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Herbivore Population Dynamics in Response to Plant Allocation Strategies

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Abstract

When herbivores feed, plants may respond by altering the quantity of edible biomass available to future feeders through mechanisms such as compensatory regrowth of edible structures or allocation of biomass to inedible reserves. Previous work showed that some forms of compensatory regrowth can drive insect outbreaks, but this work assumed regrowth occurred without any energetic cost to the plant. While this is a useful simplifying assumption for gaining preliminary insights, plants face an inherent trade-off between allocating energy to regrowth versus storage. Therefore, we cannot truly understand the role of compensatory regrowth in driving insect outbreaks without continuing on to more realistic scenarios. In this paper, we model the interaction between insect herbivores and plants that have a trade-off between compensatory regrowth and allocation to inedible reserves in response to herbivory. We found that the plant's allocation strategy, described in our model by parameters representing the strength of the overcompensatory response and the rates at which energy is stored and mobilized for growth, strongly affect whether herbivore outbreaks occur. Additional factors, such as the strength of food limitation and herbivore interference while feeding, influence the frequency of the outbreaks. Overall, we found a possible new role of overcompensation to promote herbivore fluctuations when it co-occurs with allocation to inedible reserves. We highlight the importance of considering trade-offs between tolerance mechanisms that plants use in response to herbivory by showing that new dynamics arise when different plant allocation strategies occur simultaneously.

Keywords: belowground allocation, overcompensation, plant-herbivore interaction, population dynamics, tolerance, trade-off

Introduction

Many herbivorous insect populations show fluctuating dynamics over time (Elton, 1924; Kendall et al., 1999; Turchin, 2013), and ecologists have long worked to explain these fluctuations from both theoretical (Lundberg, 1994; Vos et al., 2004) and empirical (Underwood and Rausher, 2000; Liebhold, 2019) perspectives. Many mechanisms that can drive insect outbreaks (which, following Stieha et al. (2016), we define as intrinsically generated herbivore population fluctuations) involve the plants' own responses to herbivory. In one class of responses, plants alter the quantity of edible biomass available

30 to herbivores, either increasing it through compensatory regrowth of edible tissues lost to herbivory
31 (McNaughton, 1983; Orians et al., 2011; Belsky, 1986; Agrawal, 2000), or decreasing it by allocating
32 energy to the growth of inedible storage organs (Dyer et al., 1991; Briske et al., 1996). Given a
33 finite amount of energy for growth, plants face a trade-off in their capacity to respond to herbivory
34 in either of these ways. How plants allocate energy to different structures is known to influence in-
35 sect dynamics (Miller et al., 2006), so the trade-off between compensatory regrowth of edible tissues
36 and storage of biomass in inedible ones is likely to be consequential. How, though, remains unknown.

37
38 Overcompensation, one form of compensatory plant regrowth in response to herbivory, occurs
39 when herbivore-damaged plants regrow more edible biomass than is needed to replace the losses
40 to sufficiently mild herbivory (McNaughton, 1979; Paige and Whitham, 1987; Alward and Joern,
41 1993; Lennartsson et al., 1998). Theoretically, the ability of plants to overcompensate is thought
42 to drive insect outbreak cycles (Stieha et al., 2016; Stieha et al. in prep.), at least when there is a
43 negligible energetic cost to the plant of this regrowth. This is because overcompensation exaggerates
44 the well-known “prey escape cycles” that occur when overexploitation by consumers leads to a crash
45 in the resource population, followed by a consumer crash that allows resource recovery. The ensuing
46 consumer recovery leads back to overexploitation and the cycle repeats. Overcompensation boosts
47 the boom in the herbivore population, exaggerating the crash and making eventual stabilization to
48 a point equilibrium more difficult to achieve.

49
50 For plants with inedible storage organs, such as perennial plants that experience above-ground
51 herbivory during the growing season and have overwintering roots, the ability to reallocate energy
52 to inedible storage in response to herbivory is another critical tolerance mechanism. It allows plant
53 regrowth using stored energy after an acute bout of herbivory has passed (Zhou et al., 2015). Pre-
54 vious work has shown that allocation to inedible storage influences herbivore population dynamics
55 and can lead to sustained oscillations, especially when the late-season allocation to storage tissues
56 is high enough to support a large amount of aboveground biomass next year (Thomas et al., 2017).

57
58 Overcompensation and allocation to inedible reserves have been studied separately, where both

processes can drive population cycles when acting on their own. However, because of the inevitable energetic trade-off between edible regrowth and inedible reserves in overcompensating plants, it is imperative that we consider both processes together when assessing their impact on herbivore dynamics. Past work on other plant responses to herbivory, such as food limitation, compensatory regrowth, and induced resistance, has revealed counter-intuitive effects: outbreaks can cease when two outbreak-promoting mechanisms are combined, or new outbreaks can arise from the combination of two processes neither of which drives outbreaks in isolation (Abbott et al., 2008; Stieha et al., 2016). The true effects of overcompensation and inedible storage on insect population dynamics can therefore only be understood by studying the two mechanisms, and their intrinsic trade-off, simultaneously.

Here we present a theoretical model to understand how overcompensation and allocation to inedible reserves interact to affect herbivore population dynamics. We assume that there is a trade-off between overcompensation and the ability to keep energy in inedible storage – that is, when plants use a certain portion of their energy for overcompensatory regrowth, they cannot keep the same energy in reserve for future growth. We use our model to examine properties of the insect population dynamics, such as equilibrium population size and outbreak frequency, as a function of the plant’s growth and allocation traits. We focus particularly on identifying the conditions that lead to sustained insect population fluctuations. Finally, we compare the behavior of our model to previous models of either overcompensation or inedible allocation alone (Stieha et al., 2016; Thomas et al., 2017), to determine which, if any, of our results arise from an interaction between these processes. We found that the equilibrium herbivore density increases when plants have strong overcompensatory regrowth or allocate more energy to inedible storage. Both high-frequency fluctuations characteristic of strong intraspecific density dependence (“single-species cycles” sensu Murdoch et al. (2002)) and lower-frequency fluctuations characteristic of consumer-resource feedbacks can happen when overcompensation and allocation to inedible stores occur simultaneously. In contrast, overcompensation acting on its own results only in single-species fluctuations and inedible allocation alone solely shows consumer-resource fluctuations. Overall, our results show that new dynamics arise when different plant allocation strategies occur simultaneously and suggest a new role of overcompensation to

promote herbivore fluctuations when it co-occurs with allocation to inedible reserves. This knowledge is relevant to applications such as increasing crop yield in agriculture, pest control, and forest management.

Methods

For ease of presentation, we describe a folivorous insect herbivore population, and we refer to the plant’s pool of edible plant biomass as “aboveground” and its inedible stores as “belowground”, although the same model could be applied to any overcompensating perennial plant with separate pools of biomass accessible and inaccessible to a population of herbivores. We assume insects are univoltine and plants, though perennial with potentially long-lived belowground tissues, regrow aboveground structures each growing season. These assumptions match those used in one or more of the models presented in Abbott et al. (2008), Stieha et al. (2016), and Thomas et al. (2017), allowing us to combine well-understood elements of these past models to arrive at our new model.

We use H_t to represent herbivore population density in year t and divide the perennial plant population’s biomass into an aboveground pool (A_t) and a belowground pool (B_t). We model dynamics in discrete, annual time steps that are subdivided into sequential phases of growth, herbivory, etc. (see Fig. 1 for a schematic). Variables and parameters are listed in Table 1. Except where noted, our model follows Thomas et al. (2017), and additional justification for the functional forms used can be found therein.

Early in the growing season, while herbivores are still overwintering, plants begin aboveground growth. We assume that early spring allocation of energy from belowground to aboveground follows a saturating function, $\frac{yB_{t-1}}{1+bB_{t-1}}$ (Fig. 2a), where B_{t-1} is the amount of belowground biomass that has overwintered from the previous year, and y is the maximum proportion of stored energy (measured in biomass units) that can be allocated from belowground to aboveground at the initiation of spring growth. Actual allocation saturates at $\frac{y}{b}$ (as $B_{t-1} \rightarrow \infty$) according to the parameter b . When b is small, the allocation saturates at a higher value. After stored energy is allocated from belowground,

115 the aboveground biomass grows by a factor r through photosynthesis. Thus, A'_t is the amount of
 116 aboveground biomass after spring growth in year t , such that

$$A'_t = r \frac{yB_{t-1}}{1 + bB_{t-1}}. \quad (1)$$

117 After allocating resources to initiate aboveground growth, the belowground biomass in spring,
 118 B'_t , updates to

$$B'_t = B_{t-1} - \frac{yB_{t-1}}{1 + bB_{t-1}}. \quad (2)$$

119 We maintain $0 \leq y \leq 1$, ensuring $0 \leq B'_t \leq B_{t-1}$.
 120

121 After overwintering, H_{t-1} adult herbivores emerge and begin feeding on aboveground biomass
 122 A'_t . The fraction of edible biomass that is consumed by adult herbivores, d_1 (Fig. 2b), is a saturating
 123 function of herbivores per unit edible biomass, $\frac{H_{t-1}}{A'_t}$,

$$d_1 = \frac{\frac{H_{t-1}}{A'_t}}{p_1 + \frac{H_{t-1}}{A'_t}} = \frac{H_{t-1}}{p_1 A'_t + H_{t-1}} \quad (3)$$

124 (Abbott et al., 2008), where p_1 is the half-saturation constant determining the steepness of the
 125 saturating function. The foraging success of adult herbivore levels off with increasing $\frac{H_{t-1}}{A'_t}$ because
 126 more herbivores per unit edible biomass interfere with each other's ability to find edible biomass.
 127 When the value of p_1 is low, it indicates that interference between feeding adult herbivores is weak
 128 so that the damage caused by adult herbivores per unit biomass escalates quickly. After herbivory
 129 by adults, the remaining aboveground biomass, A''_t , is

$$A''_t = (1 - d_1)A'_t. \quad (4)$$

130 Only a proportion, h_1 (Fig. 2c), of the adult herbivores survive the feeding period, so the herbivore
 131 population density updates to

$$H'_t = h_1 H_{t-1}, \quad (5)$$

132 with a saturating survivorship

$$h_1 = \frac{\frac{A'_t}{H_{t-1}}}{k_1 + \frac{A'_t}{H_{t-1}}} = \frac{A'_t}{k_1 H_{t-1} + A'_t}, \quad (6)$$

133 where k_1 determines the strength of food limitation in the adult herbivore population. Higher k_1
 134 indicates stronger food limitation and thus lower adult herbivore survival at a given level of edible
 135 biomass per herbivore (Abbott et al., 2008).

136

137 Next, adult herbivores lay eggs, then die. In the meantime, plants respond to herbivory by
 138 allocating more energy from belowground stores to aboveground biomass for compensatory regrowth.
 139 After this allocation, aboveground biomass becomes

$$A_t''' = A_t'' + \min \begin{cases} (1-z)d_1 A'_t \\ B'_t \end{cases} = \min \begin{cases} (1-zd_1)A'_t \\ A_t'' + B'_t \end{cases}. \quad (7)$$

140 That is, plants regrow a fraction $1-z$ of the biomass lost to herbivores ($d_1 A'_t$), up to a maximum
 141 of B'_t units of regrowth since only B'_t remains in the belowground stores. As the final equality in
 142 equation (7) shows, as long as sufficient belowground stores remain, the quantity $1-zd_1$ (Fig. 2d)
 143 can be thought of as the fraction of pre-herbivory aboveground biomass (A'_t) that is present after
 144 adult herbivory and compensatory regrowth (A_t'''). Although we refer to $1-z$ and $1-zd_1$ as frac-
 145 tions, note that they need not to be proper fractions; z will be negative, and $1-z$ and $1-zd_1$ will
 146 be larger than 1, when regrowth is overcompensatory (as in Stieha et al. (2016)). The addition of
 147 an overcompensatory response between two feeding insect life stages in our model is distinct from
 148 Thomas et al. (2017), who deliberately chose a partial regrowth function with parameter settings
 149 that disallowed overcompensation.

150

151 Following Stieha et al. (2016), z has the form,

$$z = 1 - \frac{1 + \frac{vH_{t-1}}{A'_t}}{1 + \left(\frac{vH_{t-1}}{A'_t}\right)^2}. \quad (8)$$

152 We use v to control the relationship between herbivore density and plant compensatory response.
 153 Small values of v mean that overcompensation is strong, with a high maximum $1 - zd_1$ and overcom-
 154 pensatory regrowth ($1 - zd_1 > 1$) occurring for a broader range of herbivore per unit edible biomass
 155 (Fig. 2d). Larger values of v indicates weaker overcompensation, and with infinitely large v , plants
 156 have no regrowth in response to herbivory.

157

158 After allocating energy for aboveground compensatory regrowth in response to adult herbivory,
 159 belowground biomass becomes,

$$B_t'' = B_t' - \min \begin{cases} (1 - z)d_1 A_t', \\ B_t' \end{cases}. \quad (9)$$

160 Next, herbivore eggs hatch into larvae. If r_p is the net reproductive rate, herbivore population
 161 density at the larval stage is,

$$H_t'' = r_p H_t'. \quad (10)$$

162 Larval herbivores then begin feeding, and a proportion of aboveground biomass d_2 is removed.
 163 The remaining biomass grows by a factor of r from photosynthetic energy until the end of the
 164 growing season. Aboveground biomass at the end of the growing season is thus,

$$A_t = (1 - d_2)rA_t''', \quad (11)$$

165 with

$$d_2 = \frac{\frac{H_t''}{A_t''}}{p_2 + \frac{H_t''}{A_t''}} = \frac{H_t''}{p_2 A_t''' + H_t''}. \quad (12)$$

166 Similar to equation (3), p_2 indicates how strongly larval herbivores interfere with each other when
 167 feeding.

168

169 Prior to the onset of winter, energy is allocated to belowground storage before aboveground

170 biomass dies back. Belowground biomass after end-of-year allocation is

$$B_t = B_t'' + \frac{qA_t}{1 + mB_t''}, \quad (13)$$

171 q is the maximum fraction of energy allocated from aboveground to belowground for storage and
 172 m indicates the density dependence of allocation (Fig. 2e). When m is large, the allocation rate
 173 drops quickly due to strong belowground density dependence. Note that we slightly depart from
 174 the assumptions in Thomas et al. (2017) here. While they modeled density dependent belowground
 175 allocation using a discrete logistic function, we instead use Beverton-Holt density dependence in
 176 equation (13) to eliminate the possibility of negative values of B_t .

177

178 After larval feeding, herbivores overwinter in the pupal stage with population density

$$H_t = h_2 H_t'', \quad (14)$$

179 with survival fraction, h_2 , written as

$$h_2 = \frac{\frac{A_t'''}{H_t''}}{k_2 + \frac{A_t'''}{H_t''}} = \frac{A_t'''}{k_2 H_t'' + A_t'''}, \quad (15)$$

180 where k_2 determines the strength of food limitation in the larval herbivore population.

181 Analysis

182 All the analyses were done in MATLAB R2019a. Model realizations were run for 10,000 annual time
 183 steps with the parameter values and initial conditions given in Table 1. The parameter ranges were
 184 chosen both for comparability to previous models (Stieha et al., 2016; Thomas et al., 2017) and to
 185 highlight noteworthy behaviors in our model.

186

187 To quantify long-term equilibrium dynamics, we calculated the mean and coefficient of variation
 188 (CV) of the population densities over the last 200 annual time steps. Our use of continuous-valued
 189 variables allows the possibility that populations drop to unrealistically low levels, and potentially

190 recover, without technically becoming extinct. To prevent this, we assumed that plant popula-
 191 tions with mean belowground biomass $B_t < 10^{-6}$, or herbivore populations with mean density
 192 $H_t < 10^{-6}$, were extinct. We used the CV of belowground biomass as an automated method for
 193 identifying whether populations are fluctuating at equilibrium (following Thomas et al. (2017)).
 194 After preliminary trials, we chose $CV = 0.02$ as the cutoff between a stable equilibrium and persis-
 195 tent fluctuations, although a slightly larger or smaller cutoff did not change our conclusions (F. Ji,
 196 unpublished results). Visual inspection of simulated time series confirmed that when $CV < 0.02$,
 197 both plant and herbivore populations reach a stable equilibrium point, and when $CV > 0.02$, the
 198 asymptotic dynamics were cyclic or chaotic. To understand the influence of different parameters on
 199 the resulting population dynamics, we map these qualitative outcomes (stable non-zero equilibrium,
 200 fluctuations, or extinction) across two-dimensional “parameter space”: combinations of two varying
 201 parameters, with all other parameter values held fixed.

202
 203 Murdoch et al. (2002) describe the distinction between shorter-period cycles due to intraspecific
 204 density dependence (what they called “single-species cycles”) and longer-period cycles due to the
 205 interaction between tightly coupled consumers and resources. We found local maxima in the simu-
 206 lated herbivore time series and measured the period of fluctuations as the modal interval between
 207 maxima during the last 200 annual time steps. We categorized the population as exhibiting the
 208 typically jagged 2^n -point cycles stemming from discrete-time intraspecific density dependence if the
 209 mode was equal to 2 years, and as the more gradual periodic or quasi-periodic consumer-resource
 210 fluctuations if the mode was larger than 2 years.

211
 212 Because we are ultimately interested in understanding how two plant defensive strategies – over-
 213 compensation and allocation to inedible structures – interact, our final step was to compare our
 214 model to models representing just one of these strategies (Stieha et al., 2016; Thomas et al., 2017).
 215 To understand the interaction, we need to pinpoint which features of our model gave rise to which
 216 new behaviors not seen in either of the previous models. To do this, we made a series of modified
 217 models that turned off overcompensation, juvenile herbivory (when herbivores respond to overcom-
 218 pensation), and/or allocation between above- and belowground biomass pools. We considered both

219 Beverton-Holt (as in our equation (13)) and discrete logistic (as in Thomas et al. (2017)) density
 220 dependence during fall biomass allocation. With the right set of modifications (Supporting In-
 221 formation), we were able to convert our model to (a) one with overcompensation only, without a
 222 cost to belowground biomass stores, equivalent to Stieha et al.’s (2016) overcompensation model
 223 (their equation 8); and (b) one with belowground allocation but no overcompensation, equivalent to
 224 Thomas et al.’s (2017) model. By adding or removing one modification at a time, we can identify
 225 which of our results are due to the interaction between overcompensation and belowground storage,
 226 and which arise from just one mechanism or the other.

227 **Interpretation**

228 We use our model to explore how plant’s allocation strategies influence the shape of population cy-
 229 cles, highlighting the distinction between single-species and consumer resource cycles. Single-species
 230 cycles result from delayed intraspecific density dependence – a high enough reproductive rate allows
 231 the population to boom, resulting in a decrease in the total number of offspring in the next time
 232 step. The characteristic 2-, 4-, $\dots$, or 2^n -point cycles are recognized by a local population peak in
 233 alternate years (Stevens, 2009). When we see biannual herbivore outbreaks, we therefore infer that
 234 intraspecific density dependence (either in the herbivore population itself, or in the plant population
 235 to which the herbivore is responding) is the primary driver of outbreaks. On the other hand, when
 236 we have a buildup of plant biomass over several years, tracked by an herbivore buildup and eventual
 237 crash, we take this as evidence that the consumer-resource interaction is primarily responsible for
 238 herbivore outbreaks.

239
 240 In interpreting the effects of the parameter v , which governs the relationship between herbivore
 241 population density and plant compensatory regrowth, care is required. Smaller values of v indicate
 242 an ability to overcompensate for greater degrees of herbivory (Fig. 2d). Note, however, that our
 243 model always assumes a finite ability to overcompensate: beyond some ratio of herbivores to plant
 244 biomass (i.e. where the curves cross the dashed horizontal 1 line in Fig. 2d), plants cannot fully
 245 make up for biomass lost to herbivory. Plants that are capable of overcompensation up to a higher
 246 threshold ratio, and those that can achieve higher levels of partial compensation when this ratio

is exceeded, will be characterized by a lower v value. However, even a plant that is capable of strong overcompensation (small v) may or may not actually exhibit overcompensation at equilibrium, depending on the equilibrium H to A ratio (Stieha et al. in prep.). In the following discussion of our results, we therefore use v as a measure of the plant's overcompensatory response, but we also specify whether or not overcompensation actually occurs ($A''' > A'$) at equilibrium. For example, for the parameter set used to create Fig. 3a, overcompensation occurs at equilibrium only within the hatched region.

Results

The plant's overcompensation and belowground allocation strategies will determine the equilibrium aboveground biomass after initial spring growth (A') and after overcompensatory regrowth (A'''), as well as the belowground biomass after overcompensation (B'') and after end-of-year belowground allocation (B). These changes in plant biomass in turn affect equilibrium herbivore population density (H ; Fig. 3). Equilibrium aboveground biomass after early-season growth and herbivory, A' , is only very weakly influenced by the plant's overcompensatory response (Fig. 3a), and is much more strongly determined by the plant's allocation strategy to belowground storage (Fig. 3b). Intuitively, we see a much stronger effect of overcompensation on later parts of the plant's seasonal progression. Post-compensation aboveground biomass, A''' , is highest at equilibrium when overcompensation is quite strong (though not so strong as to diminish end-of-year stored biomass; Fig. 3a). As a consequence of these effects on plant biomass, equilibrium herbivore density is also maximized when the plant has a strong (but not maximal, $v \rightarrow 0$) overcompensatory response and allocates heavily ($q = 1$) to belowground stores at the end of each growing season.

Various other parameters also affect how plants respond to herbivory, and the herbivore dynamics that result. For example, Fig. 4 shows that plant dynamics transition from extinction to fluctuations to stable equilibrium as we increase the strength of food limitation experienced by juvenile herbivores, k_2 . Plant dynamics in turn influence the behavior of herbivore populations, which can show ① consumer-resource cycles, ② consumer-resource chaos, ③ single-species chaos, ④ period 3

cycles (a periodic window within the chaotic regime), ⑤ single-species (period 2) cycles, and stable equilibrium. Generally, population fluctuations tend to be of the consumer-resource type with weaker food limitation and of the single-species type with stronger food limitation (this can also be seen in Figures 5b, 5c and 6c). Competition for food is the direct mechanism of density dependent regulation in the herbivore population, so this result makes intuitive sense. It is also possible for plants to persist while herbivores go extinct, though we only saw this for unrealistically strong food limitation (many orders of magnitude higher than what is shown in Fig. 4).

In sum, our model shows how the balance of overcompensation ability and belowground allocation in the plant population drives herbivore population dynamics. Intermediate levels of food limitation promote fluctuations ranging from classic consumer-resource cycles to intraspecific overcompensatory cycles, and both strong overcompensatory ability and large end-of-season allocation to storage lead to higher herbivore densities at equilibrium. These are important insights, but our complete model does not allow us to understand which features stem from the plant's overcompensatory response, versus its allocation strategy, versus the interaction between these two processes. We therefore conclude our analysis by comparing our model to earlier models with overcompensation only (no belowground storage; Stieha et al., 2016) and belowground allocation only (no overcompensation; Thomas et al., 2017). We focus in particular on the conditions that lead to herbivore cycles in each of these models, and the nature of those cycles.

The overcompensation-only model solely exhibits single-species fluctuations (Stieha et al., 2016 and Fig. 5a) because there is no long-term cost to the plant of compensatory regrowth (that model was built to represent crop plants whose density is reset each year via planting). With the addition of the trade-off between regrowth and overwinter biomass storage, both single-species and consumer-resource fluctuations are possible in our model. Our model also shows that herbivore cycles can occur when the plant exhibits actual overcompensation at equilibrium, as opposed to just having the ability to overcompensate at lower-than-equilibrium levels of herbivory. This again is in contrast to the overcompensation-only model (Fig. 5), in which herbivory is too strong in the cyclic regime for overcompensation to occur at equilibrium. In other words, in the overcompensation-only

model, overcompensation does not lead to outbreaks per se (Stieha et al. in prep.). In our model, single-species fluctuations may be triggered by overcompensation, whereas longer period consumer-resource fluctuations mostly occur outside the overcompensation region (Fig. 5). By imposing a tradeoff with belowground allocation, our model reveals a potentially new role of overcompensation per se (not just ability to overcompensate) to promote herbivore fluctuations.

To convert our model to a belowground allocation-only model comparable to Thomas et al. (2017), we remove overcompensation and the second round of herbivory within a season from our model (Supporting Information). Our resulting belowground allocation-only model can exhibit consumer-resource fluctuations but not single-species fluctuations (Fig. 6a). (Thomas et al. (2017) reported single-species cycles in their belowground-allocation-only model, but these appear to be due simply to their use of discrete logistic density dependence in the plant population, as opposed to the Beverton-Holt form we used here.) We also only see consumer-resource fluctuations in our model when overcompensation ability is weak (Fig. 6b). In this case, overcompensation only occurs at equilibrium when belowground allocation is just barely strong enough to support extant plant and herbivore populations (i.e. along the border of the fluctuation region and the extinction region; Fig. 6b). When the overcompensation is strong, weaker food limitation leads to consumer-resource fluctuations and stronger food limitation leads to single-species fluctuations; overall, overcompensation occurs throughout the fluctuation region (Fig. 6c). Again, this suggests a possible role of overcompensation in promoting some of the cycles we observe in our model.

To summarize the joint effects of overcompensation and belowground allocation on population dynamics when these two processes occur simultaneously, we plot dynamical outcomes across the $v-q$ parameter space (Fig. 7). Strong overcompensation (small v) combined with low to medium levels of belowground allocation (low to moderate q) leads to population fluctuations. A higher belowground allocation rate or weaker overcompensatory ability stabilizes the system. When overcompensatory ability is strong enough, population fluctuations may be driven by overcompensation per se (Fig. 7, hatched region).

Discussion

In this paper, we considered the trade-off between overcompensatory regrowth and allocation of energy to inedible reserves and its influence on herbivore population dynamics. Using our model, we examined how different plant allocation strategies influence the properties of insect population dynamics. The equilibrium herbivore density increases when the overcompensatory response is strong (small v) and when the belowground allocation rate is high (large q). The plant's response to herbivory and the resulting herbivore population dynamics are affected by parameters such as strength of food limitation (k_1 and k_2) and degree of herbivore interference (p_1 and p_2). If herbivores are less food limited (small k_1 and/or k_2) or if they interfere less with each other during feeding (small p_1 and/or p_2), they are able to consume more edible plant biomass when the biomass is scarce, driving the edible biomass to even lower levels and promoting consumer-resource fluctuations. These findings are consistent with the results of the classic Rosenzweig-MacArthur model, where a low half-saturation constant in predation destabilizes the system and leads to cycles (Rosenzweig, 1971).

By comparing our model to the overcompensation-only model, we have shown that consumer-resource oscillations are only possible when we additionally consider a long-term cost to plant's compensatory regrowth. In Stieha et al.'s (2016) overcompensation-only model, because the plant biomass is reset to its carrying capacity at the beginning of every year, herbivores can never overexploit the edible biomass in a way that carries over to the next time step. Adding long-term cost to the plant's compensatory regrowth enables a feedback between herbivore feeding and future years' edible biomass, therefore making consumer-resource cycles possible.

The comparison between our model and the belowground allocation-only model (with Beverton-Holt density dependence in belowground stores) shows that single-species fluctuations are only possible when we additionally incorporate strong enough overcompensation. Overcompensating plants regrow more aboveground biomass in response to moderate herbivore damage, resulting in a decrease in the energy reserved for future growth, therefore the total amount of aboveground biomass decreases in the next time step. This delayed density-dependence in resource allocation is the pri-

359 mary driver of cycles. As a consequence, when there is a trade-off between overcompensation and
360 long-term storage, we are more likely to see single-species cycles when overcompensation is strong.

361
362 Our model provides a deeper understanding of the role of overcompensatory regrowth in reg-
363 ulating herbivore population dynamics. Plants only exhibits overcompensation at equilibrium in
364 response to sufficiently mild herbivory. In the overcompensation-only model, herbivory is too strong
365 in the cyclic regime for overcompensation to occur at equilibrium and therefore, therefore herbivore
366 fluctuations are not driven by this mechanism per se. In contrast, our model shows that when there
367 is a cost to overcompensatory regrowth, plants exhibit actual overcompensation at equilibrium in
368 most of the single-species cyclic regime and some of the consumer-resource cyclic regime, suggesting
369 that overcompensation itself may directly contribute to the cyclic dynamics.

370
371 In this paper, we focused on plants with a pool of edible aboveground biomass and inedible
372 belowground storage, although our model can also be applied to any overcompensating perennial
373 plant with separate pools of biomass accessible and inaccessible to a population of herbivores. For
374 example, turfgrasses (*Poaceae* spp.) increase their aboveground biomass in response to root damage
375 by Japanese beetle grubs (*Popillia japonica*; Crutchfield and Potter, 1995). Moreover, while we
376 only consider herbivory damage and compensatory regrowth in the plant's vegetative organs in our
377 model, oftentimes plants experience damage or regrowth in reproductive organs. For example, cot-
378 ton plants (*Gossypium* spp.) increase leaf and root mass in response to early-season flowerbud loss,
379 then they can use the stored energy in roots as well as the energy from photosynthesis to support
380 fruit growth later in the growing season (Sadras, 1996). For cases such as this, our model could be
381 extended to incorporate reproductive damage or regrowth.

382
383 Overall, our analysis reveals factors that determine the equilibrium population density of her-
384 bivores or plants, that promote population fluctuations, and that affect outbreak frequency. This
385 knowledge is relevant to applications such as increasing crop yield in agriculture, pest control, and
386 forest management. By showing that new dynamics arise when different plant allocation strategies
387 occur simultaneously, we highlight the importance of considering trade-offs between different plant

388 tolerance mechanisms in response to herbivory when studying plant-herbivore interactions.

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394 **Declarations**

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398 **Conflicts of interest/Competing interests**

399 The authors have no relevant financial or non-financial interests to disclose.

400 **Availability of data and material**

401 There were no data collected for this study.

402 **Code availability**

403 Code is available upon request.

404 **Author's contributions**

405 Karen Abbott, Christopher Stieha, and Fang Ji conceived the ideas and designed methodology; Fang
406 Ji and Christopher Stieha constructed the model; Fang Ji analysed the model; Fang Ji and Karen

407 Abbott led the writing of the manuscript. All authors contributed critically to the drafts and gave
408 final approval for publication.

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465 **Figures and Tables with Captions**

Figure 1: Schematic showing seasonal progression of aboveground biomass (A), belowground biomass (B), and herbivore (H) in year t . Plants experience spring growth, herbivory by adult insects, compensatory regrowth, herbivory by juvenile insects and allocation of resource back to belowground tissues. Grey arrows indicate the direction of resource allocation (from belowground to aboveground or vice versa). Adult herbivores emerge and feed on aboveground biomass, then lay eggs and die. Juvenile herbivores hatch, start another round of herbivory, then enter pupal stage to overwinter. Description of variables is shown in Table 1.

Figure 2: Effects of (a) density dependence, b , on allocation from belowground to aboveground early in the growing season, $\frac{yB}{1+bB}$, we set $y = 0.9$; (b) interference between adult herbivores, p_1 , on the fraction of edible biomass lost to herbivory, (i.e. herbivory damage; equation (3)); (c) strength of adult herbivore's food limitation, k_1 , on herbivore survival rate (equation (6)); (d) parameter v , indicating the relationship between herbivore density and plant compensatory response, on the fraction of pre-herbivory aboveground biomass that is present after adult herbivory and compensatory regrowth, $1 - zd_1$, the fraction is larger than 1 when regrowth is overcompensatory, smaller values of v represent stronger overcompensation; and (e) density dependence, m , on allocation from aboveground to belowground prior to the onset of winter, $\frac{q}{1+mB}$, we set $q = 0.9$. AG is aboveground and BG is belowground.

Figure 3: Aboveground biomass after initial spring growth (A') and after compensatory regrowth (A'''), belowground biomass after compensatory regrowth (B'') and after end-of-year belowground allocation (B), and herbivore population density (H) at the final time step (10000th) with different levels of (a) v , which governs the relationship between herbivore population density and plant compensatory regrowth, the hatched area is where overcompensation occurs at equilibrium; and (b) q , fraction of aboveground energy allocated to belowground at the end of growing season. Only parameter combinations that lead to a stable equilibrium are considered here, so that final biomass or density can be properly interpreted as the equilibrium biomass or density. The rest of the parameters are: (a) $r = 8$, $y = 0.9$, $b = 0.01$, $q = 0.9$, $m = 0.01$, $p_1 = 0.05$, $p_2 = 10$, $r_p = 50$, $k_1 = 0.5$, $k_2 = 7$, (b) $r = 6$, $y = 0.7$, $b = 0.05$, $v = 5$, $m = 0.5$, $p_1 = 0.5$, $p_2 = 1.5$, $r_p = 2.5$, $k_1 = 0.9$, $k_2 = 0.5$.

Figure 4: Bifurcation diagram of belowground plant biomass during the last 200 annual time steps over a range of food limitation (k_2). Time-series plots show different types of herbivore population dynamics (the last 25-100 time steps) at varying k_2 : ① $k_2 = 1.19$, consumer-resource cycles, ② $k_2 = 1.2$, consumer-resource chaos, ③ $k_2 = 3.2$, single-species chaos, ④ $k_2 = 3.7$, period 3 cycles (a periodic window within the chaotic regime), and ⑤ $k_2 = 5.5$, single-species (period 2) cycles. Other parameters for the bifurcation diagram are: $r = 8$, $y = 0.9$, $b = 0.01$, $v = 1.2$, $q = 0.6$, $m = 0.01$, $p_1 = 0.05$, $p_2 = 10$, $r_p = 50$, $k_1 = 0.5$.

Figure 5: Regions of $k_2 - v$ parameter space where herbivores and plants maintain a stable equilibrium (white), undergo single-species fluctuations (orange), undergo consumer-resource fluctuations (blue), or go extinct (grey) in (a) overcompensation-only model and (b) our overcompensation+allocation model with a lower belowground allocation rate, q , and (c) our overcompensation+allocation model with a higher belowground allocation rate, q . The black hatched areas indicate where overcompensation occurs ($A''' > A'$; equation (7)). Parameters values are (a) $r = 8, y = 0.9, b = 0.01, p_1 = 0.05, p_2 = 10, r_p = 50, q = 10000000, m = 0, k_1 = 0$, in (b) $r = 8, y = 0.9, b = 0.01, p_1 = 0.05, p_2 = 10, r_p = 50, q = 0.6, m = 0.01, k_1 = 0.5$, and (c) $r = 8, y = 0.9, b = 0.01, p_1 = 0.05, p_2 = 10, r_p = 50, q = 0.9, m = 0.01, k_1 = 0.5$.

Figure 6: Regions of $k_1 - q$ parameter space where herbivores and plants maintain a stable equilibrium (white), undergo single-species fluctuations (orange), undergo consumer-resource fluctuations (blue), or go extinct (grey) in (a) belowground allocation - only model, (b) our overcompensation+allocation model with weak overcompensation (large v), and (c) our overcompensation+allocation model with strong overcompensation (small v). The black hatched area indicates where overcompensation occurs at equilibrium. The parameter values are (a) $r = 6, y = 0.7, b = 0.05, c = 0.01, m = 0.5, p_1 = 0.5, p_2 = 1.5, r_p = 2.5, k_2 = 0$ (b) $r = 6, y = 0.7, b = 0.05, p_1 = 0.5, p_2 = 1.5, r_p = 2.5, v = 10, m = 0.5, k_2 = 0.25$, (c) $r = 6, y = 0.7, b = 0.05, p_1 = 0.5, p_2 = 1.5, r_p = 2.5, v = 0.1, m = 0.5, k_2 = 0.25$.

Figure 7: Regions of $v - q$ parameter space where herbivores and plants maintain a stable equilibrium (white), undergo single-species fluctuations (orange), undergo consumer-resource fluctuations (blue), or go extinct (grey) in our model. Parameter v governs the relationship between herbivore population density and plant compensatory regrowth. Smaller v indicates that plants are capable of overcompensating for greater degrees of herbivory. The black hatched area indicates where overcompensation occurs at equilibrium. The other parameters are: $r = 6$, $y = 0.7$, $b = 0.05$, $m = 0.5$, $p_1 = 0.5$, $p_2 = 1.5$, $r_p = 2.5$, $k_1 = k_2 = 1.5$.

Table 1: Description and ranges of variables and parameters in our model. Density and biomass units are arbitrary. *AG* indicates aboveground/edible biomass, *BG* is belowground/inedible biomass.

Notation	Description	Value or range
<i>Initial conditions:</i>		
H_0	Initial herbivore population density	20
A_0	Initial amount of <i>AG</i> biomass	0
B_0	Initial amount of <i>BG</i> biomass	100
<i>Variables:</i>		
A'_t	<i>AG</i> biomass after spring growth	
A''_t	<i>AG</i> biomass after adult herbivore feeding	
A'''_t	<i>AG</i> biomass after compensatory regrowth	
A_t	<i>AG</i> biomass after juvenile herbivore feeding and photosynthetic growth	
B'_t	<i>BG</i> biomass after allocating resources to initiate spring growth	
B''_t	<i>BG</i> biomass after allocating energy for <i>AG</i> compensatory regrowth	
B_t	<i>BG</i> biomass after end-of-year allocation	
H'_t	Adult herbivore density after feeding on aboveground biomass	
H''_t	Juvenile herbivore density after hatching	
H_t	Density of herbivores in the pupal stage prior to the onset of winter	
<i>Parameters:</i>		
r	<i>AG</i> photosynthetic growth factor	1-7
y	Maximum fraction of energy allocated from <i>BG</i> to <i>AG</i> in spring	0.1-1
b	Density-dependence in spring biomass allocation	0.01-1
v	Strength of plant compensatory regrowth (lower is stronger)	0.1-10
q	Maximum fraction of energy allocated from <i>AG</i> to <i>BG</i> in fall	0.1-1
m	Density-dependence in fall energy allocation	0.01-1
p_1	Degree of adult herbivore interference during feeding	0.5-10
p_2	Degree of juvenile herbivore interference during feeding	0.5-10
k_1	Strength of adult herbivore's food limitation	0.5-5
k_2	Strength of juvenile herbivore's food limitation	0.5-5
r_p	Herbivore net reproduction ratio	1-4

Supporting Information

Our model (center column) combined both the ability for plants to exhibit overcompensatory re-
growth in response to herbivory, and the ability to allocate biomass to an inedible pool (e.g. below-
ground structure). By making four modifications to our model (rows), we were able to recover the
overcompensation-only model of Stieha et al. (2016) (left columns) or the inedible allocation-only
model of Thomas et al. (2017) (right columns). Where the same parameter names were used for
different purposes in different models, we use colors to distinguish between the parameters of our
model (black), the parameters in Stieha et al. (blue), and the parameters in Thomas et al. (red).

Overcompensation-only (Stieha et al., 2016)	Conversion ←	Overcompensation + belowground allocation (our model)	Conversion →	Belowground allocation-only (Thomas et al., 2017)
Same amount of edible plant biomass at the start of each year, p	r y $b = \frac{ry}{p}$	<ul style="list-style-type: none"> Early in growing season Plants begin to allocate to aboveground growth; adult herbivores are still overwintering $A'_t = r \frac{yB_{t-1}}{1 + bB_{t-1}}$ $B'_t = B_{t-1} - \frac{yB_{t-1}}{1 + bB_{t-1}}$	$r = r$ $y = y$ $b = b$	$V'_t = \frac{ryS_{t-1}}{1 + bS_{t-1}}$ $S'_t = S_{t-1} - \frac{yS_{t-1}}{1 + bS_{t-1}}$
$d_t = \frac{\hat{H}_{t-1}/p}{c + (\hat{H}_{t-1}/p)}$	$p_1 = c$ $k_1 = 0$	<ul style="list-style-type: none"> Adult herbivores emerge and begin feeding $A''_t = (1 - d_1)A'_t$, $d_1 = \frac{H_{t-1}}{p_1A'_t + H_{t-1}}$ $H'_t = h_1H_{t-1}$, $h_1 = \frac{A'_t}{k_1H_{t-1} + A'_t}$	$p_1 = p$ $k_1 = k$	$V''_t = (1 - d_1)V'_t$, $d_t = \frac{H_t}{pV'_t + H_t}$
$z_t = 1 - \frac{1 + v(\hat{H}_{t-1}/p)}{1 + [v(\hat{H}_{t-1}/p)]^2}$ $\hat{H}_t = r_2\hat{H}_{t-1}$ $s_t = \frac{a_t}{1 + br\hat{H}_{t-1}/[(1 - d_tz_t)p]}$	$r_p = r$ $v = v$ p_2 $q \rightarrow \infty$ $m = 0$ $k_2 = br$	<ul style="list-style-type: none"> Adult herbivores lay eggs then die. Plants respond to damage by allocating more energy aboveground from belowground storage $H''_t = r_p H'_t$ $A''_t = A'_t + \min \left\{ \frac{(1 - z)d_1A'_t}{B'_t}, z = 1 - \frac{1 + \frac{vH_{t-1}}{A'_t}}{1 + (\frac{vH_{t-1}}{A'_t})^2} \right\}$ $B''_t = B'_t - \min \left\{ \frac{(1 - z)d_1A'_t}{B'_t}, z = 1 - \frac{1 + \frac{vH_{t-1}}{A'_t}}{1 + (\frac{vH_{t-1}}{A'_t})^2} \right\}$	$r_p = r_p$ $z = 1 - cB'_t$	$V'''_t = V''_t + cd_1V''_tS'_t$ $S'_t = S''_t - cd_1V''_tS'_t$
		<ul style="list-style-type: none"> Eggs hatch and larvae begin feeding; aboveground biomass grows from photosynthesis energy is allocated back below ground for storage $A_t = (1 - d_2)rA''_t$, $d_2 = \frac{H''_t}{p_2A''_t + H''_t}$ $B_t = B''_t + \frac{qA_t}{1 + mB''_t}$ $H_t = h_2H''_t$, $h_2 = \frac{A''_t}{k_2H''_t + A''_t}$	$d_2 = 1 - \frac{1}{1 + d_1A'_t}$ $q = q$ $k_2 = 0$	$V_t = \frac{rV'''_t}{1 + d_1V''_t}$ $S_t = S''_t + \frac{qV_t}{1 + mS''_t}$ (Beverton-Holt DD instead of discrete logistic) $H_t = r_2h_{t-1}H_{t-1}$, $h_{t-1} = \frac{V'_{t-1}}{kH_{t-1} + V'_{t-1}}$

Converting our model to an overcompensation-only model

Stieha et al. (2016), imagining agricultural plants, assumed that aboveground plant biomass is re-
stored to its (constant) carrying capacity at the beginning of each growing season, while we assume
that aboveground biomass at the start of each year depends on the belowground biomass stored
through the preceding winter. To make our model identical to theirs, we first set plant biomass at

the start of each year to a constant, $A'_t = \frac{ry}{b}$. This is equivalent to assuming unlimited belowground stores (i.e. letting $B_{t-1} \rightarrow \infty$ in equation (1)). We maintain these infinite belowground stores by assuming that plants allocate infinite energy from aboveground at the end of each growing season ($q \rightarrow \infty$ in equation (13)) with no density-dependence ($m = 0$).

Because each growing season's initial edible plant biomass was set to the same carrying capacity, Stieha et al. (2016) did not explicitly model the dynamics of food limitation during the first round of herbivory. To likewise remove any effect of food limitation on adult herbivores in our model, we set adult herbivore survival rate $h_1 = 1$ (equation (6)), which is equivalent to setting food limitation experienced by adult herbivores $k_1 = 0$. Because larval feeding is still affected by food limitation, we keep $k_2 > 0$.

Converting our model to a belowground allocation-only model

To make our model equivalent to the belowground allocation-only model in Thomas et al. (2017), we turned off overcompensation by replacing equation (8) with Thomas et al.'s undercompensatory regrowth function,

$$z = 1 - cB'_t, \tag{16}$$

where c is a constant parameter chosen to be small enough so that $0 \leq z \leq 1$ for all realized values of B'_t .

Next, because Thomas et al. assumed a different insect life history and thus model only one round of herbivory, we remove effects of larval herbivory by setting

$$d_2 = 1 - \frac{1}{1 + d_1 A'_t}, \tag{17}$$

and food limitation experienced by larval herbivores $k_2 = 0$, which guarantees survival rate of larvae $h_2 = 1$.

Figures

Figure 1

Schematic showing seasonal progression of aboveground biomass (A), belowground biomass (B), and herbivore (H) in year t . Plants experience spring growth, herbivory by adult insects, compensatory regrowth, herbivory by juvenile insects and allocation of resource back to belowground tissues. Grey arrows indicate the direction of resource allocation (from belowground to aboveground or vice versa). Adult herbivores emerge and feed on aboveground biomass, then lay eggs and die. Juvenile herbivores hatch, start another round of herbivory, then enter pupal stage to overwinter. Description of variables is shown in Table 1.

Figure 2

Effects of (a) density dependence, b , on allocation from belowground to aboveground early in the growing season $y/(1+bB)$, we set $y = 0.9$; (b) interference between adult herbivores, p_1 , on the fraction of edible biomass lost to herbivory, (i.e. herbivory damage; equation (3)); (c) strength of adult herbivore's food limitation, k_1 , on herbivore survival rate (equation (6)); (d) parameter v , indicating the relationship between herbivore density and plant compensatory response, on the fraction of preherbivory

aboveground biomass that is present after adult herbivory and compensatory regrowth, $1-zd1$, the fraction is larger than 1 when regrowth is overcompensatory, smaller values of v represent stronger overcompensation; and (e) density dependence, m , on allocation from aboveground to belowground prior to the onset of winter, $q/1+mB$, we set $q = 0.9$. AG is aboveground and BG is belowground.

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Aboveground biomass after initial spring growth (A') and after compensatory regrowth (A'''), belowground biomass after compensatory regrowth (B'') and after end-of-year belowground allocation (B), and herbivore population density (H) at the final time step (10000th) with different levels of (a) v , which governs the relationship between herbivore population density and plant compensatory regrowth, the hatched area is where overcompensation occurs at equilibrium; and (b) q , fraction of aboveground energy allocated to belowground at the end of growing season. Only parameter combinations that lead to a stable equilibrium are considered here, so that final biomass or density can be properly interpreted as the equilibrium biomass or density. The rest of the parameters are: (a) $r = 8$, $y = 0.9$, $b = 0.01$, $q = 0.9$, $m = 0.01$, $p1 = 0.05$, $p2 = 10$, $rp = 50$, $k1 = 0.5$, $k2 = 7$, (b) $r = 6$, $y = 0.7$, $b = 0.05$, $v = 5$, $m = 0.5$, $p1 = 0.5$, $p2 = 1.5$, $rp = 2.5$, $k1 = 0.9$, $k2 = 0.5$.

Figure 4

Bifurcation diagram of belowground plant biomass during the last 200 annual time steps over a range of food limitation (k_2). Time-series plots show different types of herbivore population dynamics (the last 25-100 time steps) at varying k_2 : 1 $k_2 = 1:19$, consumer-resource cycles, 2 $k_2 = 1:2$, consumer-resource chaos, 3 $k_2 = 3:2$, single-species chaos, 4 $k_2 = 3:7$, period 3 cycles (a periodic window within the chaotic regime), and 5 $k_2 = 5:5$, single-species (period 2) cycles. Other parameters for the bifurcation diagram are: $r = 8$; $y = 0.9$; $b = 0.01$; $v = 1.2$; $q = 0.6$; $m = 0.01$; $p_1 = 0.05$; $p_2 = 10$; $r_p = 50$; $k_1 = 0.5$.

Figure 5

Regions of k_2 - v parameter space where herbivores and plants maintain a stable equilibrium (white), undergo single-species uctuations (orange), undergo consumer-resource uctuations (blue), or go extinct (grey) in (a) overcompensation-only model and (b) our overcompensation+allocation model with a lower belowground allocation rate, q , and (c) our overcompensation+allocation model with a higher below-ground allocation rate, q . The black hatched areas indicate where overcompensation occurs ($A'' > A'$; equation (7)). Parameters values are (a) $r = 8$; $y = 0.9$; $b = 0.01$; $p_1 = 0.05$; $p_2 = 10$; $r_p = 50$, $q = 100000000$; $m = 0$; $k_1 = 0$, in (b) $r = 8$; $y = 0.9$; $b = 0.01$; $p_1 = 0.05$; $p_2 = 10$; $r_p = 50$, $q = 0.6$; $m = 0.01$; $k_1 = 0.5$, and (c) $r = 8$; $y = 0.9$; $b = 0.01$; $p_1 = 0.05$; $p_2 = 10$; $r_p = 50$, $q = 0.9$; $m = 0.01$; $k_1 = 0.5$.

Figure 6

Regions of k_1 - q parameter space where herbivores and plants maintain a stable equilibrium (white), undergo single-species uctuations (orange), undergo consumer-resource uctuations (blue), or go extinct (grey) in (a) belowground allocation - only model, (b) our overcompensation+allocation model with weak overcompensation (large v), and (c) our overcompensation+allocation model with strong overcompensation (small v). The black hatched area indicates where overcompensation occurs at equilibrium. The parameter values are (a) $r = 6$, $y = 0.7$, $b = 0.05$, $c = 0.01$, $m = 0.5$, $p_1 = 0.5$, $p_2 = 1.5$, $r_p = 2.5$, $k_2 = 0$ (b) $r = 6$;

$y = 0.7$; $b = 0.05$; $p_1 = 0.5$; $p_2 = 1.5$; $r_p = 2.5$, $v = 10$; $m = 0.5$, $k_2 = 0.25$, (c) $r = 6$; $y = 0.7$; $b = 0.05$; $p_1 = 0.5$; $p_2 = 1.5$; $r_p = 2.5$, $v = 0.1$; $m = 0.5$, $k_2 = 0.25$.

Figure 7

Regions of v - q parameter space where herbivores and plants maintain a stable equilibrium (white), undergo single-species oscillations (orange), undergo consumer-resource oscillations (blue), or go extinct (grey) in our model. Parameter v governs the relationship between herbivore population density and plant compensatory regrowth. Smaller v indicates that plants are capable of overcompensating for greater degrees of herbivory. The black hatched area indicates where overcompensation occurs at equilibrium. The other parameters are: $r = 6$, $y = 0.7$, $b = 0.05$, $m = 0.5$, $p_1 = 0.5$, $p_2 = 1.5$, $r_p = 2.5$, $k_1 = k_2 = 1.5$.