pronounced in winter. However, the regrowth of vegetation appears to take place too rapidly to maintain low rodent population densities over several years. The lack of studies prevented assessment of time lags in the qualitative responses of vegetation to rodent herbivory. We conclude that the literature is currently insufficient to discard with confidence any of the four potential hypotheses for plant–rodent cycles discussed herein. While new methods allow analyses of plant quality across more herbivore-relevant spatial scales than previously possible, we argue that the best way forward to rejecting any of the rodent–plant hypotheses is testing specific predictions of dietary variation. Indeed, all identified hypotheses make explicit assumptions on how rodent diet taxonomic composition and quality will change across the cycle. Passing this bottleneck could help pinpoint where, when, and how plant–herbivore interactions have – or do not have – plausible effects on rodent population dynamics.

Key words: plant–herbivore interaction, arvicoline, population dynamics, vole, lemming, herbivore, bottom-up, top-down, rodent, population cycle.

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* Author for correspondence (Tel.: +47 77 64 63 92; E-mail: eeva.soininen@uit.no).

I. INTRODUCTION

Small rodents form a central link between vegetation and predators in a range of food webs (Jaksic, 2001; Krebs, 2011), and their cyclic population dynamics characterise entire food webs in the northern hemisphere (Boonstra et al., 2016; Ims & Fuglei, 2005). Small-rodent population cycles also have various implications for humans, such as damage to crops and forestry, spreading diseases, and modifying the population dynamics of game species (Huitu et al., 2009; Jacob et al., 2014; Kallio et al., 2009). Ecologists have long tried to understand why small rodent populations have cycles (Elton, 1924; Krebs, 2013). While this interest has resulted in substantial research and increased our understanding of population dynamics considerably (Berryman, 2002; Turchin, 2003; Barraquand et al., 2017), we still have no definite answer.

To date, most researchers agree that trophic interactions are the likely underlying mechanism of northern small rodent population cycles (Berryman, 2002; Turchin, 2003; Krebs, 2013; Kelt et al., 2019; Oli, 2019). Amongst trophic interactions, the role of predator–prey interactions has long been acknowledged (Gilg, Hanski & Sittler, 2003; Hanski et al., 2001). However, not all small-rodent cycles are easily explained by predation (Lambin, Bretagnolle & Yoccoz, 2006), and rodent–vegetation interactions have repeatedly been proposed either to cause or to modify small-rodent population cycles (Huitu et al., 2008; Kent, Plesner Jensen & Doncaster, 2005; Massey et al., 2008; Rammul et al., 2007). Various hypotheses on how rodent–vegetation interactions may, alone or together with other factors, cause cyclic population dynamics have been put forward since the 1960s (Freeland, 1974; Haukioja et al., 1983; Massey et al., 2008; Schultz, 1964; Plesner Jensen & Doncaster, 1999). These hypotheses are not all easy to disentangle, some are similar, some are slight modifications of others, and some are not fully specified and hence not testable. The current literature is thus unobliging in a search for scientific consensus.

In his book *Population Fluctuations in Rodents*, Krebs (2013, p. 127) suggested that 'single-factor models of food shortage causing population fluctuations in rodents have been rejected'. However, in a recent review of the 10 most essential, but remaining, questions about population fluctuations, Andreassen et al. (2021) highlighted food resources as potentially shaping population dynamics and in need of further investigation. Several authors have reviewed rodent–plant interactions using time-series data (Oksanen et al., 2008) or modelling approaches (Klemola, Pettersen & Stenseth, 2003; Turchin, 2003), but no recent review has systematically synthesised the empirical evidence for plant–rodent interactions. Identifying the key points where information gaps may exist could contribute to assessing whether we indeed should reject plants as drivers of small-rodent population cyclicity or whether key studies remain to be done.

Climate is changing rapidly in northern ecosystems, leading to documented changes in primary production (Gauthier et al., 2013; Callaghan, Cazzolla Gatti & Phoenix, 2021; Xu et al., 2013). Other changes in vegetation characteristics, such as vegetation composition and plant nutritional quality, are likely to occur as well. Climate-driven changes in vegetation have unavoidable consequences for herbivorous animals, as documented for ungulates by Fauchald et al. (2017). Concurrent with climate change, changes in rodent population dynamics (Cornulier et al., 2013; Ims, Henden & Killengreen, 2008; Schmidt et al., 2012) and distribution (Fufachev et al., 2019) have also been observed during recent decades. Indeed, some authors have proposed that changes in primary productivity are dampening population cycles (Schmidt et al., 2018). Thus, climate-driven changes in vegetation could provide a new understanding of the effects of plants on rodents, if the necessary data to quantify the potentially coupled changes are collected. Yet, to advance this task, we need to know which data to collect.

Several new methodological approaches have emerged during the last decade, allowing us to acquire previously unavailable information. DNA metabarcoding enables assessment of the taxonomic composition of herbivores' diets to a previously unseen level (Soininen et al., 2015a, 2009). It is now possible to detect food items that represent a minor proportion of the diet but have important nutritional functions. Camera trapping methods also have vastly expanded the extent and resolution of monitoring of small rodent populations, enabling year-round abundance estimates (Soininen et al., 2015b; Mölle et al., 2021). Near-infrared

spectroscopy enables analyses of plant nutritional quality across entire landscapes, sampling plant parts that match herbivore bite size (Smis *et al.*, 2014; Murguzur *et al.*, 2019; Petit Bon *et al.*, 2020*a*). The changes that northern ecosystems are undergoing and the possibilities that new methodological developments represent, thus make it timely to update our understanding of the effects of plants on rodent population dynamics, whether reciprocal or not.

The 'plant hypothesis' has gradually evolved into a collection of different hypotheses on how vegetation may create rodent population cycles. These hypotheses include both bottom-up control, i.e. cycles driven by plant properties, and top-down control *via* consumer–prey interactions, i.e. cycles driven by rodent impacts on plants and their consequent feedback. Below, we first describe rodent–vegetation interactions that have been suggested to cause rodent population cycles, as well as assumptions related to the various hypotheses. We focus on predominantly herbivorous rodents with population cycles, i.e. the arvicoline voles and lemmings of the Northern Hemisphere. We then systematically review the empirical literature related to these hypotheses. Finally, we identify research required to reject the different hypotheses and discuss potential pathways to advance our understanding of rodent–plant interactions in a changing world.

II. OVERVIEW OF THE HYPOTHESES

(1) Inherent plant cycles

Originally proposed by Kalela (1962), the inherent plant cycles hypothesis suggests that cyclic peaks in plant production provide cycles of availability of nutritious food for rodents. Rodent diet quality would then track these plant cycles, resulting in cycles of increased reproduction of rodents and thus cyclic peaks in rodent population density. Thus, rodent population densities should track plant production peaks. This bottom-up hypothesis focused in its original form on plant production in terms of reproductive organs such as flowers or berries (i.e. nutritious plant parts), but was subsequently extended to other measures of plant nutrient levels (Andersson & Jonasson, 1986). Assumptions behind the hypothesis are described in more detail in hypothesis A in Fig. 1. We are unaware of theoretical/mathematical modelling studies assessing this hypothesis.

(2) Interaction cycles

A top-down interaction between rodents and plants may also cause rodent populations to cycle. This hypothesis argues that high numbers of rodents can reduce the quality or quantity of their food resources, leading to decreasing access to good-quality food. This change in food quality or quantity should then affect rodent health negatively, and consequently either reduce reproduction rates or increase mortality, leading to a reduction in population growth rate. Furthermore,

the vegetation will require a period to recover after a rodent population peak. The resulting lower availability of good-quality food over time will thus maintain low rodent population densities over the low phase of the cycle, and a time lag between rodent abundance and the availability of good-quality food is essential for the interaction cycles to arise. In the seasonal systems where rodent cycles occur, plants cease growth during the winter season and are in many cases covered by snow. The availability of good-quality food for rodents and the energy required to acquire it, thus also have strong seasonal dynamics – as do the dynamics of rodent populations which tend to increase during summer and decrease during winter. Time lags of vegetation recovery from herbivory are superimposed on this seasonal cycle, and multi-annual time lags of recovery are required to produce multi-annual rodent population cycles. We identified three main groups of interaction cycles hypotheses based on the type of effects that rodents have on the quantity/quality of their food resources or on the dietary changes rodents exhibit during the population cycle (Fig. 1).

The hypothesis that interaction cycles are caused by a decrease in food quantity (Lack, 1954) argues that rodent feeding affects plant biomass, leading to decreased food availability at the individual level, as an increasing number of animals has a decreasing amount of food to share. At high population densities, the available food is insufficient to fulfil the nutritional needs of all rodent individuals. This leads to health consequences, such as lower reproduction, starvation or increased vulnerability to diseases and predators, and consequently, the population density decreases. Plant quantity will then remain low for a period, constraining rodent population growth rate (hypothesis B in Fig. 1). Note that rodents could avoid negative effects of reduced food quantity through dietary shifts. In addition to the assumption that consumption by rodents reduces food biomass to inadequate levels, mathematical modelling has demonstrated that another prerequisite of this interaction to create population cycles is relatively slow regrowth of depleted or grazed plants (Turchin & Batzli, 2001).

An increasing impact of rodents on their food plants may, instead of or in addition to changes in plant biomass, lead to reduced nutritional quality of plants. In this case, high feeding pressure leads to nutritionally depleted plants (Batzli *et al.*, 1980; Schultz, 1964) or induces plant defences (Haukioja & Hakala, 1975; Massey *et al.*, 2008). Thus, at high population densities, rodent individuals ingest nutritionally insufficient food, leading to a decrease in population growth rate. Plant quality will then remain poor for a period, constraining rodent population growth rate (hypothesis C in Fig. 1). Some versions of this hypothesis include multi-step pathways *via* soil and plant nutrients [e.g. the nutrient recovery hypothesis (Batzli *et al.*, 1980; Schultz, 1964)], while others are based only on plant–rodent interactions (Massey *et al.*, 2008; Seldal, Andersen & Hogstedt, 1994). Mathematical models have demonstrated that induced plant defences can, in principle, create cyclic population dynamics in herbivores (Reynolds *et al.*, 2013; Underwood, 1999) and that seasonality appears critical for maintaining cyclicity
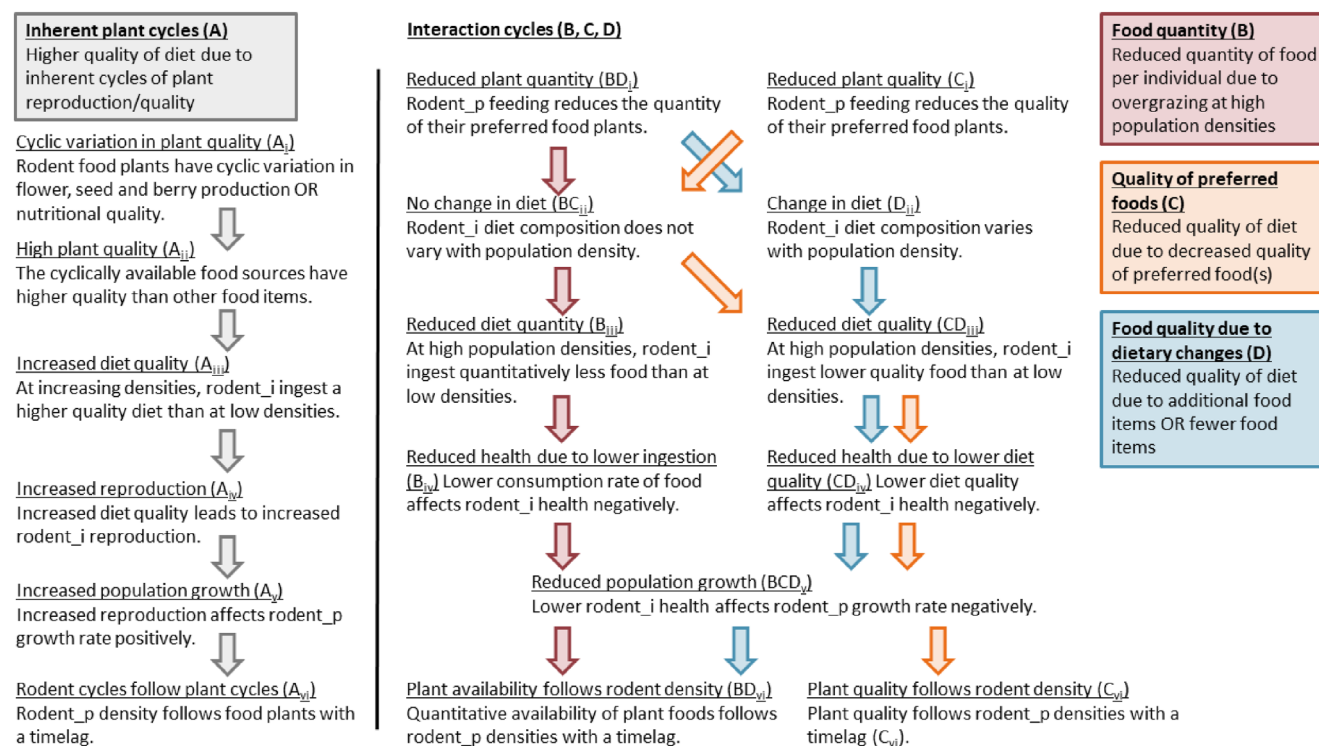
Fig. 1. Assumptions related to the inherent plant cycle hypothesis (left) and different variants of the interaction cycles hypotheses (right). Letters A–D refer to hypotheses, and subscript roman numbers i–vi refer to the related assumptions. Note that assumptions BC_{ii} and D_{ii} assess the presence/absence of the same phenomena, and they were therefore combined when coding information from the included studies. Rodent_i refers to rodent individuals and rodent_p to rodent populations. The pathways are not mutually exclusive; for instance overgrazing may result both quantitative (B) and qualitative (D) reduction of food. We do not assume that the magnitude of the effects of each assumption are equal, neither do we estimate effect thresholds in this review, but instead discuss the assumptions qualitatively.

(Reynolds *et al.*, 2013). Yet rodents may escape the negative effects of induced plant defences by feeding on alternative plants (species or groups) with different nutritional quality. None of the current modelling studies evaluates the possible impacts of dietary shifts on cyclic dynamics (Underwood, 1999; Lundberg, Jaremo & Nilsson, 1994; Reynolds *et al.*, 2013).

A third variant of the interaction cycles hypothesis states that as the biomass of preferred food plants diminishes to low levels during high rodent population densities, rodents are forced to shift to food plants of lower quality; i.e. to plants with fewer nutrients, more defence compounds or even lethal toxins (Freeland, 1974). Increased competition for good-quality food items may drive individuals to add food items of lower quality to their diet, thus resulting in a broader diet (Svanbäck & Bolnick, 2007; Stewart *et al.*, 2011; Plesner Jensen & Doncaster, 1999). Yet empirical support for the idea that intraspecific competition leads to higher diet diversity is not unequivocal (Jones & Post, 2016), and some studies have found the opposite pattern (Nicholson, Bowyer & Kie, 2006; Parent, Agashe & Bolnick, 2014). For herbivorous territorial rodents living in a heterogeneous environment, dominant individuals may potentially monopolise territories with good-quality food items, forcing subdominant individuals to feed on alternative low-value food. Thus, a broader population-level diet and decreased population-level average food quality may, in principle, arise from narrower individual diets. Note that rodent diet breadth relates to plants with different nutritional quality rather than species richness *per se*. The assumptions related to the potential of this mechanism (hypothesis D in Fig. 1) to create rodent population cycles are identical except for the exact manner of diet switches, and we therefore consider this as one hypothesis. A mathematical modelling study has provided limited support for this hypothesis. It found that constitutive defences of non-preferred plants were able to create multiannual rodent cycles only in a scenario where the plant defences marginally increased rodent mortality (Kent *et al.*, 2005). The set of assumptions that can be tested in a single study is always limited. For instance, Kent *et al.* (2005) only included two food types in their study. This hypothesis would benefit from further exploration in more extensive modelling studies before it can be rejected.

III. MATERIALS AND METHODS

We systematically searched the scientific literature to collect publications on interactions between cyclic arvicoline

populations and their plant foods. We followed the Reporting Standards for Systematic Evidence Syntheses (ROSES) statement as a guide (Haddaway *et al.*, 2018). We included publications reporting on studies that fulfilled the following criteria. (*i*) Study species is an arvicoline rodent with cyclic population dynamics from the northern hemisphere. (*ii*) The study addresses a rodent–plant interaction, related to rodent population cycles. This included studies on plant/vegetation effects on rodents, rodent effects on plants/vegetation, changes in rodent diet or food quality linked to population cycles or different population densities, and health consequences of plant food quality on rodents. However, we excluded studies that focused on tree seeds/masting years, as herbivorous arvicoline rodents involved in such dynamics exhibit population peaks linked to community-wide trophic cascades driven by other, granivorous, rodent species (Elias, Witham & Hunter, 2006; Šipoš *et al.*, 2017). (*iii*) The study presents empirical primary research data. Examples of excluded studies include studies of non-cyclic populations, diet studies that did not address a relationship between diet and population density, studies on rodent habitat selection and habitat use descriptions, and modelling studies (see online Supporting Information, Appendix S1, for full list of exclusion criteria).

We collected literature in three steps. First, we searched the ISI *Web of Science* (Core Collection) database, and the *Scopus* database, using the following search string: Topic = (rodent OR vole OR lemming) AND (plant OR vegetation OR defence OR defense) AND ('population cycle*' OR 'population dynamic*'). Access dates to ISI and *Scopus* were 08.02.2018, 22.02.2019 and 03.09.2020. Based on the title and abstract, we included publications that fulfilled all our criteria. Second, we checked for additional publications fulfilling our inclusion criteria among publications that either cited the included publications or were cited by them. For this step, we used the *Scopus* and ISI *Web of Science* features 'cited search' and 'view related records'. Access dates to ISI *Web of Science* and *Scopus* for this search were 19.03.2018, 22.02.2019 and 18.01.2021. Appendix S2 lists all papers found with information on possible exclusion criteria.

The first literature search in ISI *Web of Science* and *Scopus* resulted in 505 and 495 search hits, respectively (Fig. 2). Of these, 94 appeared to fulfil our inclusion criteria based on titles and abstracts. These articles cited 4679 references and were themselves cited in 2295 publications. After removing duplicates, we screened the titles and abstracts and retained 273 publications, for which we assessed the full text. We excluded an additional 123 publications based on full text screening (see Fig. 2 and Appendix S2 for more details).

The remaining 150 publications (Appendix S3; identified with asterisks in the main reference list) all contained one or multiple relevant results. We separated publications into multiple studies when they addressed several hypotheses or assumptions, used several methods (e.g. reported on an experiment and a long-term observational study), or several study systems. For each study, we recorded the following information

(see Appendix S4 for detailed coding sheet with definitions, and Appendix S5 for additional information).

(1) What are the general hypothesis and the specific assumption that the study assessed or provided information about? Figure 1 presents the hypotheses, related assumptions, and abbreviations used below. However, we do not expect these assumptions to be quantitatively equal, neither between assumptions nor for the same assumption in different ecological contexts. We do not attempt to estimate thresholds or effect sizes in this paper, but instead present information relating to each assumption strictly qualitatively.

(2) What kind of evidence does the study provide for or against the assumption?

(3) What is the study system: small rodent species, plant community/species, habitat, biome?

(4) What is the location and time span of the study?

(5) What is the research approach employed and how was rodent density addressed?

(6) Have aspects of rodents and their food plants been related to changed population dynamics and/or climate change?

(7) Are there issues with study quality? We assessed this using a set of criteria modified from the guidelines for systematic reviews by Collaboration for Environmental Evidence (2013). The criteria cover selection of study units, replication, existence of a control treatment (for experimental studies), apparent confounding issues, attrition (non-random loss of samples) or other variations of sampling design, and comments on whether the method description was sufficient. We used the following categories: (*i*) high risk of bias (HR): studies with a total absence of replication (e.g. an experiment with one rodent individual per treatment), strongly insufficient method description (e.g. field study without any information on locality), or major confounding factors; (*ii*) medium risk of bias (MR): lack of a transparent and systematic procedure for sample selection, lack of experimental controls, attrition bias or confounding of sampling design that was not controlled for, basing conclusions on indirect evidence, or slightly insufficient methods description. Examples are a change of methods or sampling sites between years, concluding that two time series are correlated based on visual inspection, highly unbalanced sample size (e.g. twice as many plots of treatment A than treatment B), spatial or temporal mismatch between variables (e.g. use of regional statistics in combination with local field data). If the authors analysed, discussed, or interpreted the impacts of such issues, they were not necessarily considered problematic. Note, however, that as almost no ecological studies describe transparently the rationale for the selection of the study area, we did not use the absence of such description as a criterion for MR; (*iii*) low risk of bias (LR): the remaining studies.

Risk of bias was first assessed by E. M. S.; for unclear cases both authors discussed potential disagreements to achieve consensus. We included studies with MR/LR in our evidence
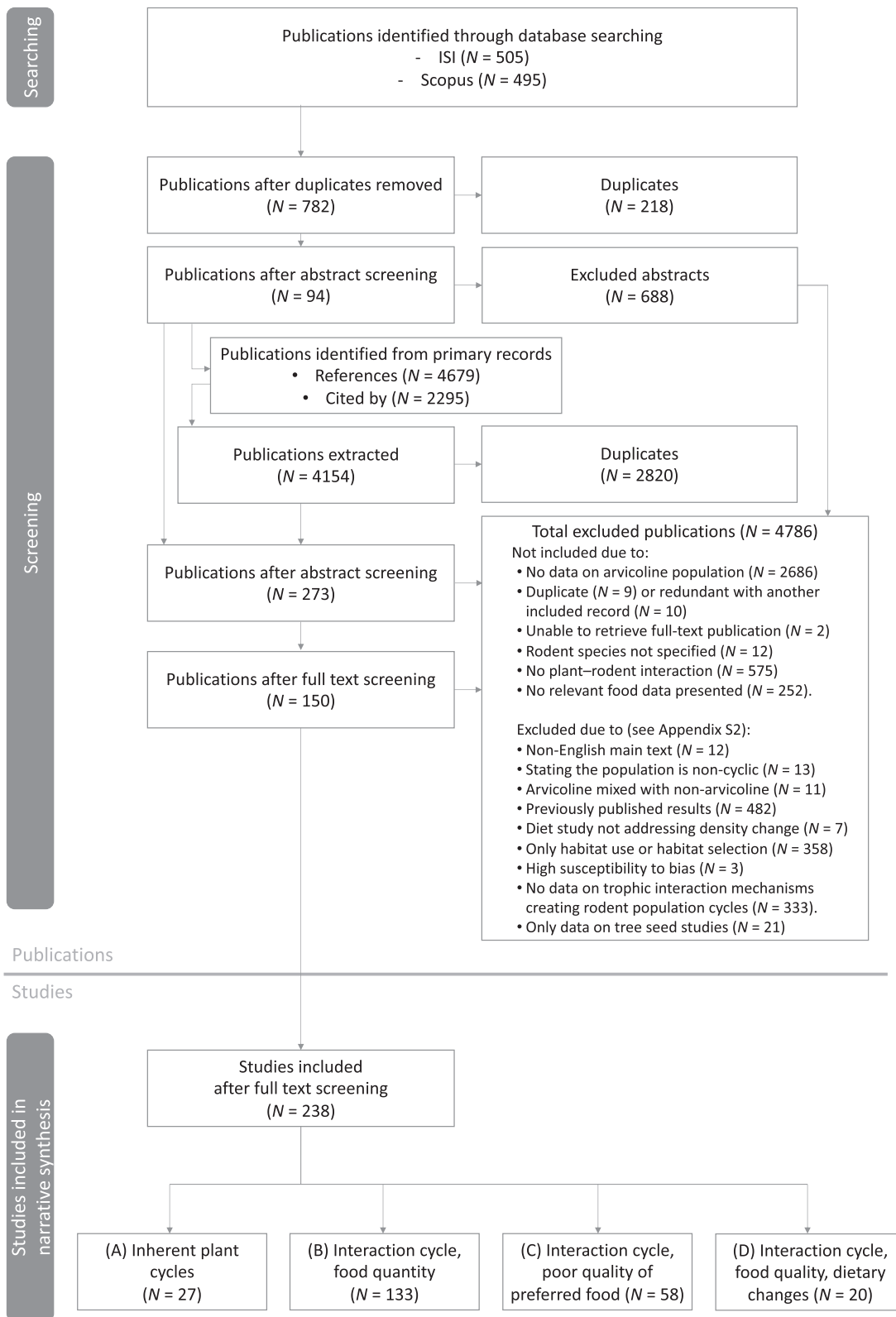
Fig. 2. Flow diagram of the selection process used for inclusion of studies in this review, using the Reporting Standards for Systematic Evidence Syntheses (ROSES) statement as guide (Haddaway *et al.*, 2018). Note that each publication could contribute more than one study to our synthesis.

base but excluded studies with HR. However, in Section IV we focus our interpretations on studies with LR. Due to considerable variation among studies, with very few replicates of identical response and predictor variables, we did not perform a quantitative meta-analysis, but rather synthesised similar studies narratively. We summarised findings only for repeatedly ($N \geq 3$ studies) studied topics. Singular studies are included in summary tables, but are not discussed in detail.

IV. RESULTS

(1) Summary of the evidence base

We included a total of 150 publications, published from 1941 to 2020 (Fig. 3), containing 238 studies (Fig. 2). All four main hypotheses (Fig. 1) have been studied, although across different time periods (Fig. 3). The earliest studies were on food quantity interactions, but since the late 1970s all hypotheses have been addressed. Overall, 78% of the studies stated that they aimed to test a hypothesis on plant–rodent interactions or an assumption derived from such hypotheses. Some assumptions have been studied more frequently than others (Tables 1 and 2), such as the impact of rodents on food quantity or quality (BD_i, C_i). By contrast, no study directly measured whether individual rodents ingest quantitatively less food during periods of high rodent densities than during low densities (B_{iii}).

The interaction cycles hypotheses were most often studied experimentally, whereas inherent plant cycles were mostly studied by observational means (Tables 1 and 2). Data collection for most studies (87%) spanned less than 10 years,
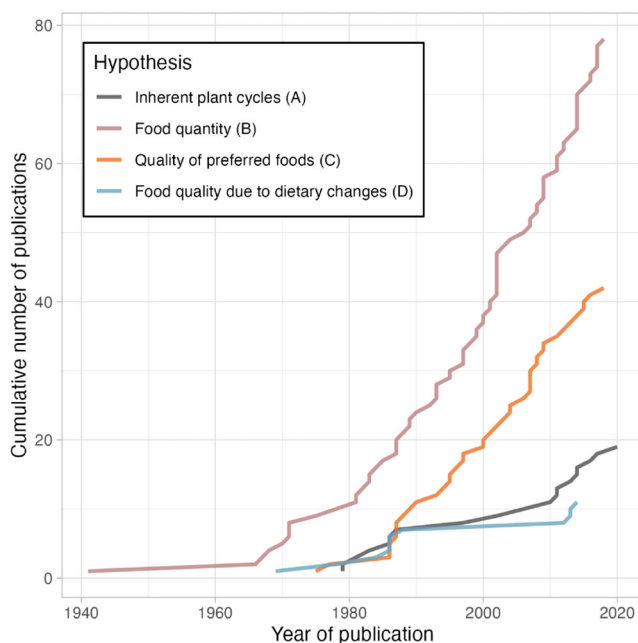

Fig. 3. Cumulative count (i.e. publication rate) of included publications from 1941 to 2020.

although one observational study lasted for 50 years (Fig. S1). Most studies contained data collected in the field (88%), although studies for changes in food quality (hypothesis C) also encompassed greenhouse and laboratory studies (Tables 1 and 2). More than half the studies focused on rodent population level (55%), followed by studies on community level (25%, especially for hypotheses A and B) and on individual level (20%, especially for hypothesis C; Appendix S3).

The studies ranged from high-Arctic tundra to the temperate biome, the latter having the most studies (34%, Fig. 4). Forested regions (i.e. all regions other than tundra) represented 72% of the studies (Fig. 4). Fennoscandia was the most studied region with 134 studies, while 69 studies were from North America, and only four studies included data from Russia (Fig. 4). Many different rodent species ($N = 20$) were investigated, with the genus *Microtus* (especially for hypotheses C and D) and *Myodes* (especially for hypothesis A) particularly well represented. Only 17% of the studies included lemming species (*Lemmus* or *Dicrostonyx*). Rodents interacted with many different plant species, although the genus *Vaccinium* ($N = 52$) was the most common, followed by *Carex*, *Salix*, and *Solidago* ($N = 29$, $N = 24$, $N = 22$, respectively; Appendix S3).

Fourteen publications (with the first published in 1999) set their research in the context of climate change and/or changes in small rodent population dynamics. These publications varied in how they related temporal changes to their study topics, ranging from climate impacts on the studied food plants (Selås, 2020; Forbes *et al.*, 2014b) to direct climate effects on rodents (Boulanger-Lapointe *et al.*, 2017; Korslund & Steen, 2006). Our evidence base included no studies that explicitly addressed the impacts of climate change on plant–rodent interactions.

We excluded four studies from three publications due to high susceptibility to bias – due to inadequate method description, lack of a control treatment or lack of replicate treatments. We found 85 studies with medium susceptibility to bias whereas the remaining 153 studies had low susceptibility to bias.

(2) Evidence for the inherent plant cycles hypothesis

Evidence for the inherent plant cycles hypothesis was found in 27 studies (Table 1). One study system was addressed by several studies: fruiting of dwarf shrubs in boreal regions, with a focus on ericoid berries and mainly *Myodes* voles ($N = 13$ studies). Evidence for cyclic berry production was inconclusive; the only LR study found a different pattern than the MR studies (Table 3). Evidence for a correlation between berry production and vole population dynamics was more consistent, although not all studies found such patterns (Table 3). Note that these correlations were based on vole abundance indices; population growth rates were estimated in only two cases (Table 3). We found no studies that tested assumptions A_{ii} and A_v in this study system. Nine of the 13 ericoid/vole studies were focused on one region (southern Norway, taiga–temperate ecotone). Therefore, we could not assess whether contradictory results in different studies were related to different ecological contexts.

Among the remaining studies addressing the inherent plant cycles hypothesis ($N = 14$), 10 addressed plant

Table 1. Number of studies providing evidence for the inherent plant cycles hypothesis (number of studies assessed as having a low risk of bias are given in parentheses). Assumptions A_{ii} (high plant quality) and A_v (increased population growth) are not included here as the evidence base contained no studies assessing these aspects. Note that some studies include data from multiple categories (e.g. several rodent genera) and are included in the counts for each of these categories. For example, a study with data from both *Microtus* and *Myodes* would be included in the sum of both genera.

Study system/characteristics		Cyclic variation in plant quality (A_i)	Increased diet quality (A_{iii})	Increased reproduction (A_{iv})	Rodent cycles follow plant cycles (A_{vi})
Sample size (low risk of bias)		8 (2)	1 (1)	2 (1)	16 (5)
Rodents	*Myodes*	7 (1)	–	–	13 (4)
	Microtus	2 (0)	1 (1)	2 (1)	8 (2)
	Lemmus	3 (0)	–	–	2 (1)
	Arvicolinae/vole	1 (1)	–	–	1 (0)
Biomes	Temperate	–	1 (1)	1 (0)	1 (0)
	Taiga–temperate ecotone	3 (0)	–	–	8 (2)
	Taiga	–	–	1 (1)	4 (1)
	Tundra–taiga ecotone	3 (1)	–	–	3 (2)
	Tundra	2 (1)	–	–	–
Regions	Fennoscandia	8 (2)	–	–	13 (4)
	Other parts of Europe	–	1 (1)	1 (0)	–
	North America	–	–	1 (1)	3 (1)
Methods	Field experiments	–	–	1 (1)	1 (1)
	Observational field studies	6 (2)	1 (1)	1 (0)	14 (4)
	Other observational	2 (0)	–	–	1 (0)
Approach to cycle	Temporal contrast 1 peak	1 (0)	–	–	1 (0)
	Temporal contrast >1 peaks	7 (2)	–	1 (0)	13 (5)
	Spatial contrast	–	–	–	2 (0)
	Other	–	1 (1)	1 (1)	–

nutritional quality, and four addressed cyclic plant reproduction. These studies were scattered across biomes and vegetation types (Tables 1 and 3). Evidence for cyclic variation in plant reproduction was inconsistent, and too few studies assessed cyclic variation in plant nutrient quality to allow meaningful synthesis (Table 3). We note that the studies assessing plant quality under the interaction cycles hypotheses (see Section IV.3.*b*) also do not provide strong evidence for cyclic variations in plant quality but do indicate that high rodent densities are linked to higher ingestion of nitrogen and structural carbohydrates. Evidence that rodent cycles follow plant cycles with a time lag was inconsistent (Table 3), with studies in different ecological contexts reporting different results; replicates within an ecological context were too sparse for synthesis. Information related to the remaining assumptions was also too scarce for synthesis (Table 3).

(3) Evidence for the interaction cycles hypotheses

(a) Reduced plant quantity (BD_i)

Most studies provided support for the assumption that high rodent numbers lead to quantitative changes in their food plants (Table 4) and 54% of these studies measured effects of rodents on plant biomass, either total biomass or for specific preferred plant foods (Table 4). Evidence for these effects being long lasting is missing. By contrast, several studies explicitly stated that an abnormally high rodent density

would be needed to induce quantitative changes in food availability. There was no difference in this context between findings from observational field studies with natural rodent densities and experimental studies that manipulated rodent densities.

The large number of studies testing this assumption (BD_i, $N = 72$; Table 2), allowed us to explore sources of variation among the results. We found that studies reporting on herbivory during winter ($N = 26$) tended to report stronger effects during winter than in other seasons ($N = 2$ for seed removal, $N = 2$ plant cutting frequency, $N = 1$ for species composition, $N = 4$ for biomass) or report tree damage only in winter ($N = 1$), where we define winter as the period when vegetation does not regenerate. The remaining winter studies did not contrast winter data with other seasons. Only two winter studies (8%) found no evidence for an effect of vole herbivory on vegetation, as compared to seven studies (13% of the 56 studies including data for summer only or for summer and winter) that found no clear evidence during summer. We found no clear pattern between study biome and the quantitative effects of rodent herbivory of vegetation.

(b) Reduced plant quality (C_i)

In response to herbivory, some plants produce harmful defensive compounds. The best studied are phenolic

Table 2. Number of studies providing evidence for the interaction cycles hypothesis (number of studies assessed as having a low risk of bias are given in parentheses). Assumption B_{iii} (reduced diet quantity) is not included here, as we found no studies assessing it. B_{other} includes food supplementation studies that assessed the impact of supplemental food on only population-level aspects. C_{other} includes a study assessing whether plant quality explained the abundance of signs of vole herbivory. Note that some studies include data from multiple categories (e.g. several rodent genera) and are included in the counts for each of these categories. For example, a study with data from both *Microtus* and *Myodes* would be included in the sum of both genera.

Study system/characteristic/method	Reduced plant quantity (BD_i)	Reduced plant quality (C_i)	No change in diet or a change in diet (BCD_{ii})	Reduced diet quality (CD_{iii})	Reduced health due to lower ingestion (B_{iv})	Reduced health due to lower diet quality (CD_{iv})	Reduced population growth (BCD_v)	Plant availability follows rodent density (BD_{vi})	Plant quality follows rodent density (C_{vi})	B_{other}	C_{other}
Sample size (low risk of bias)	72 (52)	21 (17)	12 (6)	10 (6)	21 (18)	24 (18)	16 (9)	20 (9)	7 (4)	7 (4)	1 (1)
Rodents *Myodes*	39 (26)	4 (2)	6 (2)	1 (0)	10 (8)	3 (3)	7 (3)	11 (3)	2 (2)	4 (1)	1 (1)
Microtus	43 (31)	12 (10)	11 (6)	9 (6)	13 (11)	20 (14)	9 (5)	11 (3)	4 (2)	3 (3)	—
Lemmus	22 (20)	2 (1)	1 (1)	—	2 (1)	1 (1)	—	5 (5)	1 (0)	—	—
Dicrostonyx	3 (3)	1 (1)	—	—	—	—	—	1 (1)	—	1 (1)	—
Lasiopodomys	—	—	—	—	1 (1)	—	1 (1)	—	—	—	—
Arvicolinae/vole	5 (3)	—	—	—	—	—	—	4 (2)	—	—	—
Not relevant	—	3 (3)	—	—	—	—	—	—	—	—	—
Biomes Temperate	16 (12)	10 (8)	3 (2)	6 (3)	10 (9)	15 (11)	7 (3)	5 (2)	3 (1)	2 (1)	—
Taiga–temperate ecotone	10 (8)	1 (1)	6 (3)	2 (2)	3 (3)	4 (3)	3 (3)	2 (0)	—	1 (1)	—
Taiga	10 (4)	1 (1)	1 (0)	2 (1)	7 (5)	4 (3)	6 (3)	3 (0)	1 (1)	2 (0)	—
Tundra–taiga ecotone	1 (1)	—	—	—	—	—	—	—	1 (1)	—	—
Tundra	35 (27)	9 (7)	2 (1)	3 (2)	1 (1)	1 (1)	—	9 (6)	2 (1)	2 (2)	1 (1)
Regions Fennoscandia	47 (32)	9 (7)	8 (4)	3 (2)	10 (9)	7 (6)	7 (7)	14 (6)	3 (3)	4 (2)	1 (1)
Other parts of Europe	8 (7)	6 (6)	—	3 (2)	1 (1)	4 (4)	1 (0)	2 (0)	2 (1)	—	—
North America	16 (13)	6 (4)	5 (3)	4 (2)	8 (6)	12 (7)	7 (1)	4 (3)	1 (0)	2 (2)	—
Russia/China	1 (0)	—	1 (1)	—	1 (1)	1 (1)	1 (1)	—	1 (0)	—	—
Japan	—	—	—	—	1 (1)	—	—	1 (1)	1 (0)	1 (0)	—
Methods Field experiment	38 (32)	10 (8)	2 (2)	2 (2)	18 (16)	7 (5)	15 (8)	6 (4)	2 (2)	7 (4)	1 (1)
Field quasi-experimental	3 (1)	1 (1)	1 (0)	—	—	—	—	1 (0)	—	—	—
Field other	1 (1)	—	—	—	—	—	—	—	—	—	—
Field observational	25 (13)	5 (3)	9 (4)	8 (4)	1 (1)	4 (3)	1 (1)	12 (4)	5 (2)	—	1 (1)
Greenhouse experiment	3 (3)	5 (5)	—	—	1 (0)	—	—	—	—	—	—
Laboratory experiment	—	—	—	—	1 (1)	12 (9)	—	1 (1)	—	—	—
Other observational	2 (2)	—	—	—	—	1 (1)	—	—	—	—	—
Other experiments	—	—	—	—	—	—	—	—	—	—	—
Approach to cycle Density manipulation	16 (12)	9 (7)	1 (1)	1 (1)	1 (0)	3 (3)	—	1 (0)	2 (2)	1 (1)	—
Temporal contrast 1 peak	14 (8)	2 (1)	8 (4)	5 (3)	—	2 (1)	1 (1)	5 (3)	2 (1)	—	1 (1)
Temporal contrast >1 peaks	10 (3)	—	2 (1)	2 (1)	1 (1)	1 (1)	—	10 (3)	1 (1)	—	—
Spatial contrast	6 (5)	4 (3)	2 (0)	1 (0)	—	1 (1)	—	1 (0)	2 (0)	—	—
Exclosure	22 (21)	2 (2)	—	—	—	—	—	2 (2)	—	—	—
Simulated herbivory	1 (0)	4 (4)	—	—	—	—	—	—	—	—	—
Other	4 (4)	—	1 (1)	1 (1)	19 (17)	16 (11)	15 (8)	1 (1)	—	6 (3)	—
Not relevant	—	—	—	—	—	1 (1)	—	—	—	—	—
Not reported	—	—	—	—	—	—	—	—	—	—	—

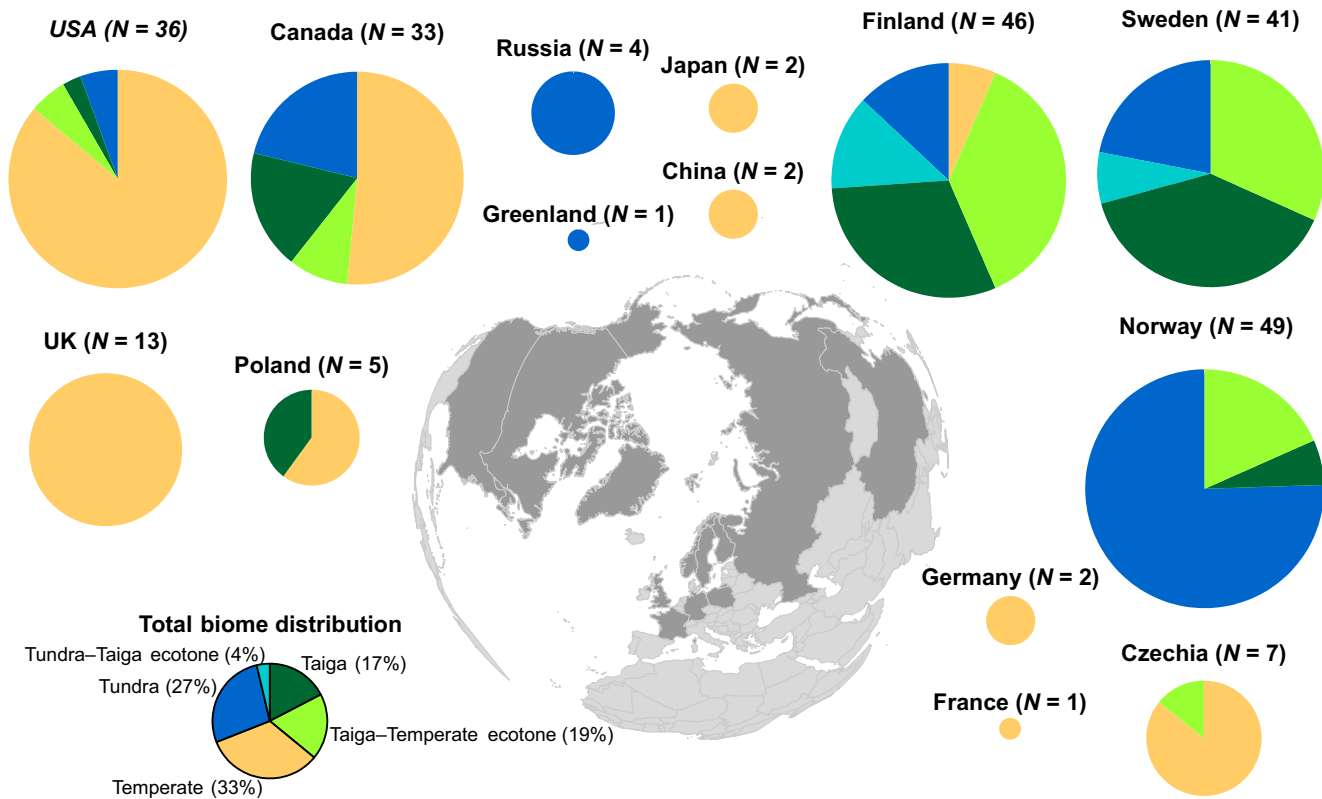Eeva M. Soininen and Magne Neby

Fig. 4. Distribution of studies included in the evidence base ($N = 238$). The countries that are represented are shown in dark grey on the image of the globe. Pie diagrams depict the distribution of studies among biomes, with colours representing type of biome as labelled on the pie diagram for total biome distribution. The number of studies per country is given in parentheses and reflected by the relative size of the pie diagram. Note that some studies include data from multiple countries and are included in the counts for each of these countries.

compounds and silica (Table 5A), with the evidence suggesting that rodent herbivory can, in some cases, induce increased concentrations (Table 5A). Induction of silica production in response to vole herbivory was reported for several grass species in both greenhouse and field studies. The only field study testing multiple species found that not all species responded similarly, including one species that did respond to herbivory by silica induction in field study from a different ecosystem. While replicate studies remain needed, these results suggest that there is variation among grass species both within/among ecosystems and within/among grass species. The evidence was less clear for phenolics, with impacts of rodent herbivory ranging from no effects to negative or positive effects. For other defensive compounds, we found reports that rodent herbivory did not result in increased levels of trypsin inhibitors (Table 5A). There were no other harmful compounds with three or more replicate studies, preventing any synthesis (Table 5A).

57% of studies addressing plant defences included measures of nutrients. For proteins/nitrogen, both positive, negative and no relationships with current rodent population density were found, while for carbon-based compounds, both negative and no relationships were found (Table 5A). Further synthesis of these results is difficult as the measured compounds, methodological approaches, and ecological contexts differed among

studies (Appendix S3). Evidence for an effect of herbivory on other measures of plant quality was also too limited for synthesis (Table 5B). Note that the delayed responses of plant quality to rodent herbivory are addressed in Section IV.3.*i*.

(c) No change in diet or a change in diet (BCD_ii)

We found some evidence for changes in diet composition related to population density; some, but not all, studies found an increased use of less-palatable food items during periods of high population density (Table 6). A low number of replicate studies from specific ecological contexts prevents further assessments on when and where such patterns arise. As no studies were carried out across two consecutive population cycles, it remains unclear whether these patterns were persistent over time. The number of studies addressing diet diversity or food preferences was too low to allow synthesis (Table 6).

(d) Reduced diet quality (CD_iii)

For total phenolics, protein/nitrogen and carbohydrates there was sufficient evidence available for synthesis (Table 5A). The evidence suggests that current or recent high rodent densities are linked with higher concentrations of nitrogen and structural carbohydrates in ingested food, but

Table 3. Summary of published evidence on the inherent plant cycles hypothesis. Assumptions A_{ii} (high plant quality) and A_v (increased population growth) are not included here as the evidence base contained no studies assessing these aspects. Studies with low risk of bias are identified with an asterisk; other studies cited in the table were classified as medium risk of bias. Note that some publications included multiple studies and/or informed on multiple characteristics, see Tables 1 and 2 and Appendix S3 for quantitative assessment. When studies within a publication had a different risk of bias, the reference is given with the appropriate risk denotation and may occur twice.

Study system	Cyclic variation in plant quality (A_i)	Increased diet quality (A_{iii})	Increased reproduction (A_{iv})	Rodent cycles follow plant cycles (A_{vi})
Ericoid berries and voles in boreal biome ($N = 13$ studies)	No evidence (Boulanger-Lapointe *et al.*, 2017*); evidence for (Selås, 1997; Selås *et al.*, 2002; Selås, 2006).	–	–	Vole abundance index related to previous year's berry production (Selås, 1997; Selås, 2006; Krebs *et al.*, 2010; Selås *et al.*, 2011; Selås *et al.*, 2013*; Selås, 2020*); no such pattern (Hansson, 1979; Tornberg *et al.*, 2011). Vole abundance index related to current year's berry production (Selås, 2006); no such pattern (Hansson, 1979). Vole population growth during summer was related to current (Selås *et al.*, 2002; Krebs *et al.*, 2010) or previous (Selås *et al.*, 2002) year's berry production. Vole population growth during winter was unrelated to previous year's berry production (Selås *et al.*, 2002) or depended on species (Krebs *et al.*, 2010). No relationship between nutritional quality of berry-producing plants and vole abundance (Selås *et al.*, 2011).
Other ($N = 14$ studies)	Flowering of tundra plants was mostly not synchronous across species (Oksanen & Ericson, 1987*). Cyclic variation in plant reproduction (Laine & Henttonen, 1983); no such variation (Oksanen & Oksanen, 1981). No cyclic variation in plant nutrient content (Andersson & Jonasson, 1986).	Voles ingested higher quality diet during high population densities than during low population densities in arable temperate landscapes (Janova *et al.*, 2016*).	Female reproduction was higher in fertilised taiga forest vegetation but not in non-fertilised forest (Sullivan & Sullivan, 2014*). Female reproduction related to vegetation productivity index (Pinot *et al.*, 2014).	Fluctuations of plant nutrient content in low alpine heaths were unrelated to rodent abundance (Andersson & Jonasson, 1986*; Jonasson *et al.*, 1986*). Population cycles only present in fertilised taiga forest vegetation but not in non-fertilised forest (Sullivan & Sullivan, 2014*). Vole abundance related to plant nutrient content in boreal forest (Hansson, 1979), and to plant reproduction in alpine vegetation (Laine & Henttonen, 1983). Vole abundance not related to plant nutrient content in temperate grassland (Cole & Batzli, 1979) or to plant reproduction in boreal heath forest (Oksanen & Ericson, 1987).

the evidence for phenolics was uncertain. These studies often addressed ingestion through levels of compounds in faeces or stomach contents. However, not all ingested compounds are absorbed from the dietary tract, and the absorbed concentrations and concentration excreted in faeces are not necessarily correlated. Note that evidence was available only for voles for assumption CD_{iii} (Table 2).

(e) Reduced health due to lower ingestion (B_{iv})

None of the studies in our database tested assumption B_{iv} directly. Furthermore, all but one of the studies that provided potentially relevant information used food supplementation experiments to manipulate the food consumption rate (i.e. lacked direct measurement of lower food consumption at the individual level). It is methodologically difficult to test directly whether individual rodents ingest lower quantity food at high population densities than at low densities, as direct observations of ingestion are much less feasible than in larger herbivores. Thus, experimental food supplementation is a common strategy in such research. However, this strategy assumes a close relationship between availability and consumption, which may not be justified. The studies used various ways to assess individual health (Table 7A) and overall reported that increased food supply was beneficial to one or more

Table 4. Summary of published evidence for the interaction cycles hypotheses on the impacts of rodent herbivory on quantitative aspects of vegetation. Studies with low risk of bias are identified with an asterisk; other studies cited in the table were classified as medium risk of bias. Note that some publications included multiple studies and/or informed on multiple characteristics, see Tables 1 and 2 and Appendix S3 for quantitative assessment. When studies within a publication had a different risk of bias, the reference is given with the appropriate risk denotation and may occur twice.

Characteristic of vegetation	Reduced plant quantity (BD_i)	Plant availability follows rodent density (BD_{vi})
Biomass/plant abundance	Rodents markedly reduced the biomass of several plant species (Andersson & Jonasson, 1986*; Batzli & Pitelka, 1970*; Bergeron & Jodoin, 1989; Bergeron & Jodoin, 1993*; Chitty et al., 1968*; Dahlgren et al., 2007*; Dahlgren et al., 2009a*; Ford & Pitelka, 1984*; Hoset et al., 2014*; Howe, 2008*; Johnson et al., 2011*; Moen et al., 1993a*; Moen et al., 1993b*; Olofsson et al., 2012*; Ostfeld et al., 1993; Ravolainen et al., 2011*; Ruffino et al., 2016*; Smirnov & Tomakova, 1971; Virtanen et al., 2002). Some plant species/groups responded stronger than others e.g. Vaccinium myrtillus/ericoids/shrubs (Dahlgren et al., 2009a*; Dahlgren et al., 2009b*; Grellman, 2002*; Hambäck & Ekerholm, 1997*; Hambäck et al., 2004*; Hoset et al., 2017*; Oksanen & Oksanen, 1981), Empetrum nigrum (Dahlgren et al., 2009b*), mosses (Kalela & Koponen, 1971*; Oksanen & Oksanen, 1981; Virtanen et al., 1997*), herbs (Moen & Oksanen, 1998*), deciduous shrubs (Norrdahl et al., 2002*), Medicago sativa (Truszkowski, 1982*), Desmanthus illinoensis (Sullivan & Howe, 2011*). Response was greatest (or only present) in winter season (Hambäck et al., 2004*; Howe & Brown, 2000*; Norrdahl et al., 2002*; Ravolainen et al., 2014*). Quantitative effects of grazing were negligible (Agrell et al., 1995*; Bergeron & Jodoin, 1995; Bilodeau et al., 2014*; Ericson & Oksanen, 1987*), or evidence present in one cycle but not another (Summerhayes, 1941*), or in one habitat/site but not another (Kalela & Koponen, 1971*; Moen, 1990*; Oksanen & Oksanen, 1981; Ravolainen et al., 2011*)	Plant biomass in grazed plots was lower the year after rodent population peak, but sometimes differed among plant species (Howe, 2008*; Moen et al., 1993b*). Direct density dependence with reduced biomass during peak, but recovery during post-peak/low-density year (Ostfeld et al., 1993; Andersson & Jonasson, 1986; Olofsson et al., 2012*). No plant biomass variation between years (Bilodeau et al., 2014*).
Plant species composition, richness, diversity	Rodents changed the plant species composition (Andersson & Jonasson, 1986*; Summerhayes, 1941*; Virtanen et al., 1997*) or species richness/diversity (Fox, 1985*; Norrdahl et al., 2002*), but sometimes only in winter (Howe & Brown, 2000*). No effects on plant composition (Agrell et al., 1995*; Moen, 1990*), or in one site but not another (Sirotnak & Huntly, 2000*)	Palatable species fluctuated more than unpalatable species (Olofsson et al., 2012*).
NDVI (normalised difference vegetation index)	Rodent population peaks correlated with reduced NDVI in satellite imagery during the following year (Olofsson et al., 2012*)	Rodent population peaks correlated with reduced NDVI in satellite imagery during the following year (Olofsson et al., 2012*)
Seed removal/ seedlings	Increased rodent numbers were correlated with increased seed removal (Ashby, 1967*; Batzli & Pitelka, 1970*; Hansson, 1999; Hansson, 2002a), although sometimes only/more during winter (Ashby, 1967*; Howe & Brown, 2000*), or not at all (Hansson, 1999; Hansson, 2002b), or even with seed increase (Nystuen et al., 2014*). More seedlings emerging in the rodent low-density year than in the year of the rodent population peak (Nystuen et al., 2014*). Variation among sites despite equal rodent disturbance (Nystuen et al., 2014*). Repeated clipping reduced seed production in Desmanthus illinoensis (Sullivan & Howe, 2011*).	High seed consumption only during high vole density (Hansson, 2002a)

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Table 4. *(Cont.)*

Characteristic of vegetation	Reduced plant quantity (BD$_i$)	Plant availability follows rodent density (BD$_{vi}$)
Flower frequency/ berry production	Increased numbers of rodents reduced the flowering frequency of food plants (Andersson & Jonasson, 1986*; Andersson & Jonasson, 1986; Järvinen, 1987; Moen & Oksanen, 1998*; Oksanen & Ericson, 1987). Abundance of rodents was negatively related to the subsequent year's flower and berry abundance (Boulanger-Lapointe *et al.*, 2017*)	Grazing during the two preceding years was related to smaller individual plants with fewer flowers on grazed than non-grazed *Ranunculus glacialis*; no effect on leaf number (Järvinen, 1987). Annual variation of flower frequency or survival of flowers from spring to fall was explained by rodent densities (Oksanen & Ericson, 1987), but not in both rodent density peaks (Oksanen & Ericson, 1987). The abundance of rodents during the preceding year had a negative effect on the current year's flower abundance (Boulanger-Lapointe *et al.*, 2017).
Cutting frequency of ramets/ saplings	High vole density led to more clipping (Dahlgren *et al.*, 2007*). Most of the plant mortality (80%) occurred over the winter when rodents were abundant (Hambäck *et al.*, 2004*; Ravolainen *et al.*, 2014*).	Rodent winter grazing signs more evident during a post-peak spring than a pre-peak spring, with differences among habitats (Ruffino *et al.*, 2016*), or the effect lasting into the following growing season for some plant species but not others (Sullivan & Howe, 2011*). Vole density patterns across years mirrored patterns of shoot/sapling damage (Elmqvist *et al.*, 1988; Suchomel *et al.*, 2016*). Shoot mortality remained low throughout (Oksanen *et al.*, 1999*).
Ramet density	Rodent grazing led to higher density of ramets of *Vaccinium myrtillus* (Dahlgren *et al.*, 2007*). Genet or bark scars on *Salix* correlated with number of shoots during the spring/summer (Ericson *et al.*, 1992, Predavec & Danell, 2001*)	Winters with extensive damage from voles on willow bark were followed by summers with high shoot production (Ericson *et al.*, 1992)
Damage on bark/ trees, scars	High vole abundance was associated with increased amount of damage (Elmqvist *et al.*, 1988; Ericson *et al.*, 1992; Hansson, 1999; Hansson, 2002*a*; Hansson, 2002*b*; Heroldová *et al.*, 2012*; Hörnfeldt *et al.*, 1986; Imholt *et al.*, 2017; Klemola *et al.*, 2000*a*; Krojerová-Prokešováa *et al.*, 2018*; Predavec & Danell, 2001*), but not all present vole species caused significant damage (Suchomel *et al.*, 2016*), or mainly in winter (Imholt *et al.*, 2017).	Vole damage on trees/bark reflected vole density patterns (Hansson, 2002*b*; Hörnfeldt *et al.*, 1986; Imholt *et al.*, 2017; Suchomel *et al.*, 2016*).
Survival of marked shoots	Seedling survival was reduced by high vole density, but depended on seedling size, habitat, and species (Hambäck & Ekerholm, 1997*; Hambäck *et al.*, 2004*; Huitu *et al.*, 2007*; Ostfeld *et al.*, 1997*; Ravolainen *et al.*, 2014*). Green shoots of overwintered mosses, grasses and/or dicotyledons were less abundant during high vole abundance (Huitu *et al.*, 2003*; Huitu *et al.*, 2007*; Klemola *et al.*, 2000*a*; Moen, 1990*), or *Solidago virgaurea* specifically (Oksanen & Ericson, 1987); others did not find such reduction (Oksanen *et al.*, 1999*). Some studies found winter mortality of shoots related to vole density (Elmqvist *et al.*, 1988; Hambäck *et al.*, 2004*; Huitu *et al.*, 2009*); others did not (Hambäck & Ekerholm, 1997*).	Shoot mortality of the main winter food plant, *Vaccinium myrtillus*, was low and had no obvious relationship with vole density (Oksanen *et al.*, 1999*).

of these health indices, such as body mass, growth, reproductive onset/activity, and immune response. A single observational study used nearby agricultural production as an index of food-plant production and found that the body condition index of overwintered voles was positively related to food availability. The three studies with MR

Table 5. Summary of published evidence for the interaction cycles hypotheses relating rodent herbivory to qualitative changes in plants. Note that some studies tested several types of responses and are therefore included multiple times. Studies with low risk of bias are identified with an asterisk; other studies cited in the table were classified as medium risk of bias. Note that some publications included multiple studies and/or informed on multiple characteristics, see Tables 1 and 2 and Appendix S3 for quantitative assessment. When studies within a publication had a different risk of bias, the reference is given with the appropriate risk denotation and may occur twice. The single study assessing whether plant quality explained the abundance of signs of vole herbivory (C_{other}) is denoted with grey.

A. Chemical compounds, endophytic fungi, and nutrients

Compound	Reduced plant quality (C_i)	Reduced diet quality (CD_{iii}, C_{other})	Reduced health due to lower diet quality (CD_{iv})	Plant quality follows rodent density (C_{vi})
Silica	Rodent herbivory increased grass silica content in greenhouse experiments for all tested grass species (Massey & Hartley, 2006*; Massey et al., 2007*; Reynolds et al., 2012*). Simulated herbivory increased grass silica content of some tested species (Soininen et al., 2013a*) or had no effect (Massey et al., 2007*). Field experiments with vole density manipulation and one grass species showed silica induction in the tested grass species (Huitu et al., 2014*; Ruffino et al., 2018*). Field experiment with vole exclosures and multiple grass species showed silica induction in some grass species (Soininen et al., 2013a*).	Vole dental abrasion, presumably due to silica in food, was unrelated to population density (Calandra et al., 2016*).	Reduced body mass (Massey et al., 2008*; Wieczorek et al., 2015*); higher food consumption concurrent with changes in intestinal morphology (Wieczorek et al., 2015*). High-vole-density treatment led to (i) changes in grass silica content, not reflected in vole health (Ruffino et al., 2018*); and (ii) changes in both silica and phenolic content of grasses, reduced body mass, and higher female mortality (Huitu et al., 2014).	Spatial contrasts in silica levels were related to population cycle phase (Massey et al., 2008). Vole density manipulation led to changes in silica levels, but the differences did not persist beyond the density manipulation (Ruffino et al., 2018*).
Endophytic fungi	–	–	Reduced body mass (Huitu et al., 2008*); increased body mass of females but not males (Fortier et al., 2000*); effect on body mass depending on vole sex and grass grazing history (Huitu et al., 2014); increased haematocrit levels of female voles (Huitu et al., 2014).	–
All phenolics [note that this group of compounds is reported in very variable ways; we use the terms reported by the authors and group them below into flavonoids, phenolic acids	Studies with no effect were most common (Lindroth & Batzli, 1986*; Bergeron & Jodoin, 1993*; Agrell et al., 1995*; Bergeron & Jodoin, 1995; Bergeron, 1997), followed by studies with variable responses among plant species (Oksanen & Oksanen, 1981; Bergeron & Jodoin, 1989*; Saetnan &	Concentration in vole faeces was higher during periods of high vole densities than during lower densities (Bergeron, 1996*) and in a low-food-availability treatment (Bergeron & Jodoin, 1995*). Levels of phenolic-detoxification metabolites were not related to population	Reduced body mass and increased mortality (Huitu et al., 2014).	No correlation with the current year's rodent density (Jonasson et al., 1986*; Lindroth & Batzli, 1986; Laine & Henttonen, 1987*); no correlation with the preceding year's rodent density (Jonasson et al., 1986*).

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Table 5. *(Cont.)*

A. Chemical compounds, endophytic fungi, and nutrients

Compound	Reduced plant quality (C_i)	Reduced diet quality (CD_{iii}, C_{other})	Reduced health due to lower diet quality (CD_{iv})	Plant quality follows rodent density (C_{vi})
and phenolic glycosides according to Crozier *et al.*, (2006)]	Batzli, 2009*). One study reported a positive relationship with rodent herbivory (Huitu *et al.*, 2014*); one reported a negative relationship with rodent herbivory (Oksanen *et al.*, 1987).	density and did not vary multi-annually (Lindroth & Batzli, 1986). Intensity of vole herbivory was negatively related to plant phenolic content (Hambäck *et al.*, 2002*).		
Flavonoids	No overall relationship with vole density (Olofsson *et al.*, 2007*). Catechins: increase induced by simulated herbivory (Berg, 2003*); no relationship with vole density (Olofsson *et al.*, 2007*). Condensed tannins: peak concentration during summer after highest vole densities (Bergeron & Jodoin, 1989*); no relationship with vole density (Olofsson *et al.*, 2007*). Glycosides: 3 compounds for which grazing effects were found, 2 for which grazing effects depended on grass endophyte status, and 3 for which no grazing effects (Huitu *et al.*, 2014*). Flavonoid derivates: 2 compounds for which grazing effects were found, 1 for which not found (Huitu *et al.*, 2014*).	–	Slower growth (Lindroth & Batzli, 1984*, quercetin); feeding inhibition (Lindroth & Batzli, 1984*, querbracho, a condensed tannin).	–
Phenolic acids	No relationship with vole density (phenolic acids as a group; Olofsson *et al.*, 2007*, gentisic acid and neochlorogenic acid; Huitu *et al.*, 2014*). Increase due to vole herbivory (Huitu *et al.*, 2014*, chlorogenic acid).	–	Increased metabolic rate and decreased body mass (Thomas *et al.*, 1988*, gallic acid); slower growth (Lindroth & Batzli, 1984*, tannic acid).	–
Phenolic glycosides	No relationship with vole density (Olofsson *et al.*, 2007*).	–	–	–
Trypsin inhibitors	No evidence for an effect of either simulated herbivory (Lindgren *et al.*, 2007*; Saetnan & Batzli, 2009*) or observed herbivory in the field (Bråthen *et al.*, 2004*).	Relative size of pancreas and liver (an index of metabolisation of trypsin inhibitors) was not related to phase of rodent cycle (Klemola *et al.*, 1997*).	Increased mass of pancreas, decreased proportion of reproductively active females (Erlinge *et al.*, 2011*).	Ratio between trypsin inhibitors and soluble plant proteins was negatively correlated with lemming density. Spatial contrasts in cycle phase were related to this ratio (Erlinge *et al.*, 2011).

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Table 5. *(Cont.)*

A. Chemical compounds, endophytic fungi, and nutrients

Compound	Reduced plant quality (C_i)	Reduced diet quality (CD_{iii}, C_{other})	Reduced health due to lower diet quality (CD_{iv})	Plant quality follows rodent density (C_{vi})
Saponins	No difference between exclosure treatment and control (Lindroth & Batzli, 1986*).	–	–	No relationship with vole density (Lindroth & Batzli, 1986).
Protein/nitrogen	Decrease related to simulated herbivory (Lindgren *et al.*, 2007*); positive relationship between rodent density and protein/nitrogen levels (Oksanen *et al.*, 1987; Olofsson *et al.*, 2007*; Agrell *et al.*, 1995*); no clear relationship (Lindroth & Batzli, 1986*; Bergeron & Jodoin, 1989*; Bergeron & Jodoin, 1993*; Bergeron, 1997; Bråthen *et al.*, 2004*).	Nitrogen concentration in vole stomach contents related to current high population density (Palo & Olsson, 2009; Janova *et al.*, 2015; Janova *et al.*, 2016*). In one of the MR studies this was found only in reproductive females, not in males or non-reproductive females (Janova *et al.*, 2015).	Low protein diet led to (*i*) lighter offspring at weaning, but effect did not persist until sexual maturity, (*ii*) delayed female but not male sexual maturity. No effect on litter size, adult female body mass or weaning success (Andreassen & Ims, 1990*).	No relationships between nitrogen concentration and rodent abundance of the current year (Laine & Henttonen, 1987*; Jonasson *et al.*, 1986*) or the previous year (Jonasson *et al.*, 1986*; Klemola *et al.*, 2000*b**).
Carbohydrates	For sugars, starch, fibres, and non-structural carbohydrates, no evidence for an effect of herbivory (Bergeron & Jodoin, 1993*; Bergeron & Jodoin, 1995; Agrell *et al.*, 1995*; Bergeron, 1997; Bråthen *et al.*, 2004*); negative relationship between rodent density and sugars (Agrell *et al.*, 1995*) or fibres (Bergeron & Jodoin, 1989*).	Concentration of total non-structural carbohydrates in vole faeces was higher during population peak than during lower densities, but neutral detergent-soluble carbohydrates did not show this pattern (Bergeron, 1996*). Low-food-availability treatment led to higher concentration of neutral detergent-soluble carbohydrates in faeces (Bergeron & Jodoin, 1995*). Carbon concentration in vole stomachs was positively related to population density (Palo & Olsson, 2009)	–	No relationship with previous year's vole abundance (Jonasson *et al.*, 1986*; Klemola *et al.*, 2000*b**) or with current year's abundance (Jonasson *et al.*, 1986*).
Calcium	–	–	Increased survival and growth of young, no effect on litter frequency or litter size (Batzli, 1986*).	No relationship with previous/current year's vole abundance (Jonasson *et al.*, 1986*).
Sodium	–	–	Increased litter frequency and litter size, no effect on survival and growth of young (Batzli, 1986*).	
Magnesium	–	–	–	No relationship with previous/current year's vole abundance (Jonasson *et al.*, 1986*).
Potassium	–	–	–	No relationship with previous/current years vole abundance (Jonasson *et al.*, 1986*).

B. Other measures of plant quality.

Food quality characteristic/ treatment	Reduced plant quality (C_i)	Reduced diet quality (CD_{iii})	Reduced health due to lower diet quality (CD_{iv})
Palatability	Positive relationship with vole herbivory (Dahlgren *et al.*, 2007*, quantified as availability of young ramets).	Probability of damage to woody plant saplings increased with vole density and appeared to depend on palatability (Gilbert *et al.*, 2013*b**).	In an experiment with four diet groups (moss, mixed, *Brachypodium*, or high-quality laboratory food), all voles but those in the moss treatment gained weight, but the high-nutrient laboratory food resulted in the highest weight gain (Chitty *et al.*, 1968*).
Vegetation manipulation through vole herbivory/ density treatments	–	–	High-vole-density treatment led to changes in food quality and rodent health. Agrell *et al.* (1995*): rodent health: slower body growth, lower proportion of reproductive females; food quality: increased protein levels, decreased sugar levels, no changes in starch or phenolics content. Bergeron & Jodoin (1989): rodent health: indication of digestion of toxic compounds, signs of chronic malnutrition; food quality: low energy content and acid detergent fibre (ADF), condensed tannins peaking a year after the peak, no changes in phenolics, proteins or acid detergent lignin (ADL).
High-quality food supplementation	–	–	Larger litters (Batzli, 1986*; Cole & Batzli, 1979; Ylönen & Eccard, 2004*), faster growth of offspring (Ylönen & Eccard, 2004*), faster growing individuals (Ylönen & Eccard, 2004*), higher mass at weaning (Cole & Batzli, 1979), greater number of litters (Batzli, 1986*; Cole & Batzli, 1979). No changes in survival at birth (Ylönen & Eccard, 2004*), birth mass (Ylönen & Eccard, 2004*), timing of parturition (Eccard & Ylönen, 2001*), or winter mortality (Eccard & Ylönen, 2001*).
Difference between high- and low-quality vegetation	–	–	Voles in habitats considered to contain the highest quality food had: earlier reproduction (Cole & Batzli, 1979), higher body mass (Cole & Batzli, 1979*; Cole & Batzli, 1979), high individual growth rates (Cole & Batzli, 1979*; Cole & Batzli, 1979), higher mass gain (Ostfield & Klosterman, 1986*), larger litters (Cole & Batzli, 1979*), greater body fat reserves (Cole & Batzli, 1979*).
Extracts of different commonly eaten plant species	–	–	No effects, except for the highest doses of *Phalaris* grass (i.e. unrealistically high dosage needed to create an effect), which led to increase in liver mass but no effect on growth or kidney mass (Jean & Bergeron, 1986*)

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Table 5. *(Cont.)*

B. Other measures of plant quality.

Food quality characteristic/ treatment	Reduced plant quality (C_i)	Reduced diet quality (CD_{iii})	Reduced health due to lower diet quality (CD_{iv})
Birch twig powder supplementation	–	–	Increased food intake, liver size, activation of detoxification enzymes. No effect on body mass (Harju & Tahvanainen, 1994*).
Toxic plants	–	No clear pattern of toxic plants in vole faeces during a population cycle (Batzli & Pitelka, 1975).	Voles fed with toxic plant extracts got renal lesions, but not liver lesions. Voles fed on a balanced diet that was supplemented with toxic plant extracts did not develop irreversible lesions or intoxification (Bergeron *et al.*, 1987).

Table 6. Summary of published evidence on relationships between diet composition and population density (no change in diet or a change in diet; BCD_{ii}). All studies assessing this assumption were field studies. Studies with low risk of bias are identified with an asterisk; other studies cited in the table were classified as medium risk of bias. Note that some publications included multiple studies and/or informed on multiple characteristics, see Tables 1 and 2 and Appendix S3 for quantitative assessment. When studies within a publication had a different risk of bias, the reference is given with the appropriate risk denotation and may occur twice.

Test/analysis	Diet diversity	Diet composition	Food preference
Plant species/organ proportions in faeces or stomach contents, compared across population densities	No relationship (Bergeron & Jodoin, 1989*, Soininen *et al.*, 2013b, Soininen *et al.*, 2014*). Density-dependent habitat use and habitat-specific diets may lead to variation in population diet diversity (Soininen *et al.*, 2014*).	High vole densities related to higher proportions of bark, and lower proportions of forbs in the diet (Hansson & Larsson, 1978; Larsson & Hansson, 1977*). The same studies found higher proportions of grasses (Hansson & Larsson, 1978) and fewer seeds (Larsson & Hansson, 1977*). Little evidence of variation related to population density (Batzli & Pitelka, 1971; Bergeron & Jodoin, 1989*; Hansson, 1969; Soininen *et al.*, 2014): one grass species eaten more commonly during high-density periods (Bergeron & Jodoin, 1989*).	No clear evidence for variation of food preferences/selection across rodent densities (Soininen *et al.*, 2013b).
Herbivory signs across population densities	The number of plant species grazed was higher during peak years than in years with increasing populations (Hansson, 1988*).	Vole damage of woody plant seedlings was positively related to population density (Bergeron, 1996; Gilbert *et al.*, 2013b*; Hansson, 1986).	–
Manipulation of food availability and vole density	–	Low food availability was related to increased use of less palatable plants (Bergeron & Jodoin, 1995*).	–

provided less support for assumption B_{iv} than the LR studies.

(f) Reduced health due to lower diet quality (CD_{iv})

Studies investigating the production of defensive compounds by plants provided support for negative health effects on rodents of silicates and phenolics, and some, although context-dependent, evidence on the health effects of endophytic fungi (Table 5A). The effects of phenolics ranged from feeding inhibition to increased mortality, depending on the specific compound involved (Table 5A). Studies that assessed positive health impacts of nutrients were too scarce for synthesis (Table 5A).

Table 7. Summary of published evidence for a relationship between food consumption rate and rodent individual health (reduced health due to lower ingestion; B_{iv}) and whether individual health is related to population growth rate (reduced population growth; BCD_v). B_{other} includes food supplementation studies that assessed the impact of supplemental food on only population-level aspects. (A) summarises individual level effects from food supplementation studies; (B) summarises population-level effects from food supplementation studies and the single study that directly related health effects to population growth (in grey). Studies with low risk of bias (LR) are identified with an asterisk; other studies cited in the table were classified as medium risk of bias. Note that some publications included multiple studies and/or informed on multiple characteristics, see Tables 1 and 2 and Appendix S3 for quantitative assessment. When studies within a publication had a different risk of bias, the reference is given with the appropriate risk denotation and may occur twice.

(A) Individual measures (B_{iv})

Body mass	$\mathcal{N} = 11$	All LR studies including body mass found a positive correlation with food availability (Andrzejewski, 1975*; Desy & Thompson, 1983*; Fey *et al.*, 2008*; Haapakoski & Ylönen, 2013*; Kusumoto, 2009*; Taitt & Krebs, 1981*; Taitt & Krebs, 1983*; Yin *et al.*, 2017*), except one that concurred only when predators were excluded and with sex-dependent effects (Haapakoski *et al.*, 2012*). One found weight loss in some species, but not others (Moen *et al.*, 1993*a*). No effects (Gilbert & Krebs, 1981).
Reproductive status/activity/ stage, juvenile production, litter size, breeding onset	$\mathcal{N} = 12$	Positive effects on various reproduction-related measures (Andrzejewski, 1975*; Desy & Batzli, 1989*; Desy & Thompson, 1983*; Fey *et al.*, 2008*; Haapakoski *et al.*, 2012*; Haapakoski & Ylönen, 2013*; Ims, 1987*; Schweiger & Boutin, 1995*; Taitt & Krebs, 1983*; Yin *et al.*, 2017*). No relationship (Gilbert & Krebs, 1981).
Survival	$\mathcal{N} = 7$	Positive relationship (Cole & Batzli, 1978*; Desy & Thompson, 1983*; Korslund & Steen, 2006*; Schweiger & Boutin, 1995*); positive relationship during non-breeding season and negative during breeding season (Yin *et al.*, 2017*). No effects/no clear positive relationship (Desy & Batzli, 1989*; Haapakoski *et al.*, 2012*).
Growth/growth rate	$\mathcal{N} = 5$	Positive effects on growth/growth rate (Cole & Batzli, 1978*; Desy & Batzli, 1989*; Desy & Thompson, 1983*; Krebs, 1966); no effects (Gilbert & Krebs, 1981).
Condition index based on mass/size	$\mathcal{N} = 4$	Positive relationship, including the single observational study (Norrdahl & Korpimäki, 2002*), but in one only for females during winter (Haapakoski & Ylönen, 2013*), and in another only at low and medium population densities (not at high densities) (Forbes *et al.*, 2014*a**). No relationship (conducted during summer) (Forbes *et al.*, 2014*b**).
Immune responses	$\mathcal{N} = 3$	Three studies (LR) measured internal immune responses, two of which included multiple such measures. In one study, female (not male) haematocrit was higher (Forbes *et al.*, 2014*b**). Another study found that plasma albumin levels did not respond to food supplementation, but monocyte and leucocyte levels did (Forbes *et al.*, 2015*). Another study found that food restriction led to weakened immune response, as well as hypertrophy of kidney, heart and liver (Kusumoto, 2009*).

(B) Population-level measures (BCD_v, B_{other})

Vole density/abundance	$\mathcal{N} = 23$	Food supplementation increased population density (Desy & Batzli, 1989*; Desy & Thompson, 1983; Forbes *et al.*, 2014*a**; Forbes *et al.*, 2015*; Ford & Pitelka, 1984*; Huitu *et al.*, 2007*; Saitoh, 1989; Schweiger & Boutin, 1995; Taitt & Krebs, 1981; Taitt & Krebs, 1983; Yoccoz *et al.*, 2001; Yin *et al.*, 2017*), sometimes only/mostly over winter/spring (Andrzejewski, 1975; Fey *et al.*, 2008*; Haapakoski & Ylönen, 2013*), only with certain types of supplements (Gilbert & Krebs, 1981), or differed between vole species (Batzli & Lesieutre, 1995*). Other studies did not find density effects (Forbes *et al.*, 2014*b**; Hambäck & Ekerholm, 1997*; Haapakoski *et al.*, 2012*), one of which also found no health effects from food. Food supplementation prevented a dramatic decline in density during winter, but unknown or no effect in late summer (Forbes *et al.*, 2015*; Huitu *et al.*, 2003*; Johnsen *et al.*, 2017). Other studies found a similar effect in concert with predation release (Huitu *et al.*, 2003*) or did not prevent a decline to low density (Krebs, 1966; Desy & Thompson, 1983).
Proportion of reproducing females/recruitment of young to the population/sex ratio	$\mathcal{N} = 8$	Food supplementation increased proportion of adults (Desy & Batzli, 1989*) or proportion of reproducing females or recruitment (Andrzejewski, 1975; Taitt & Krebs, 1981); others found varied/unclear effects (Ford & Pitelka, 1984*), increased female-biased sex ratio (Saitoh, 1989; Taitt & Krebs, 1983), no effect on sex-ratio (Desy & Batzli, 1989*; Forbes *et al.*, 2015*), increased population reproductive output (Saitoh, 1989), or elongated breeding season (Gilbert & Krebs, 1981; Saitoh, 1989).
Survival/persistence	$\mathcal{N} = 9$	Food supplementation increased survival indices (Huitu *et al.*, 2003*; Johnsen *et al.*, 2017; Schweiger & Boutin, 1995); in other studies effects unclear (Ford & Pitelka, 1984*; Yin *et al.*, 2017*) or no effects (Forbes *et al.*, 2014*b**; Forbes *et al.*, 2015*; Haapakoski *et al.*, 2012*; Gilbert & Krebs, 1981)

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Table 7. *(Cont.)*

(A) Individual measures (B_{iv})		
Population growth	$\mathcal{N} = 5$	Population growth rates higher in vole populations that received supplementary food compared to controls (Ford & Pitelka, 1984*; Forbes *et al.*, 2014*a**; Forbes *et al.*, 2014*b**; Forbes *et al.*, 2015*; Huitu *et al.*, 2003*).
Relationship between health measures and population growth rate	$\mathcal{N} = 1$	Condition index of voles, as well as blood levels of haematocrit, proteins, free fatty acids and immunoglobulin G, were positively related to population growth rate when populations were declining. When populations were increasing, these variables tended to be negatively related to population growth rate. Highest indices of physiological condition occurred when populations were stable or increasing slightly (Huitu *et al.*, 2007*).

The evidence base also included studies that contrasted high- and low-quality diets composed of different plant species or diets collected from different habitats (Table 5B). These studies are challenging to compare in detail, as their definitions of food quality and treatments, as well as measures of health, differ (Table 5B). Overall, they do provide support for high-quality diets being related to higher body mass and increased reproduction rates. Ingestion of toxic compounds was linked to signs of detoxification, but whether this can be caused by natural concentrations, whether such signs (e.g. renal lesions) are irreversible, and whether detoxification affects growth and reproduction cannot be synthesised from our evidence base.

(g) Reduced population growth (BCD$_v$)

The evidence base included only one study (Huitu *et al.*, 2007) which directly related rodent health to population growth (Table 7B). It showed that reduced vole individual condition was related to population growth rate, thus supporting the assumption. The remaining studies used supplemental feeding and were designed to measure the effects of increased food availability on rodent health and population trajectories. These studies mainly showed that food supplementation increased rodent health and population growth rate (or related variables), but several studies did not find a positive relationship with rodent health (Table 7B). However, all food supplementation studies that measured population growth rates did identify an increase, while results for other population-level variables were less consistent (Table 7B). Five studies related the effect of food supplements to population density during the population decline phase; while four of these found that supplementation resulted in a slower density decline, none measured widespread or long-lasting effects (Table 7B).

(h) Plant availability follows rodent density (BD$_{vi}$)

Most of the 72 studies assessing impacts of rodent herbivory on quantitative aspects of vegetation (BD$_i$) did not assess assumption BD$_{vi}$, despite covering multiple years (Table 2). Of those 20 studies that did, there was generally no support for a time lag, with relatively rapid plant recovery the following year (Table 4). Proper evaluation of this assumption is,

however, hampered by the limited number of studies, e.g. only three LR studies assessed this assumption over more than one rodent peak. We note that studies on lemmings in Fennoscandia (Tables 2 and 4) found reduced plant biomass and changed vegetation composition the year after rodent peak, but a study on a different lemming species from Canada did not replicate this result.

(i) Plant quality follows rodent density (C$_{vi}$)

For plant defences, three studies found no correlation with current year rodent density and total phenolics. Only one study (Jonasson *et al.*, 1986) assessed the propensity of phenolics to follow rodent density with a time lag, sample size thus being too low for synthesis. For all other plant defence compounds, a low number of studies (less than three studies, Table 5A) prevents synthesis of their co-variation with rodent population dynamics, including time lags.

For nutrients, protein/nitrogen showed no relationship with rodent abundance (Table 5A) in the current or previous year; for all other nutrients sample sizes are too small for synthesis. We found only one study that assessed the relationship between vegetation quality and rodent population dynamics across two or more population peaks (Table 2), and no consistent responses in plant quality (levels of phenolics) to rodent peaks.

V. DISCUSSION

This review aimed to assess evidence for the hypothesis that plant–rodent interactions could drive rodent population dynamics. Below, we discuss our findings and their implications for the four plant–rodent hypotheses presented in Fig. 1: inherent plant cycles (hypothesis A), food quantity (hypothesis B), quality of preferred foods (hypothesis C), and food quality due to dietary changes (hypothesis D). We then focus on the potential pathways to advance our understanding of plant–rodent interactions.

(1) Inherent plant cycles

The evidence base for the inherent plant cycles hypothesis was largely limited to correlative evidence between time

series of plants and rodent population measures, with more mechanistic studies scarce and scattered among study systems. The relationships between *Myodes* voles and ericoid berry production in boreal forests were studied in sufficient detail to allow synthesis. In this case, studies tested whether berry production is cyclical, and whether the dynamics of berries and voles were correlated. Most of these studies were from a single study region in Fennoscandia, where the dynamics of *Vaccinium myrtillus* berry crops and *Myodes glareolus* populations have been studied in detail (Selås, 1997, 2006, 2020; Selås, Kobro & Sonerud, 2013; Selås, Framstad & Spidso, 2002). Evidence from other parts of the boreal biome is scarce and less consistent (Krebs *et al.*, 2010; Tornberg, Helle & Korpimäki, 2011; Hansson, 1979; Boulanger-Lapointe *et al.*, 2017), with more diversified methodological approaches and ecological contexts needed for a more robust assessment of the potential of berry cycles to cause arvicoline cycles throughout the boreal biome.

Taken together, evidence for cycles of high-quality plant food availability acting as a cause of rodent population cycles throughout their spatial range still remains unclear. Several assumptions related to this hypothesis have never been tested. In particular, only a handful of studies have linked increased availability of presumed high-quality food items to actual ingestion of those foods (Janova, Heroldova & Cepelka, 2016) and consequently increased reproduction rates (but see Sullivan & Sullivan, 2014; Pinot, Gauffre & Bretagnolle, 2014). While there is no question that food quality does affect a range of aspects of herbivore health (e.g. Forbey *et al.*, 2018), we still require clear demonstrations of changes in diet quality in free-living rodents throughout population cycles. Such studies are needed to understand how rodent reproduction is related to available food quality, and to clarify processes underlying population growth rates. An interesting parallel is rodent population outbreaks that occur during/after seed masting in temperate trees. Such tree seeds represent good-quality food for sympatric granivorous rodents but not necessarily for herbivorous arvicoline rodents (Onodera *et al.*, 2017). The community-wide population peaks observed likely arise through effects on shared predators and represent an example of how increased food availability for some species can lead to a community-wide trophic cascade (Elias *et al.*, 2006; Šipoš *et al.*, 2017). However, clearly articulated hypotheses on how trophic cascades related to specific inherent plant food cycles (such as berries eaten by *Myodes* voles) could lead to synchronous cycles across the small rodent guild seem to be missing from the literature.

We propose that future empirical studies of the inherent plant cycles hypothesis should include: (*i*) assessments of whether individuals acquire a high-quality diet through ingestion of high-quality foods during the increase phase of population cycles; and (*ii*) in which regions these specific cycles in plant reproduction, such as cycles of ericoid berry production, are present. Ideally, the latter should be established by excluding rodents. Distinguishing inherent cycles in plants from those induced by rodents would allow assessment of the direction of causality.

(2) Food quantity

This hypothesis was the most frequently studied in our evidence base. We found that high-density populations of rodents can affect vegetation in various ways, reducing biomass, inflicting plant mortality, and changing vegetation composition. However, whether impacts of rodents on vegetation fluctuate with rodent cycles is less clear, as only some rodent–plant combinations show such patterns. The observed time lags of vegetation regeneration do not fit the typical 3–5-year period (Oksanen *et al.*, 2008) common in arvicoline population cycles. However, such long-term lags might not be detected if rodents depend on specific plant parts (e.g. floral shoots), or rare plant species (Hansson, 1987). Furthermore, the strength of plant–herbivore interactions can vary over time (Hansson, 1999), or between population cycles (Soininen *et al.*, 2018). We found no studies that assessed patterns of biomass for longer than 2 cycles, and only seven studies that contained 2 cycles. Thus, the evidence base is insufficient to assess the conditions or ecosystems in which quantitative effects of rodents persist – with a time lag – over several cycles.

Our evidence base also does not allow us to conclude whether diet composition throughout rodent cycles is constant, or whether a decrease in food availability translates to a decrease in the quantity of ingested food. These are prerequisites for rodents to be affected by reduced food quantity, as opposed to switching to alternative food sources when a preferred food becomes scarce. Several studies indicate that diet changes can occur (e.g. Gilbert *et al.*, 2013*a*; Bergeron & Jodoin, 1995). Arvicolines have diverse diets with substantial seasonal and spatial variation (Hjältén, Danell & Ericson, 1996; Soininen *et al.*, 2013*b*, 2017). This large variation makes it challenging to assess the value of specific food items, and thus complicates our interpretation of potential diet shifts during a population cycle. Furthermore, it implies that multiple population cycles should be studied to tease apart seasonal, spatial, and cycle-phase-dependent dietary variation.

Despite the absence of observational studies assessing variation in ingested food quantity across population cycles – admittedly methodologically difficult studies – inferences on the impacts of food availability on individual- and population-level variables can be gained from food supplementation studies. In our evidence base, such studies show relatively consistently that individual health and population growth improve with increasing food availability. However, some studies found no effects, or results that depended on e.g. food type, season, population density, or sex. Some of this variability may be explained by methodological issues: it can be challenging to supply food at a representative spatial and temporal scale (Boutin, 1990). In addition, some of the common metrics used to describe health, such as body mass and breeding status, are rather indirect proxies; reliable estimates of body condition may require the use of newer methods (Peig & Green, 2009). Furthermore, food availability can, in

addition to direct health effects, also modify vole reproductive behaviour (Pierce, Ferkin & Williams, 2005), predation risk (Ylönen *et al.*, 2002), and disease risk (Kusumoto, 2009), and the presence of such indirect effects could easily impact the results. Finally, we found no consistent evidence that food supplementation could prevent a population decline [but see Johnsen *et al.* (2017) for a study where this happened], in line with the conclusions of a previous narrative review (Oli, 2019). Such discrepancies among and between studies could also be interpreted to show that increased food availability can improve conditions for individual rodents, but that other factors override its importance in the control of population cycles.

Several publications note that rodent herbivory was more pronounced during the winter period when vegetation does not regenerate (e.g. Ashby, 1967; Howe & Brown, 2000). Some found effects during winter but not summer (Fey, Banks & Korpimäki, 2008; Hambäck *et al.*, 2004; Norrdahl & Korpimäki, 2002). Furthermore, food supplementation often had a stronger impact during winter than summer (Norrdahl & Korpimäki, 2002; Forbes *et al.*, 2015). Food is less available during the winter for arvicolines, as vegetation does not regenerate outside the growing season, rodent movements are limited by snow, and their feeding becomes concentrated in smaller areas (Kausrud *et al.*, 2008; Berteaux *et al.*, 2016; Korslund & Steen, 2006). Concurrently, cold temperatures increase their energetic requirements (Voltura & Wunder, 1998), making winter the season with highest potential for food availability to impact rodents. The snow-covered season in general represents a bottleneck of food availability for herbivores, and winter food availability can have large repercussions on herbivore population dynamics (Albon *et al.*, 2017; Gurnell, 1996). However, our evidence base provides little opportunity to assess seasonal variation, other than for the effects of rodent grazing on plants. In particular, relationships among seasonal herbivory, seasonal plant regrowth patterns and seasonal impacts of plants on rodents, as well as the relationships of these with multi-annual patterns or rodent cycles are far from clear. For example, do wintertime herbivory effects lead to a time lag of plant recovery during the next summer(s) or winter(s)? When and how do feedbacks from vegetation on rodents manifest?

Overall, several issues weaken the evidence for the hypothesis that overgrazing by rodents results in starvation and thereby to population cycles. In particular, the time lags in food-plant regeneration appear too short to explain arvicoline population cycles (May, 1973), and are inconsistent across habitats and regions. For instance, studies on lemmings in Fennoscandia found reduced plant biomass and altered vegetation composition the year after a rodent population peak (Kalela & Koponen, 1971; Moen, Lundberg & Oksanen, 1993*b*), but a study on a different lemming species in Canada did not find the same patterns (Bilodeau *et al.*, 2014). Furthermore, one important assumption of this hypothesis remains unexplored: there are no studies assessing how quantitative ingestion of food varies between cycle phases, if at all. Overgrazing by vertebrate herbivores has mainly been related to introduced populations or populations that are maintained at high densities through management (Mysterud, 2006). Indeed, overgrazing of winter foods is rarely observed for snowshoe hares (*Lepus americanus*), even though its potential role in population cycles of this species has been investigated (Krebs, Boonstra & Boutin, 2018; Krebs *et al.*, 1986). It is likely that regeneration times of different functional groups of plants will be an important determinant of whether overgrazing leads to a population crash (Crawley *et al.*, 2021). Clearly, links between herbivore overgrazing and population crashes are not straightforward; even when overgrazing is observed, it does not necessarily cause population cycles.

We propose that to assess whether interactions with food quantity can cause arvicoline population cycles, future empirical studies could target: (*i*) variation in quantitative ingestion of food in natural populations; (*ii*) potential dietary switches rendering the quantity of main food items less important; and (*iii*) seasonal variation (e.g. shorter growing season, lower summer reproduction *sensu* Reynolds *et al.*, 2013), in particular with a focus on food quantity during the winter.

(3) Quality of preferred foods

Studies addressing this hypothesis focussed mainly on two plant defence compounds: silicates (e.g. Ruffino *et al.*, 2018) and phenolics (e.g. Huitu *et al.*, 2014). The evidence suggests that concentrations of these compounds can increase due to rodent herbivory, but too few studies are available to assess the ecological contexts in which such induction takes place. Evidence relating to a reduced availability of nutrients (e.g. Agrell *et al.*, 1995) as a factor contributing to interaction cycles was sparse. The few studies assessing this hypothesis did not provide consistent evidence that rodent herbivory reduces plant nutritional quality. Whether reduced plant quality, either as a defence or in terms of nutrient content, follows rodent cycles with a time lag was assessed by a very limited number of studies that provided no support for this pattern. This could either indicate that small-rodent herbivory does not induce long-lasting reductions in plant quality, or that the relevant compounds and/or food plants have not been investigated. Studies that assessed the composition and quality of ingested diets throughout a population cycle were rare and identified no consistent patterns, while studies that assessed health effects of food quality were scattered across a range of compounds. Still, the negative health effects of silica and phenolics, and the argument that improved food quality will improve rodent health, both were supported by our evidence base. Finally, evidence from food-supplementation experiments supports the suggestion that reduced individual health will affect population growth rates negatively.

Taken together, we identified no consistent reductions in food quality that could be related to rodent population cycles or to increased herbivory by rodents. However, given the complex chemistry of plants and the interactions between ingested compounds (DeGabriel *et al.*, 2014; Kaspari, 2021; Burkepile & Parker, 2017; McArthur *et al.*, 2014), the

possibility that relevant aspects of plant chemistry have yet to be identified and assessed appears almost endless. For instance, phenolics are a diverse group of chemicals with a range of effects on rodents (Lindroth & Batzli, 1984), and the analysis of 'total phenolics' could easily mask opposing effects of rodent herbivory on different phenolic compounds. New methods allowing analysis of specific compounds and larger numbers of samples will provide powerful tools to explore variation in plant and diet chemistry across herbivore 'foodscapes' (Windley & Foley, 2015; Jean *et al.*, 2015; Petit Bon *et al.*, 2020*a*). Combining analyses of several nutrients through geometric or stoichiometric frameworks could also enable better assessments of their combined effects (Raubenheimer, Simpson & Mayntz, 2009; Elser, 2006). Addressing integrated qualitative changes in rodent food plants at a grain size relevant to foraging, across a spatial extent relevant to population dynamics, and across the time span necessary to uncover delayed effects will undoubtedly provide new insights on many aspects of plant–rodent interactions. However, this is unlikely to be the most fruitful approach to reducing the number of hypotheses that could explain rodent population cycles.

The probability of ingesting health-reducing amounts of a given plant defence hinges on the taxonomic and chemical diversity of the available vegetation and diet. If rodents can compensate for reduced quality of their main food items by dietary switching to other available foods, they are likely to do so, given that they are known to be flexible in selecting foods (Underwood, 1999; Huitu *et al.*, 2014). Whether a taxonomic switch of diet is equivalent to a qualitative switch is, however, not clear, as herbivores may select their diet based on phytochemical quality rather than taxonomic composition (Felton *et al.*, 2021; Hecker, Edwards & Nielsen, 2021). Furthermore, we note that even for specialised herbivores that feed on a narrow range of food items, such as forest lepidopterans, a link between herbivore-induced plant quality changes and population cycles may not be present (Myers & Cory, 2013). The challenges that complex diets present to linking plant defence compounds to mammal population dynamics are also known from other wild herbivores (Hartley & DeGabriel, 2016). Although some studies find such links, the general support for plant defences regulating herbivore populations is variable or limited (Myers, 2018; DeGabriel *et al.*, 2014; Fowler & Lawton, 1985; Karban & Baldwin, 2007). As our knowledge of dietary quality variation of arvicoline rodents across their population cycles remains very limited, we propose that to assess whether cycles are created by the quality of preferred food plants, future studies should target variability in diet composition and especially quality across population cycles.

(4) Food quality due to dietary changes

Evidence for the assumptions related to this variant of the interaction cycles hypothesis was summarised above (see Sections V.2 and V.3). Regarding this hypothesis, it appears that the effects of arvicoline rodents on food quantity

appear particularly prevalent during the winter. Yet, to what extent seasonal changes in biomass of preferred vegetation cause changes in rodent diet composition and quality is not evident from our evidence base, as most studies of diet compositional differences between cycle phases focussed on summer diets. We also found that among the studies that assessed diet quality or health impacts of low-quality food, very few targeted compounds could be expected to result from a dietary shift, such as toxins present in *Empetrum nigrum* (Plesner Jensen & Doncaster, 1999) or constituent defences of woody plants (see e.g. Harju & Tahvanainen, 1994). This prevents us from drawing general conclusions on the prevalence of such compounds in diets and whether, at realistic concentrations, they can reduce individual condition. We note, however, that plant phenolics, discussed in Section IV.3.*b*, include constitutive defence compounds. However, as the evidence base related to these was very sparse, we cannot confidently conclude that ingestion of phenolic compounds is related to population cycles. While switching to poorer quality food plants in times of scarcity has been observed in other herbivores (Vogel *et al.*, 2020; Hecker *et al.*, 2021), the links between individual-level foraging behaviour and population dynamics are, in general, poorly understood for herbivores [but see DeGabriel *et al.* (2009) for an example of spatial configuration of food quality]. To assess this hypothesis empirically, we propose that future studies focus on rodent feeding ecology during the winter. In particular, assessing the prevalence of dietary switches across population cycle phases in terms of dietary composition and ingestion of targeted quality components would be informative.

VI. FUTURE DIRECTIONS

Our evidence base covered a wide range of rodent species, plant species, and suggested specific characteristics of plants that could affect rodents (ranging from specific compounds to plant reproduction). Yet, the lack of replicate studies addressing the same assumptions with identical response and predictor variables challenges synthesis of many of the findings. Thus, the current knowledge is insufficient to discard 'the plant hypothesis' or even to assess the ecological contexts in which some of the specific interactions may take place. For example, the evidence base was highly biased towards forested regions and voles, with few studies on tundra and lemmings. This was surprising, as cyclic populations in lemmings have repeatedly been hypothesised to result from a plant quantity interaction (Turchin *et al.*, 2000; Oksanen *et al.*, 2008). However, simply replicating studies on all topics and contexts where such studies appear to be lacking is unlikely to be the most fruitful path forward. Rather, we argue that a structured assessment of quantitative assumptions will enable us to develop consensus on the feasibility of different hypotheses.

In this review, we focused on the empirical evidence related to plant–rodent cycles. However, we could only

outline the different hypotheses qualitatively, without any quantitative analyses. This means that we were unable to establish when studies provide evidence for an effect of sufficient magnitude to be a likely cause of population cycles. Deducing quantitative relationships for plant–rodent cycles is challenging, as the chains of assumptions result in complex processes characterised by delayed density dependence, rodent cycles take place in highly seasonal environments, and rodents have complex multivoltine season-specific life histories. The best tools for this are, therefore, theoretical analyses or models, but these have been applied to different hypotheses – and specific cases of plant–rodent interactions – to different degrees. For instance, no theoretical analyses have been carried out on the inherent cycles hypothesis, while plant quantity interactions (Turchin & Batzli, 2001) and plant quality interactions due to decreased quality of preferred foods (Reynolds *et al.*, 2012) have been shown to lead to realistic cycles under specific assumptions. We therefore highlight theoretical analyses, and comparisons of the existing empirical evidence with the results of theoretical analyses, as a major focus of future research. Such analyses should progress through several steps, with each step having potential to reduce the number of feasible hypotheses. First, can theoretical models of specific hypotheses produce realistic cycles in terms of length and shape? Second, are the deduced quantitative assumptions, such as effect sizes, time lags, and functional forms, also realistic? Third, how does the current evidence align with those quantitative assumptions? To obtain suitable data to test the predictions from theoretical models, and based on our findings in this review, we summarise the key empirical gaps below.

The most important empirical gap is knowledge of rodent diets – the hypothesised plant–rodent cycles outlined in Fig. 1 currently rely on untested assumptions of changes in composition and/or quality of diets. For instance, studies on plant–rodent interactions focusing on quality of preferred food items often assume that the diet is dominated by that plant species [e.g. *Vaccinium myrtillus* in Selås (2020) and *Deschampsia caespitosa* in Massey *et al.* (2008)], but this assumption is rarely confirmed. Furthermore, the presence – or lack of – dietary shifts is a shared assumption for all plant–rodent hypotheses, but the prevalence of such shifts is currently unclear. Until recent advances in high-throughput sequencing, diet analyses have had coarse taxonomic resolution and temporal limitations, despite known seasonal dependence (e.g. Schweiger & Boutin, 1995). Indeed, improving knowledge on dietary variation has been highlighted as a general issue to advance understanding on how plants affect herbivore population dynamics (DeGabriel *et al.*, 2014). Thus, assessing whether rodent diets have population cycle phase-dependent variation and whether such variation corresponds to the predicted patterns will shed light on the degree of coupling between rodent dynamics and the dynamics of important dietary items.

Our evidence base demonstrates that the impact of rodent herbivory on vegetation may be stronger in winter (i.e. the period with no or limited plant regeneration) than in summer. Still, very few studies include data from winter or address seasonal patterns. For instance, we know little about

variation in diet composition and quality between winters (but see Bergeron, 1996). Below-snow ecology of rodents is poorly understood in general, as suitable methodologies have been lacking (Krebs, 2013; Ehrich *et al.*, 2020). New approaches include below-snow camera trapping (Mölle *et al.*, 2021) and non-invasive diet analyses from faeces, both in terms of diet taxonomic composition (Soininen *et al.*, 2015*a*; Lopes *et al.*, 2020) and nutritional quality (Čepelka *et al.*, 2021). However, new molecular methods may be less informative than traditional methods for some aspects of diet, such as dietary restriction to particular plant organs (Batzli & Henttonen, 1990). Below-snow studies of individual condition, life-history traits, and food availability are likely to remain challenging until new methods become available. A better understanding of winter rodent–plant interactions may also help us to understand the impacts of changing climate on rodents, as shorter winters imply longer growing seasons of plants and thus improved access to food (Schmidt *et al.*, 2018), whereas changes in the snowpack structure can have an opposite effect (Berteaux *et al.*, 2016). We recommend that future work should focus on the quantitative aspects of seasonal variation, explicitly considering when in the seasonal cycle food characteristics may affect rodent demography and how the seasonal and multi-annual patterns in rodent herbivory, plant recovery, and plant impacts on rodents are expected to interact.

Given a history of long-term studies of rodent population dynamics (Ehrich *et al.*, 2020; Krebs, 2013), our evidence base included surprisingly few studies that assessed plant–rodent interactions across several cycles. For instance, we were unable to assess whether there are time lags in plant quality responses to rodent herbivory, and no studies assessed phase-dependent diets for longer than one population cycle. Yet, the strength of plant–rodent interactions can differ between population cycles (Soininen *et al.*, 2018), and understanding the extent of such variation would enable assessments of plant–rodent interactions to be more robust. In parallel, our evidence base was dominated by studies that did not consider the spatial structure of vegetation or population dynamics. The spatial structure of available food quality is known to influence mammalian herbivore feeding ecology with repercussions on reproductive output (DeGabriel *et al.*, 2014). Nutrient analyses at herbivore-relevant spatial scales are increasingly feasible (Windley & Foley, 2015; Jean *et al.*, 2015; Petit Bon *et al.*, 2020*b*) and could elucidate whether variability in plant chemistry corresponds to spatial and temporal extents with contrasting rodent population densities/dynamics. We propose that future empirical studies on plant–rodent interactions aim to incorporate relevant timescales (e.g. through long-term studies of both rodents and plants) and spatial structure of vegetation (e.g. through measurements at rodent-relevant spatial extents and resolution).

VII. CONCLUSIONS

(1) The food hypothesis as an explanation for population cycles in rodents has many variants, and the continued

addition of new hypotheses seems counter-productive for scientific consensus. Rather, time should be spent on reduction/falsification of existing explanations.

(2) The literature is currently insufficient to reject any of the four potential pathways for the creation of plant–rodent cycles discussed herein. This is largely due to a lack of replicate studies addressing the same question across different localities and multiple rodent population cycles, preventing synthesis of assumptions.

(3) For most specific plant–rodent contexts there are no theoretical/mathematical analyses available that identify quantitative assumptions to be tested. Even where they exist, the empirical literature rarely uses them as bases for explicit predictions. A key path forward is therefore to create quantitative assumptions through theoretical studies, compare them with existing empirical data, and use them as guideline to determine which empirical studies to conduct.

(4) There are insufficient data available to test many of the key assumptions of the plant–rodent cycle hypotheses. Key empirical gaps that we identified relate to rodent diets and seasonality, as all identified hypotheses make explicit assumptions on how rodent diet taxonomic and nutritional composition will change across the cycle. Addressing dietary changes especially during the snow-cover season would be valuable, as our evidence base indicates that this may be a key period of food limitation and is the season for which there has been the least empirical study. Passing these bottlenecks could help pinpoint where, when, and how plant–herbivore interactions are (or are not) a plausible cause of rodent population dynamics.

VIII. ACKNOWLEDGEMENTS

IX. REFERENCES

References identified with an asterisk (*) were included in our systematic synthesis.

*Agrell, J., Erlinge, S., Nelson, J., Nilsson, C. & Persson, I. (1995). Delayed density-dependence in a small-rodent population. *Proceedings of the Royal Society of London series B: Biological Sciences* **262**(1363), 65–70.

Albon, S. D., Irvine, R. J., Halvorsen, O., Langvatn, R., Loe, L. E., Ropstad, E., Veiberg, V., Van Der Wal, R., Bjorkvoll, E. M., Duff, E. I., Hansen, B. B., Lee, A. M., Tveraa, T. & Stien, A. (2017). Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. *Global Change Biology* **23**(4), 1374–1389.

*Andersson, M. & Jonasson, S. (1986). Rodent cycles in relation to food resources on an alpine heath. *Oikos* **46**(1), 93–106.

*Andreassen, H. P. & Ims, R. A. (1990). Responses of female grey-sided voles *Clethrionomys rufocanus* to malnutrition: a combined laboratory and field experiment. *Oikos* **59**(1), 107–114.

Andreassen, H. P., Sundell, J., Ecke, F., Halle, S., Haapakoski, M., Henttonen, H., Huitu, O., Jacob, J., Johnsen, K., Koskela, E., Luque-Larena, J. J., Lecomte, N., Leirs, H., Marien, J., Neby, M., et al. (2021). Population cycles and outbreaks of small rodents: ten essential questions we still need to solve. *Oecologia* **195**(3), 601–622.

*Andrzejewski, R. (1975). Supplementary food and the winter dynamics of bank vole populations. *Acta Theriologica* **20**(1–14), 23–40.

*Ashby, K. R. (1967). Studies on ecology of field mice and voles (*Apodemus sylvaticus*, *Clethrionomys glareolus* and *Microtus agrestis*) in Houghall Woods, Durham. *Journal of Zoology* **152**, 389–513.

Barraquand, F., Louca, S., Abbott, K. C., Cobbold, C. A., Cordoleani, F., DeAngelis, D. L., Elderd, B. D., Fox, J. W., Greenwood, P., Hilker, F. M., Murray, D. L., Stieha, C. R., Taylor, R. A., Vitense, K., Wolkowicz, G. S. K. & Tyson, R. C. (2017). Moving forward in circles: challenges and opportunities in modelling population cycles. *Ecology Letters* **20**(8), 1074–1092.

*Batzli, G. O. (1986). Nutritional ecology of the California vole: effects of food quality on reproduction. *Ecology* **67**(2), 406–412.

Batzli, G. O. & Henttonen, H. (1990). Demography and resource use by microtine rodents near Toolik Lake, Alaska, U.S.A. *Arctic and Alpine Research* **22**(1), 51–64.

*Batzli, G. O. & Lesieutre, C. (1995). Community organization of arvicoline rodents in northern Alaska. *Oikos* **72**(1), 88–98.

*Batzli, G. O. & Pitelka, F. A. (1970). Influence of meadow mouse populations on California grassland. *Ecology* **51**(6), 1027–1039.

*Batzli, G. O. & Pitelka, F. A. (1971). Condition and diet of cycling populations of the California vole, *Microtus californicus*. *Journal of Mammalogy* **52**(1), 141–163.

*Batzli, G. O. & Pitelka, F. A. (1975). Vole cycles: test of another hypothesis. *American Naturalist* **109**(968), 482–487.

Batzli, G. O., White, R. G., MacLean, S. F., Pitelka, F. A. & Collier, B. D. (1980). The herbivore- based trophic system. In *An Arctic Ecosystem – the Coastal Tundra at Barrow, Alaska* (eds J. Brown, P. C. Miller, L. L. Tieszen and F. L. Bunnell), p. 571. Dowden, Hutchinson & Ross, Stroudsburg, PA.

*Berg, T. B. (2003). Catechin content and consumption ratio of the collared lemming. *Oecologia* **135**(2), 242–249.

*Bergeron, J.-M. (1996). Chemical constituents of vole feces as indicators of bark use in sapling plantations. *Annales Zoologici Fennici* **33**(2), 249–257.

*Bergeron, J.-M. (1997). Changes in habitat and in quality of food intake after a summer of grazing by fenced voles (*Microtus pennsylvanicus*). *Annales Zoologici Fennici* **34**(2), 105–113.

*Bergeron, J. M. & Jodoin, L. (1989). Patterns of resource use, food quality, and health status of voles (*Microtus pennsylvanicus*) trapped from fluctuating populations. *Oecologia* **79**(3), 306–314.

*Bergeron, J. M. & Jodoin, L. (1993). Intense grazing by voles (*Microtus pennsylvanicus*) and its effect on habitat quality. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **71**(9), 1823–1830.

*Bergeron, J. M. & Jodoin, L. (1995). Winter use of food by fenced voles (*Microtus pennsylvanicus*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **73**(5), 907–915.

*Bergeron, J. M., Jodoin, L. & Jean, Y. (1987). Pathology of voles (*Microtus pennsylvanicus*) fed with plant extracts. *Journal of Mammalogy* **68**(1), 73–79.

Berryman, A. A. (2002). *Population Cycles: The Case of Trophic Interactions*. Oxford University Press, Oxford.

Berteaux, D., Gauthier, G., Domine, F., Ims, R. A., Lamoureux, S. F., Lévesque, E. & Yoccoz, N. (2016). Effects of changing permafrost and snow conditions on tundra wildlife: critical places and times. *Arctic Science* **3**(2), 65–90.

*Bilodeau, F., Gauthier, G., Fauteux, D. & Berteaux, D. (2014). Does lemming winter grazing impact vegetation in the Canadian Arctic? *Polar Biology* **37**(6), 845–857.

Boonstra, R., Andreassen, H. P., Boutin, S., Husek, J., Ims, R. A., Krebs, C. J., Skarpe, C. & Wabakken, P. (2016). Why do the boreal forest ecosystems of northwestern Europe differ from those of western North America? *Bioscience* **66**(9), 722–734.

*Boulanger-Lapointe, N., Järvinen, A., Partanen, R. & Herrmann, T. M. (2017). Climate and herbivore influence on *Vaccinium myrtillus* over the last 40 years in Northwest Lapland, Finland. *Ecosphere* **8**(1), e01654.

Boutin, S. (1990). Food supplementation experiments with terrestrial vertebrates – patterns, problems, and the future. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **68**(2), 203–220.

*Bråthen, K. A., Agrell, J., Berteaux, D. & Jónsdoottir, I. S. (2004). Intraclonal variation in defence substances and palatability: a study on *Carex* and lemmings. *Oikos* **105**, 461–470.

Burkepile, D. E. & Parker, J. D. (2017). Recent advances in plant-herbivore interactions. *F1000Research* **6**, 119.

*Calandra, I., Zub, K., Szafranska, P. A., Zalewski, A. & Merceron, G. (2016). Silicon-based plant defences, tooth wear and voles. *Journal of Experimental Biology* **219**(4), 501–507.

Callaghan, T. V., Cazzolla Gatti, R. & Phoenix, G. (2021). The need to understand the stability of Arctic vegetation during rapid climate change: an assessment of imbalance in the literature. *Ambio* **51**, 1034–1044.

Cepelka, L., Jánová, E., Suchomel, J. & Heroldová, M. (2021). Use of NIRS in wild rodents' research: a review of timid beginnings. *Remote Sensing* **13**(16), 3268.

*Chitty, D., Pimentel, D. & Krebs, C. J. (1968). Food supply of overwintered voles. *Journal of Animal Ecology* **37**(1), 113–120.

*Cole, F. R. & Batzli, G. O. (1978). Influence of supplemental feeding on a vole population. *Journal of Mammalogy* **59**(4), 809–819.

*Cole, F. R. & Batzli, G. O. (1979). Nutrition and population dynamics of the prairie vole, *Microtus ochrogaster*, in Central Illinois. *Journal of Animal Ecology* **48**(2), 455–470.

Collaboration for Environmental Evidence (2013). Guidelines for systematic review and evidence synthesis in environmental management. Version 4.2.

Cornulier, T., Yoccoz, N. G., Bretagnolle, V., Brommer, J. E., Butet, A., Ecke, F., Elston, D. A., Framstad, E., Henttonen, H., Hörnfeldt, B., Huitu, O., Imholt, C., Ims, R. A., Jacob, J., Jedrzejewska, B., et al. (2013). Europe-wide dampening of population cycles in keystone herbivores. *Science* **340**(6128), 63–66.

Crawley, M. J., Pakeman, R. J., Albon, S. D., Pilkington, J. G., Stevenson, I. R., Morrissey, M. B., Jones, O. R., Allan, E., Bento, A. I., Hipperson, H., Asefa, G. & Pemberton, J. M. (2021). The dynamics of vegetation grazed by a food-limited population of Soay sheep on St Kilda. *Journal of Ecology* **109**(12), 3988–4006.

Crozier, A., Jaganath, I. B. & Clifford, M. N. (2006). Phenols, polyphenols and tannins: an overview. In *Plant Secondary Metabolites: Occurrence, Structure and Role in the Human Diet* (Volume **1**), pp. 1–25. Blackwell Pub., Oxford.

*Dahlgren, J., Oksanen, L., Oksanen, T., Olofsson, J., Hambäck, P. A. & Lindgren, A. (2009a). Plant defences to no avail? Responses of plants of varying edibility to food web manipulations in a low arctic scrubland. *Evolutionary Ecology Research* **11**(8), 1189–1203.

*Dahlgren, J., Oksanen, L., Olofsson, J. & Oksanen, T. (2009b). Plant defences at no cost? The recovery of tundra scrubland following heavy grazing by grey–sided voles, *Myodes rufocanus*. *Evolutionary Ecology Research* **11**(8), 1205–1216.

*Dahlgren, J., Oksanen, L., Sjodin, M. & Olofsson, J. (2007). Interactions between gray-sided voles (*Clethrionomys rufucanus*) and bilberry (*Vaccinium myrtillus*), their main winter food plant. *Oecologia* **152**(3), 525–532.

DeGabriel, J. L., Moore, B. D., Felton, A. M., Ganzhorn, J. U., Stolter, C., Wallis, I. R., Johnson, C. N. & Foley, W. J. (2014). Translating nutritional ecology from the laboratory to the field: milestones in linking plant chemistry to population regulation in mammalian browsers. *Oikos* **123**(3), 298–308.

DeGabriel, J. L., Moore, B. D., Foley, W. J. & Johnson, C. N. (2009). The effects of plant defensive chemistry on nutrient availability predict reproductive success in a mammal. *Ecology* **90**(3), 711–719.

*Desy, E. A. & Batzli, G. O. (1989). Effects of food availability and predation on prairie vole demography: a field experiment. *Ecology* **70**(2), 411–421.

*Desy, E. A. & Thompson, C. F. (1983). Effects of supplemental food on a *Microtus pennsylvanicus* population in Central Illinois. *Journal of Animal Ecology* **52**(1), 127–140.

*Eccard, J. A. & Ylönen, H. (2001). Initiation of breeding after winter in bank voles: effects of food and population density. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **79**(10), 1743–1753.

Ehrich, D., Schmidt, N. M., Gauthier, G., Alisauskas, R., Angerbjörn, A., Clark, K., Ecke, F., Eide, N. E., Framstad, E., Frandsen, J., Franke, A., Gilg, O., Giroux, M. A., Henttonen, H., Hörnfeldt, B., et al. (2020). Documenting lemming population change in the Arctic: can we detect trends? *Ambio* **49**(3), 786–800.

Elias, S. P., Witham, J. W. & Hunter, J. M. L. (2006). A cyclic red-backed vole (*Clethrionomys gapperi*) population and seedfall over 22 years in Maine. *Journal of Mammalogy* **87**(3), 440–445.

*Elmqvist, T., Ericson, L., Danell, K. & Salomonson, A. (1988). Latitudinal sex-ratio variation in willows, *Salix* spp, and gradients in vole herbivory. *Oikos* **51**(3), 259–266.

Elser, J. (2006). Biological stoichiometry: a chemical bridge between ecosystem ecology and evolutionary biology. *The American Naturalist* **168**(S6), S25–S35.

Elton, C. S. (1924). Periodic fluctuations in the numbers of animals: their causes and effects. *Journal of Experimental Biology* **2**(1), 119–163.

*Ericson, L., Elmqvist, T., Jakobsson, K., Danell, K. & Salomonson, A. (1992). Age structure of boreal willows and fluctuations in herbivore populations. *Proceedings of the Royal Society of Edinburgh Section B: Biological Sciences* **98**, 75–89.

*Ericson, L. & Oksanen, L. (1987). The impact of controlled grazing by *Clethrionomys rufocanus* on experimental guilds of boreal forest floor herbs. *Oikos* **50**(3), 403–416.

*Erlinge, S., Hasselquist, D., Hogstedt, G., Seldal, T., Frodin, P. & Svensson, M. (2011). Lemming-food plant interactions, density effects, and cyclic dynamics on the Siberian tundra. *Arctic* **64**(4), 421–428.

Fauchald, P., Park, T., Tømmervik, H., Myneni, R. & Hausner, V. H. (2017). Arctic greening from warming promotes declines in caribou populations. *Science Advances* **3**(4), e1601365.

Felton, A. M., Wam, H. K., Felton, A., Simpson, S. J., Stolter, C., Hedwall, P. O., Malmsten, J., Eriksson, T., Tigabo, M. & Raubenheimer, D. (2021). Macronutrient balancing in free-ranging populations of moose. *Ecology and Evolution* **11**(16), 11223–11240.

*Fey, K., Banks, P. B. & Korpimäki, E. (2008). Voles on small islands: effects of food limitation and alien predation. *Oecologia* **157**(3), 419–428.

*Forbes, K. M., Henttonen, H., Hirvelä-Koski, V., Kipar, A., Mappes, T., Stuart, P. & Huitu, O. (2015). Food provisioning alters infection dynamics in populations of a wild rodent. *Proceedings of the Royal Society B: Biological Sciences* **282**(1816), 20151939.

*Forbes, K. M., Stuart, P., Mappes, T., Henttonen, H. & Huitu, O. (2014a). Food resources and intestinal parasites as limiting factors for boreal vole populations during winter. *Ecology* **95**(11), 3139–3148.

*Forbes, K. M., Stuart, P., Mappes, T., Hoset, K. S., Henttonen, H. & Huitu, O. (2014b). Diet quality limits summer growth of field vole populations. *PLoS One* **9**(3), e91113.

Forbey, J. S., Liu, R., Caughlin, T. T., Matocq, M. D., Vucetich, J. A., Kohl, K. D., Dearing, M. D. & Felton, A. M. (2018). Review: using physiologically based models to predict population responses to phytochemicals by wild vertebrate herbivores. *Animal* **12**(s2), s383–s398.

*Ford, R. G. & Pitelka, F. A. (1984). Resource limitation in populations of the California vole. *Ecology* **65**(1), 122–136.

*Fortier, G. M., Bard, N., Jansen, M. & Clay, K. (2000). Effects of tall fescue endophyte infection and population density on growth and reproduction in prairie voles. *Journal of Wildlife Management* **64**(1), 122–128.

Fowler, S. V. & Lawton, J. H. (1985). Rapidly induced defenses and talking trees: the devil's advocate position. *The American Naturalist* **126**(2), 181–195.

*Fox, J. F. (1985). Plant diversity in relation to plant production and disturbance by voles in Alaskan tundra communities. *Arctic and Alpine Research* **17**(2), 199–204.

Freeland, W. J. (1974). Vole cycles: another hypothesis. *The American Naturalist* **108**(960), 238–245.

Fufachev, I. A., Ehrich, D., Sokolova, N. A., Sokolov, V. A. & Sokolov, A. A. (2019). Flexibility in a changing arctic food web: can rough-legged buzzards cope with changing small rodent communities? *Global Change Biology* **25**(11), 3669–3679.

Gauthier, G., Bety, J., Cadieux, M. C., Legagneux, P., Doiron, M., Chevallier, C., Lai, S., Tarroux, A. & Berteaux, D. (2013). Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra. *Philosophical Transactions of the Royal Society B-Biological Sciences* **368**(1624), 20120482.

*Gilbert, B. S. & Krebs, C. J. (1981). Effects of extra food on *Peromyscus* and *Clethrionomys* populations in the southern Yukon. *Oecologia* **51**(3), 326–331.

Gilbert, S., Martel, J., Klemola, T. & Norrdahl, K. (2013a). Increasing vole numbers cause more lethal damage to saplings in tree monocultures than in mixed stands. *Basic and Applied Ecology* **14**(1), 12–19.

*Gilbert, S., Norrdahl, K., Martel, J. & Klemola, T. (2013b). Vole damage to woody plants reflects cumulative rather than peak herbivory pressure. *Annales Zoologici Fennici* **50**(4), 189–199.

Gilg, O., Hanski, I. & Sittler, B. (2003). Cyclic dynamics in a simple vertebrate predator-prey community. *Science* **302**(5646), 866–868.

*Grellmann, D. (2002). Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. *Oikos* **98**(2), 190–204.

Gurnell, J. (1996). The effects of food availability and winter weather on the dynamics of a grey squirrel population in southern England. *Journal of Applied Ecology* **33**(2), 325–338.

*Haapakoski, M., Sundell, J. & Ylönen, H. (2012). Predation risk and food: opposite effects on overwintering survival and onset of breeding in a boreal rodent. *Journal of Animal Ecology* **81**(6), 1183–1192.

*Haapakoski, M. & Ylönen, H. (2013). Snow evens fragmentation effects and food determines overwintering success in ground-dwelling voles. *Ecological Research* **28**(2), 307–315.

Haddaway, N. R., Macura, B., Whaley, P. & Pullin, A. S. (2018). ROSES RepOrting standards for systematic evidence syntheses: pro forma, flow-diagram and descriptive summary of the plan and conduct of environmental systematic reviews and systematic maps. *Environmental Evidence* **7**(1), 7.

*Hambäck, P. A. & Ekerholm, P. (1997). Mechanisms of apparent competition in seasonal environments: an example with vole herbivory. *Oikos* **80**(2), 276–288.

*Hambäck, P. A., Grellmann, D. & Hjältén, J. (2002). Winter herbivory by voles during a population peak: the importance of plant quality. *Ecography* **25**(1), 74–80.

*Hambäck, P. A., Oksanen, L., Ekerholm, P., Lindgren, A., Oksanen, T. & Schneider, M. (2004). Predators indirectly protect tundra plants by reducing herbivore abundance. *Oikos* **106**(1), 85–92.

Hanski, I., Henttonen, H., Korpimäki, E., Oksanen, L. & Turchin, P. (2001). Small-rodent dynamics and predation. *Ecology* **82**(6), 1505–1520.

*Hansson, L. (1969). Spring populations of small mammals in central Swedish Lapland in 1964–68. *Oikos* **20**(2), 431–450.

*Hansson, L. (1979). Food as a limiting factor for small rodent numbers. *Oecologia* **37**(3), 297–314.

*Hansson, L. (1986). Bark consumption of voles in relation to snow cover, population density and grazing impact. *Ecography* **9**(4), 312–316.

Hansson, L. (1987). An interpretation of rodent dynamics as due to trophic interactions. *Oikos* **50**, 308–318.

*Hansson, L. (1988). Grazing impact by small rodents in a steep cyclicity gradient. *Oikos* **51**(1), 31–42.

*Hansson, L. (1999). Intraspecific variation in dynamics: small rodents between food and predation in changing landscapes. *Oikos* **86**(1), 159–169.

*Hansson, L. (2002*a*). Dynamics and trophic interactions of small rodents: landscape or regional effects on spatial variation? *Oecologia* **130**(2), 259–266.

*Hansson, L. (2002*b*). Consumption of bark and seeds by voles in relation to habitat and landscape structure. *Scandinavian Journal of Forest Research* **17**(1), 28–34.

*Hansson, L. & Larsson, T.-B. (1978). Vole diet on experimentally managed reforestation areas in northern Sweden. *Ecography* **1**(1), 16–26.

*Harju, A. & Tahvanainen, J. (1994). The effect of silver birch (*Betula pendula*) powder on physiological performance of field voles (*Microtus agrestis*). *Annales Zoologici Fennici* **31**(2), 229–234.

Hartley, S. E. & DeGabriel, J. L. (2016). The ecology of herbivore-induced silicon defences in grasses. *Functional Ecology* **30**(8), 1311–1322.

Haukioja, E. & Hakala, T. (1975). Herbivore cycles and periodic outbreaks. Formulation of a general hypothesis. *Reports from the Kevo Subarctic Research Station* **12**, 1–9.

Haukioja, E., Kapiainen, K., Niemelä, P. & Tuomi, J. (1983). Plant availability hypothesis and other explanations of herbivore cycles – complementary or exclusive alternatives. *Oikos* **40**(3), 419–432.

Hecker, L. J., Edwards, M. A. & Nielsen, S. E. (2021). Assessing the nutritional consequences of switching foraging behavior in wood bison. *Ecology and Evolution* **11**(22), 16165–16176.

*Heroldová, M., Bryja, J., Janova, E., Suchomel, J. & Homolka, M. (2012). Rodent damage to natural and replanted mountain forest regeneration. *Scientific World Journal* **2012**, 872536. https://doi.org/10.1100/2012/872536.

Hjältén, J., Danell, K. & Ericson, L. (1996). Food selection by two vole species in relation to plant growth strategies and plant chemistry. *Oikos* **76**(1), 181.

*Hörnfeldt, B., Löfgren, O. & Carlsson, B. G. (1986). Cycles in voles and small game in relation to variations in plant production indices in Northern Sweden. *Oecologia* **68**(4), 496–502.

*Hoset, K. S., Kyro, K., Oksanen, T., Oksanen, L. & Olofsson, J. (2014). Spatial variation in vegetation damage relative to primary productivity, small rodent abundance and predation. *Ecography* **37**(9), 894–901.

*Hoset, K. S., Ruffino, L., Tuomi, M., Oksanen, T., Oksanen, L., Makynen, A., Johansen, B. & Moe, T. (2017). Changes in the spatial configuration and strength of trophic control across a productivity gradient during a massive rodent outbreak. *Ecosystems* **20**(8), 1421–1435.

*Howe, H. F. (2008). Reversal of fortune: plant suppression and recovery after vole herbivory. *Oecologia* **157**(2), 279–286.

*Howe, H. F. & Brown, J. S. (2000). Early effects of rodent granivory on experimental forb communities. *Ecological Applications* **10**(3), 917–924.

*Huitu, O., Forbes, K. M., Helander, M., Julkunen-Titto, R., Lambin, X., Saikkonen, K., Stuart, P., Sulkama, S. & Hartley, S. (2014). Silicon, endophytes and secondary metabolites as grass defenses against mammalian herbivores. *Frontiers in Plant Science* **5**, 10.

*Huitu, O., Helander, M., Lehtonen, P. & Saikkonen, K. (2008). Consumption of grass endophytes alters the ultraviolet spectrum of vole urine. *Oecologia* **156**(2), 333–340.

*Huitu, O., Jokinen, I., Korpimäki, E., Koskela, E. & Mappes, T. (2007). Phase dependence in winter physiological condition of cyclic voles. *Oikos* **116**(4), 565–577.

*Huitu, O., Kiljunen, N., Korpimäki, E., Koskela, E., Mappes, T., Pietiäinen, H., Pöysä, H. & Henttonen, H. (2009). Density-dependent vole damage in silviculture and associated economic losses at a nationwide scale. *Forest Ecology and Management* **258**(7), 1219–1224.

*Huitu, O., Koivula, M., Korpimäki, E., Klemola, T. & Norrdahl, K. (2003). Winter food supply limits growth of northern vole populations in the absence of predation. *Ecology* **84**(8), 2108–2118.

*Imholt, C., Reil, D., Plašil, P., Rödiger, K. & Jacob, J. (2017). Long-term population patterns of rodents and associated damage in German forestry. *Pest Management Science* **73**(2), 332–340.

*Ims, R. A. (1987). Responses in spatial organization and behaviour to manipulations of the food resource in the vole *Clethrionomys rufocanus*. *Journal of Animal Ecology* **56**(2), 585–596.

Ims, R. A. & Fuglei, E. (2005). Trophic interaction cycles in tundra ecosystems and the impact of climate change. *Bioscience* **55**(4), 311–322.

Ims, R. A., Henden, J. A. & Killengreen, S. T. (2008). Collapsing population cycles. *Trends in Ecology & Evolution* **23**(2), 79–86.

*Järvinen, A. (1987). Microtine cycles and plant production: what is cause and effect? *Oikos* **49**(3), 352–357.

Jacob, J., Manson, P., Barfknecht, R. & Fredricks, T. (2014). Common vole (*Microtus arvalis*) ecology and management: implications for risk assessment of plant protection products. *Pest Management Science* **70**(6), 869–878.

Jaksic, F. M. (2001). Ecological effects of El Niño in terrestrial ecosystems of western South America. *Ecography* **24**(3), 241–250.

*Janova, E., Bryja, J., Cizmar, D., Cepelka, L. & Heroldová, M. (2015). A new method for assessing food quality in common vole (*Microtus arvalis*) populations. *European Journal of Wildlife Research* **61**(1), 57–62.

*Janova, E., Heroldova, M. & Cepelka, L. (2016). Rodent food quality and its relation to crops and other environmental and population parameters in an agricultural landscape. *Science of the Total Environment* **562**, 164–169.

Jean, P.-O., Bradley, R. L., Tremblay, J.-P. & Côté, S. D. (2015). Combining near infrared spectra of feces and geostatistics to generate forage nutritional quality maps across landscapes. *Ecological Applications* **25**(6), 1630–1639.

*Jean, Y. & Bergeron, J.-M. (1986). Can voles (*Microtus pennsylvanicus*) be poisoned by secondary metabolites of commonly eaten foods? *Canadian Journal of Zoology* **64**(1), 158–162.

*Johnsen, K., Boonstra, R., Boutin, S., Devineau, O., Krebs, C. J. & Andreassen, H. P. (2017). Surviving winter: food, but not habitat structure, prevents crashes in cyclic vole populations. *Ecology and Evolution* **7**(1), 115–124.

*Johnson, D. R., Lara, M. J., Shaver, G. R., Batzli, G. O., Shaw, J. D. & Tweedie, C. E. (2011). Exclusion of brown lemmings reduces vascular plant cover and biomass in Arctic coastal tundra: resampling of a 50+ year herbivore exclosure experiment near Barrow, Alaska. *Environmental Research Letters* **6**(4), 45507.

*Jonasson, S., Bryant, J. P., Chapin, F. S. I. & Andersson, M. (1986). Plant phenols and nutrients in relation to variations in climate and rodent grazing. *The American Naturalist* **128**(3), 394–408.

Jones, A. W. & Post, D. M. (2016). Does intraspecific competition promote variation? A test via synthesis. *Ecology and Evolution* **6**(6), 1646–1655.

Kalela, O. (1962). On the fluctuations in the numbers of arctic and boreal small rodents as a problem of production biology. *Annales Academiae Scientiarum Fennicae Series A* **4**(66), 1–38.

*Kalela, O. & Koponen, T. (1971). Food consumption and movements of the Norwegian lemming in areas characterized by isolated fells. *Annales Zoologici Fennici* **8**(1), 80–84.

Kallio, E. R., Begon, M., Henttonen, H., Koskela, E., Mappes, T., Vaheri, A. & Vapalahti, O. (2009). Cyclic hantavirus epidemics in humans—predicted by rodent host dynamics. *Epidemics* **1**(2), 101–107.

Karban, R. & Baldwin, I. T. (2007). Induced resistance against herbivores. In *Induced Responses to Herbivory*. The University Press of Chicago, Chicago.

Kaspari, M. (2021). The invisible hand of the periodic table: how micronutrients shape ecology. *Annual Review of Ecology, Evolution, and Systematics* **52**, 199–219.

Kausrud, K. L., Mysterud, A., Steen, H., Vik, J. O., Ostbye, E., Cazelles, B., Framstad, E., Eikeset, A. M., Mysterud, I., Solhoy, T. & Stenseth, N. C. (2008). Linking climate change to lemming cycles. *Nature* **456**(7218), 93–97.

Kelt, D., Heske, E., Lambin, X., Oli, M., Orrock, J., Ozgul, A., Pauli, J., Prugh, L., Sollmann, R. & Sommer, S. (2019). Advances in population ecology and species interactions in mammals. *Journal of Mammalogy* **100**, 965–1007.

Kent, A., Plesner Jensen, S. & Doncaster, C. P. (2005). Model of microtine cycles caused by lethal toxins in non-preferred food plants. *Journal of Theoretical Biology* **234**, 593–604.

*Klemola, T., Koivula, M., Korpimäki, E. & Norrdahl, K. (1997). Size of internal organs and forage quality of herbivores: are there differences between cycle phases in *Microtus* voles? *Oikos* **80**(1), 61–66.

*Klemola, T., Koivula, M., Korpimäki, E. & Norrdahl, K. (2000*a*). Experimental tests of predation and food hypotheses for population cycles of voles. *Proceedings of the Royal Society B: Biological Sciences* **267**(1441), 351–356.

*Klemola, T., Norrdahl, K. & Korpimäki, E. (2000*b*). Do delayed effects of overgrazing explain population cycles in voles? *Oikos* **90**(3), 509–516.

Klemola, T., Pettersen, T. & Stenseth, N. C. (2003). Trophic interactions in population cycles of voles and lemmings: a model-based synthesis. *Advances in Ecological Research* **33**(33), 75–160.

*Korslund, L. & Steen, H. (2006). Small rodent winter survival: snow conditions limit access to food resources. *Journal of Animal Ecology* **75**, 156–166.

*Krebs, C. J. (1966). Demographic changes in fluctuating populations of *Microtus californicus*. *Ecological Monographs* **36**(3), 239–273.

KREBS, C. J. (2011). Of lemmings and snowshoe hares: the ecology of northern Canada. *Proceedings of the Royal Society B: Biological Sciences* **278**(1705), 481–489.

KREBS, C. J. (2013). *Population Fluctuations in Rodents*. The University Press Of Chicago, Chicago.

KREBS, C. J., BOONSTRA, R. & BOUTIN, S. (2018). Using experimentation to understand the 10-year snowshoe hare cycle in the boreal forest of North America. *Journal of Animal Ecology* **87**(1), 87–100.

*KREBS, C. J., COWCILL, K., BOONSTRA, R. & KENNEY, A. J. (2010). Do changes in berry crops drive population fluctuations in small rodents in the southwestern Yukon? *Journal of Mammalogy* **91**(2), 500–509.

KREBS, C. J., GILBERT, B. S., BOUTIN, S., SINCLAIR, A. R. E. & SMITH, J. N. M. (1986). Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon, 1976–84. *Journal of Animal Ecology* **55**(3), 963–982.

*KROJEROVÁ-PROKEŠOVÁÁ, J., HOMOLKA, M., HEROLDOVÁ, M., BARANCEKOVA, M., BANAR, P., KAMLER, J., MODLINGER, R., PURCHART, L., ZEJDA, J. & SUCHOMEL, J. (2018). Patterns of vole gnawing on saplings in managed clearings in Central European forests. *Forest Ecology and Management* **408**, 137–147.

*KUSUMOTO, K. (2009). Effect of food availability on immune function of gray red-backed voles (*Myodes rufocanus*) exposed to low temperature and short photoperiod. *Journal of Mammalogy* **90**(2), 416–422.

LACK, D. (1954). *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford.

*LAINE, K. & HENTTONEN, H. (1983). The role of plant-production in microtine cycles in northern Fennoscandia. *Oikos* **40**(3), 407–418.

*LAINE, K. M. & HENTTONEN, H. (1987). Phenolics/nitrogen ratios in the blueberry *Vaccinium myrtillus* in relation to temperature and microtine density in Finnish Lapland. *Oikos* **50**, 389–395.

LAMBIN, X., BRETAGNOLLE, V. & YOCCOZ, N. (2006). Vole population cycles in northern and southern Europe: is there a need for different explanations for single pattern? *Journal of Animal Ecology* **75**, 340–349.

*LARSSON, T. B. & HANSSON, L. (1977). Vole diet on experimentally managed afforestation areas in northern Sweden. *Oikos* **28**(2/3), 242–249.

*LINDGREN, A., KLINT, J. & MOEN, J. (2007). Defense mechanisms against grazing: a study of trypsin inhibitor responses to simulated grazing in the sedge *Carex bigelowii*. *Oikos* **116**(9), 1540–1546.

*LINDROTH, R. L. & BATZLI, G. O. (1984). Plant phenolics as chemical defenses – effects of natural phenolics on survival and growth of prairie voles (*Microtus ochrogaster*). *Journal of Chemical Ecology* **10**(2), 229–244.

*LINDROTH, R. L. & BATZLI, G. O. (1986). Inducible plant chemical defences: a cause of vole population cycles? *Journal of Animal Ecology* **55**(2), 431–449.

LOPES, C. M., DE BARBA, M., BOYER, F., MERCIER, C., GALIANO, D., KUBIAK, B. B., MAESTRI, R., DA SILVA FILHO, P. J. S., GIELLY, L. & COISSAC, E. (2020). Ecological specialization and niche overlap of subterranean rodents inferred from DNA metabarcoding diet analysis. *Molecular Ecology* **29**(16), 3143–3153.

LUNDBERG, S., JAREMO, J. & NILSSON, P. (1994). Herbivory, inducible defense and population oscillations – a preliminary theoretical-analysis. *Oikos* **71**(3), 537–540.

*MASSEY, F. P. & HARTLEY, S. E. (2006). Experimental demonstration of the antiherbivore effects of silica in grasses: impacts on foliage digestibility and vole growth rates. *Proceedings of the Royal Society B: Biological Sciences* **273**(1599), 2299–2304.

*MASSEY, F. P., ROLAND ENNOS, A. & HARTLEY, S. E. (2007). Herbivore specific induction of silica-based plant defences. *Oecologia* **152**, 677–683.

*MASSEY, F. P., SMITH, M. J., LAMBIN, X. & HARTLEY, S. E. (2008). Are silica defences in grasses driving vole population cycles? *Biology Letters* **4**(4), 419–422.

MAY, R. M. (1973). Time-delay versus stability in population models with two and three trophic levels. *Ecology* **54**, 315–325.

MCARTHUR, C., BANKS, P. B., BOONSTRA, R. & FORBEY, J. S. (2014). The dilemma of foraging herbivores: dealing with food and fear. *Oecologia* **176**(3), 677–689.

*MOEN, J. (1990). Summer grazing by voles and lemmings upon subarctic snow-bed and tall herb meadow vegetation: an enclosure experiment. *Holarctic Ecology* **13**(4), 316–324.

*MOEN, J., GARDFJELL, H., OKSANEN, L., ERICSON, L. & EKERHOLM, P. (1993a). Grazing by food-limited microtine rodents on a productive experimental plant community: does the 'green desert' exist? *Oikos* **68**(3), 401–413.

*MOEN, J., LUNDBERG, P. A. & OKSANEN, L. (1993b). Lemming grazing on snowbed vegetation during a population peak, northern Norway. *Arctic and Alpine Research* **25**(2), 130–135.

*MOEN, J. & OKSANEN, L. (1998). Long-term exclusion of folivorous mammals in two arctic-alpine plant communities: a test of the hypothesis of exploitation ecosystems. *Oikos* **82**(2), 333–346.

MÖLLE, J. P., KLEIVEN, E. F., IMS, R. A. & SOININEN, E. M. (2021). Using subnivean camera traps to study Arctic small mammal community dynamics during winter. *Arctic Science* **8**(1), 183–199.

MURGUZUR, F. J. A., BISON, M., SMIS, A., BÖHNER, H., STRUYF, E., MEIRE, P. & BRÅTHEN, K. A. (2019). Towards a global arctic-alpine model for Near-infrared reflectance spectroscopy (NIRS) predictions of foliar nitrogen, phosphorus and carbon content. *Scientific Reports* **9**(1), 1–10.

MYERS, J. H. (2018). Population cycles: generalities, exceptions and remaining mysteries. *Proceedings of the Royal Society B: Biological Sciences* **285**(1875), 20172841.

MYERS, J. H. & CORY, J. S. (2013). Population cycles in forest Lepidoptera revisited. *Annual Review of Ecology, Evolution, and Systematics* **44**, 565–592.

MYSTERUD, A. (2006). The concept of overgrazing and its role in management of large herbivores. *Wildlife Biology* **12**(2), 129–141.

NICHOLSON, M. C., BOWYER, R. T. & KIE, J. G. (2006). Forage selection by mule deer: does niche breadth increase with population density? *Journal of Zoology* **269**, 39–49.

*NORRDAHL, K., KLEMOLA, T., KORPIMÄKI, E. & KOIVULA, M. (2002). Strong seasonality may attenuate trophic cascades: vertebrate predator exclusion in boreal grassland. *Oikos* **99**(3), 419–430.

*NORRDAHL, K. & KORPIMÄKI, E. (2002). Changes in individual quality during a 3-year population cycle of voles. *Oecologia* **130**(2), 239–249.

*NYSTUEN, K. O., EVJU, M., RUSCH, G. M., GRAAE, B. J. & EIDE, N. E. (2014). Rodent population dynamics affect seedling recruitment in alpine habitats. *Journal of Vegetation Science* **25**(4), 1004–1014.

*OKSANEN, L. & ERICSON, L. (1987). Dynamics of tundra and taiga populations of herbaceous plants in relation to the Tihomirov-Fretwell and Kalela-Tast hypotheses. *Oikos* **50**(3), 381–388.

*OKSANEN, L. & OKSANEN, T. (1981). Interactions between gray-sided voles (*Clethrionomys rufucanus*) and bilberry (*Vaccinium myrtillus*), their main winter food plant. *Reports from the Kevo Subarctic Research Station* **17**, 7–31.

*OKSANEN, L., OKSANEN, T., LUKKARI, A. & SIREN, S. (1987). The role of phenol-based inducible defense in the interaction between tundra populations of the vole *Clethrionomys rufocanus* and the dwarf shrub *Vaccinium myrtillus*. *Oikos* **50**(3), 371–380.

OKSANEN, T., OKSANEN, L., DAHLGREN, J. & OLOFSSON, J. (2008). Arctic lemmings, *Lemmus* spp. and *Dicrostonyx* spp.: integrating ecological and evolutionary perspectives. *Evolutionary Ecology Research* **10**(3), 415–434.

*OKSANEN, T., SCHNEIDER, M., RAMMUL, U., HAMBÄCK, P. & AUNAPUU, M. (1999). Population fluctuations of voles in North Fennoscandian tundra: contrasting dynamics in adjacent areas with different habitat composition. *Oikos* **86**(3), 463–478.

OLI, M. K. (2019). Population cycles in voles and lemmings: state of the science and future directions. *Mammal Review* **49**(3), 226–239.

*OLOFSSON, J., DAHLGREN, J. & WITZELL, J. (2007). Grey-sided voles increase the susceptibility of Northern willow, *Salix glauca*, to invertebrate herbivory. *Ecoscience* **14**(1), 48–54.

*OLOFSSON, J., TOMMERVIK, H. & CALLAGHAN, T. V. (2012). Vole and lemming activity observed from space. *Nature Climate Change* **2**(12), 880–883.

ONODERA, R., AKIMOTO, Y., SHIMADA, T. & SAITOH, T. (2017). Different population responses of three sympatric rodent species to acorn masting-the role of tannin tolerance. *Population Ecology* **59**(1), 29–43.

*OSTFELD, R. & KLOSTERMAN, L. L. (1986). Demographic substructure in a California vole population inhabiting a patchy environment. *Journal of Mammalogy* **67**(4), 693–696.

*OSTFELD, R. S., CANHAM, C. D. & PUGH, S. R. (1993). Intrinsic density-dependent regulation of vole populations. *Nature* **366**(6452), 259–261.

*OSTFELD, R. S., MANSON, R. H. & CANHAM, C. D. (1997). Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* **78**(5), 1531–1542.

*PALO, R. T. & OLSSON, G. E. (2009). Nitrogen and carbon concentrations in the stomach content of bank voles (*Myodes glareolus*). Does food quality determine abundance? *Open Ecology Journal* **2**, 86–90.

PARENT, C. E., AGASHE, D. & BOLNICK, D. I. (2014). Intraspecific competition reduces niche width in experimental populations. *Ecology and Evolution* **4**(20), 3978–3990.

PEIG, J. & GREEN, A. J. (2009). New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* **118**(12), 1883–1891.

PETIT BON, M., BÖHNER, H., KAINO, S., MOE, T. & BRÅTHEN, K. A. (2020a). One leaf for all: chemical traits of single leaves measured at the leaf surface using near-infrared reflectance spectroscopy. *Methods in Ecology and Evolution* **11**(9), 1061–1071.

PETIT BON, M., GUNNARSDOTTER INGA, K., JÓNSDÓTTIR, I. S., UTSI, T. A., SOININEN, E. M. & BRÅTHEN, K. A. (2020b). Interactions between winter and summer herbivory affect spatial and temporal plant nutrient dynamics in tundra grassland communities. *Oikos* **129**(8), 1229–1242.

PIERCE, A. A., FERKIN, M. H. & WILLIAMS, T. K. (2005). Food-deprivation-induced changes in sexual behaviour of meadow voles, *Microtus pennsylvanicus*. *Animal Behaviour* **70**(2), 339–348.

*PINOT, A., GAUFFRE, B. & BRETAGNOLLE, V. (2014). The interplay between seasonality and density: consequences for female breeding decisions in a small cyclic herbivore. *BMC Ecology* **14**(1), 1–14.

PLESNER JENSEN, S. & DONCASTER, C. P. (1999). Lethal toxins in non-preferred foods: how plant chemical defences can drive microtine cycles. *Journal of Theoretical Biology* **199**, 63–85.

*Predavec, M. & Danell, K. (2001). The role of lemming herbivory in the sex ratio and shoot demography of willow populations. *Oikos* **92**(3), 459–466.

*Rammul, Ü., Oksanen, T., Oksanen, L., Lehtelä, J., Virtanen, R., Olofsson, J., Strengbom, J., Rammul, I. & Ericson, L. (2007). Vole-vegetation interactions in an experimental, enemy free taiga floor system. *Oikos* **116**(9), 1501–1513.

Raubenheimer, D., Simpson, S. J. & Mayntz, D. (2009). Nutrition, ecology and nutritional ecology: toward an integrated framework. *Functional Ecology* **23**(1), 4–16.

*Ravolainen, V. T., Brathen, K. A., Ims, R. A., Yoccoz, N. G., Henden, J. A. & Killengreen, S. T. (2011). Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. *Basic and Applied Ecology* **12**(8), 643–653.

*Ravolainen, V. T., Bråthen, K. A., Yoccoz, N. G., Nguyen, J. K. & Ims, R. A. (2014). Complementary impacts of small rodents and semi-domesticated ungulates limit tall shrub expansion in the tundra. *Journal of Applied Ecology* **51**(1), 234–241.

*Reynolds, J. J. H., Lambin, X., Massey, F. P., Reidinger, S., Sherratt, J. A., Smith, M. J., White, A. & Hartley, S. E. (2012). Delayed induced silica defences in grasses and their potential for destabilising herbivore population dynamics. *Oecologia* **170**(2), 445–456.

Reynolds, J. J. H., Sherratt, J. A., White, A. & Lambin, X. (2013). A comparison of the dynamical impact of seasonal mechanisms in a herbivore-plant defence system. *Theoretical Ecology* **6**(2), 225–239.

*Ruffino, L., Hartley, S. E., DeGabriel, J. L. & Lambin, X. (2018). Population-level manipulations of field vole densities induce subsequent changes in plant quality but no impacts on vole demography. *Ecology and Evolution* **8**(16), 7752–7762.

*Ruffino, L., Oksanen, T., Hoset, K. S., Tuomi, M., Oksanen, L., Korpimäki, E., Bugli, A., Hobson, K. A., Johansen, B. & Makynen, A. (2016). Predator-rodent-plant interactions along a coast-inland gradient in Fennoscandian tundra. *Ecography* **39**(9), 871–883.

*Saetnan, E. R. & Batzli, G. O. (2009). Effects of simulated herbivory on defensive compounds in forage plants of Norwegian alpine rangelands. *Journal of Chemical Ecology* **35**(4), 469–475.

*Saitoh, T. (1989). Effects of added food on some attributes of an enclosed vole population. *Journal of Mammalogy* **70**(4), 772–782.

Schmidt, J. H., Rexstad, E. A., Roland, C. A., McIntyre, C. L., MacCluskie, M. C. & Flamme, M. J. (2018). Weather-driven change in primary productivity explains variation in the amplitude of two herbivore population cycles in a boreal system. *Oecologia* **186**(2), 435–446.

Schmidt, N. M., Ims, R. A., Hoye, T. T., Gilg, O., Hansen, L. H., Hansen, J., Lund, M., Fuglei, E., Forchhammer, M. C. & Sittler, B. (2012). Response of an arctic predator guild to collapsing lemming cycles. *Proceedings of the Royal Society of London series B: Biological Sciences* **279**(1746), 4417–4422.

Schultz, A. M. (1964). The nutrient-recovery hypothesis for arctic microtine cycles. II. Ecosystem variables in relation to arctic microtine cycles. In *Grazing in Terrestrial and Marine Environments* (ed. D. J. Crisp), pp. 57–68. Blackwell Scientific Publications, Blackwell, Oxford.

*Schweiger, S. & Boutin, S. (1995). The effects of winter food addition on the population-dynamics of *Clethrionomys rutilus*. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **73**(3), 419–426.

*Selås, V. (1997). Cyclic population fluctuations of herbivores as an effect of cyclic seed cropping of plants: the mast depression hypothesis. *Oikos* **80**(2), 257–268.

*Selås, V. (2006). Explaining bank vole cycles in southern Norway 1980–2004 from bilberry reports 1932–1977 and climate. *Oecologia* **147**, 625–631.

*Selås, V. (2020). Evidence for different bottom-up mechanisms in wood mouse (*Apodemus sylvaticus*) and bank vole (*Myodes glareolus*) population fluctuations in Southern Norway. *Mammal Research* **65**, 267–275.

*Selås, V., Framstad, E. & Spidso, T. K. (2002). Effects of seed masting of bilberry, oak and spruce on sympatric populations of bank vole (*Clethrionomys glareolus*) and wood mouse (*Apodemus sylvaticus*) in southern Norway. *Journal of Zoology* **258**, 459–468.

*Selås, V., Holand, O. & Ohlson, M. (2011). Digestibility and N-concentration of bilberry shoots in relation to berry production and N-fertilization. *Basic and Applied Ecology* **12**(3), 227–234.

*Selås, V., Kobro, S. & Sonerud, G. A. (2013). Population fluctuations of moths and small rodents in relation to plant reproduction indices in southern Norway. *Ecosphere* **4**(10), 1–11.

Seldal, T., Andersen, K.-J. & Hogstedt, G. (1994). Grazing-induced proteinase inhibitors: a possible cause for lemming population cycles. *Oikos* **70**(1), 3–11.

Sipoš, J., Suchomel, J., Purchart, L. & Kindlmann, P. (2017). Main determinants of rodent population fluctuations in managed Central European temperate lowland forests. *Mammal Research* **62**(3), 283–295.

*Sirotnak, J. M. & Huntly, N. J. (2000). Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. *Ecology* **81**(1), 78–87.

*Smirnov, V. S. & Tokmakova, S. G. (1971). Preliminary data on the influence of different numbers of voles upon the forest tundra vegetation. *Annales Zoologici Fennici* **8**(1), 154–156.

Smis, A., Ancin Murguzur, F. J., Struyf, E., Soininen, E. M., Herranz Jusdado, J. G., Meire, P. & Bråthen, K. A. (2014). Determination of plant silicon content with near infrared reflectance spectroscopy. *Frontiers in Plant Science* **5**, 496.

*Soininen, E. M., Bråthen, K. A., Jusdado, J. G. H., Reidinger, S. & Hartley, S. E. (2013a). More than herbivory: levels of silica-based defences in grasses vary with plant species, genotype and location. *Oikos* **122**(1), 30–41.

*Soininen, E. M., Ehrich, D., Lecomte, N., Yoccoz, N. G., Tarroux, A., Berteaux, D., Gauthier, G., Gielly, L., Brochmann, C., Gussarova, G. & Ims, R. A. (2014). Sources of variation in small rodent trophic niche: new insights from DNA metabarcoding and stable isotope analysis. *Isotopes in Environmental and Health Studies* **50**(3), 361–381.

Soininen, E. M., Gauthier, G., Bilodeau, F., Berteaux, D., Gielly, L., Taberlet, P., Gussarova, G., Bellemain, E., Hassel, K., Stenøien, H. K., Epp, L., Schrøder-Nielsen, A., Brochmann, C. & Yoccoz, N. G. (2015a). Highly overlapping winter diet in two sympatric lemming species revealed by DNA metabarcoding. *PLoS One* **10**(1), e0115335.

Soininen, E. M., Henden, J. A., Ravolainen, V. T., Yoccoz, N. G., Bråthen, K. A., Killengreen, S. T. & Ims, R. A. (2018). Transferability of biotic interactions: temporal consistency of arctic plant–rodent relationships is poor. *Ecology and Evolution* **8**(19), 9697–9711.

Soininen, E. M., Jensvoll, I., Killengreen, S. & Ims, R. A. (2015b). Under the snow: a new camera trap opens the wite box of subnivean ecology. *Remote Sensing in Ecology and Conservation* **1**(1), 29–38.

*Soininen, E. M., Ravolainen, V. T., Bråthen, K. A., Yoccoz, N. G., Gielly, L. & Ims, R. A. (2013b). Arctic small rodents have diverse diets and flexible food selection. *PLoS One* **8**(6), e68128.

Soininen, E. M., Valentini, A., Coissac, E., Miquel, C., Gielly, L., Brochmann, C., Brysting, A. K., Sonstebo, J. H., Ims, R. A., Yoccoz, N. G. & Taberlet, P. (2009). Analysing diet of small herbivores: the efficiency of DNA barcoding coupled with high-throughput pyrosequencing for deciphering the composition of complex plant mixtures. *Frontiers in Zoology* **6**, 16.

Soininen, E. M., Zinger, L., Gielly, L., Yoccoz, N. G., Henden, J.-A. & Ims, R. A. (2017). Not only mosses: lemming winter diets as described by DNA metabarcoding. *Polar Biology* **40**(10), 2097–2103.

Stewart, K. M., Bowyer, R. T., Dick, B. L. & Kie, J. G. (2011). Effects of density dependence on diet composition of North American elk *Cervus elaphus* and mule deer *Odocoileus hemionus*: an experimental manipulation. *Wildlife Biology* **17**, 417–430.

*Suchomel, J., Purchart, L., Cepelka, L. & Heroldová, M. (2016). Factors influencing vole bark damage intensity in managed mountain-forest plantations of Central Europe. *European Journal of Forest Research* **135**(2), 331–342.

*Sullivan, A. T. & Howe, H. F. (2011). Response of two prairie forbs to repeated vole herbivory. *Oecologia* **165**(4), 1007–1015.

*Sullivan, T. P. & Sullivan, D. S. (2014). Fertilisation, cattle grazing and voles: collapse of meadow vole populations in young forests? *Wildlife Research* **41**(5), 367–378.

*Summerhayes, V. S. (1941). The effect of voles (*Microtus agrestis*) on vegetation. *Journal of Ecology* **29**, 14–48.

Svanbäck, R. & Bolnick, D. I. (2007). Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences* **274**(1611), 839–844.

*Taitt, M. J. & Krebs, C. J. (1981). The effect of extra food on small rodent populations: ii. Voles (*Microtus townsendii*). *Journal of Animal Ecology* **50**(1), 125–137.

*Taitt, M. J. & Krebs, C. J. (1983). Predation, cover, and food manipulations during a spring decline of *Microtus townsendii*. *Journal of Animal Ecology* **52**(3), 837–848.

*Thomas, D. W., Samson, C. & Bergeron, J. M. (1988). Metabolic costs associated with the ingestion of plant phenolics by *Microtus pennsylvanicus*. *Journal of Mammalogy* **69**(3), 512–515.

*Tornberg, R., Helle, P. & Korpimäki, E. (2011). Vulnerability of black grouse hens to goshawk predation: result of food supply or predation facilitation? *Oecologia* **166**(2), 577–584.

*Truszkowski, J. (1982). The impact of the common vole on the vegetation of agroecosystems. *Acta Theriologica* **27**(13–2), 305–345.

Turchin, P. (2003). *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton University Press, Princeton and Oxford.

Turchin, P. & Batzli, G. O. (2001). Availability of food and the population dynamics of arvicoline rodents. *Ecology* **82**(6), 1521–1534.

Turchin, P., Oksanen, L., Ekerholm, P., Oksanen, T. & Henttonen, H. (2000). Are lemmings prey or predators? *Nature* **405**, 562–565.

Underwood, N. (1999). The influence of plant and herbivore characteristics on the interaction between induced resistance and herbivore population dynamics. *The American Naturalist* **153**(3), 282–294.

*Virtanen, R., Henttonen, H. & Laine, K. (1997). Lemming grazing and structure of a snowbed plant community: a long-term experiment at Kilpisjärvi, Finnish Lapland. *Oikos* **79**(1), 155–166.

*Virtanen, R., Parviainen, J. & Henttonen, H. (2002). Winter grazing by the Norwegian lemming (*Lemmus lemmus*) at Kilpisjarvi (NW Finnish Lapland) during a moderate population peak. *Annales Zoologici Fennici* **39**(4), 335–341.

Vogel, S. M., Blumenthal, S. A., de Boer, W. F., Masake, M., Newton, I., Songhurst, A. C., McCulloch, G., Stronza, A., Henley, M. D. & Coulson, T. (2020). Timing of dietary switching by savannah elephants in relation to crop consumption. *Biological Conservation* **249**, 108703.

Voltura, M. B. & Wunder, B. A. (1998). Effects of ambient temperature, diet quality, and food restriction on body composition dynamics of the prairie vole, *Microtus ochrogaster*. *Physiological Zoology* **71**(3), 321–328.

*Wieczorek, M., Szafranska, P. A., Labecka, A. M., Lazaro, J. & Konarzewski, M. (2015). Effect of the abrasive properties of sedges on the intestinal absorptive surface and resting metabolic rate of root voles. *Journal of Experimental Biology* **218**(2), 309–315.

Windley, H. R. & Foley, W. J. (2015). Landscape-scale analysis of nutritional traits of New Zealand tree foliage using near-infrared spectroscopy. *Forest Ecology and Management* **357**, 161–170.

Xu, L., Myneni, R. B., Chapin Iii, F. S., Callaghan, T. V., Pinzon, J. E., Tucker, C. J., Zhu, Z., Bi, J., Ciais, P., Tømmervik, H., Euskirchen, E. S., Forbes, B. C., Piao, S. L., Anderson, B. T., Ganguly, S., et al. (2013). Temperature and vegetation seasonality diminishment over northern lands. *Nature Climate Change* **3**(6), 581–586.

*Yin, B. F., Li, G. L., Wan, X. R., Shang, G. Z., Wei, W. H. & Zhang, Z. B. (2017). Large manipulative experiments reveal complex effects of food supplementation on population dynamics of Brandt's voles. *Science China Life Sciences* **60**(8), 911–920.

*Ylönen, H. & Eccard, J. A. (2004). Does quality of winter food affect spring condition and breeding in female bank voles (*Clethrionomys glareolus*)? *Ecoscience* **11**(1), 1–5.

Ylönen, H., Jacob, J., Davies, M. J. & Singleton, G. R. (2002). Predation risk and habitat selection of Australian house mice, *Mus domesticus*, during an incipient plague: desperate behaviour due to food depletion. *Oikos* **99**(2), 284–289.

*Yoccoz, N. G., Nils Chr, S., Henttonen, H. & Prevot-Julliard, A.-C. (2001). Effects of food addition on the seasonal density-dependent structure of bank vole *Clethrionomys glareolus* populations. *Journal of Animal Ecology* **70**(5), 713–720.

X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Additional information on excluded studies.
Appendix S2. List of all retrieved publications with reasons for exclusion. See https://doi.org/10.18710/ONEYAM/ELZ7WK
Appendix S3. Publications included in the systematic review, with data derived from each publication. See https://doi.org/10.18710/ONEYAM/ILZMRU
Appendix S4. Coding template used for data entry, including definitions of variables and eligible values.
Appendix S5. Additional information on assigning study evidence to particular hypothesis assumptions.
Fig. S1. Study durations for different categories of study design in our database.