



Density regulation of co-occurring herbivores via two indirect effects mediated by biomass and non-specific induced plant defenses

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Received: 13 March 2020 / Accepted: 18 August 2020 / Published online: 26 August 2020
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Abstract

Two herbivorous species that share a single plant can interact indirectly with one another, even without direct interaction. One type of indirect interaction is exploitative resource competition, which results from a reduction in plant biomass; another type is that caused by changes in plant traits. These are referred to as indirect effects, mediated, respectively, by biomass and plant traits. The two indirect effect types often occur simultaneously, and they are difficult to partition. To investigate the roles of the two indirect effects on both herbivores, a dynamic one-plant, two-herbivore system model was analyzed assuming the spatiotemporal co-occurrence of the herbivores and the plants' non-specific induced defenses. Our analysis revealed that the densities of coexisting competitively superior and subordinate herbivores were regulated by negative indirect effects mediated by plant biomass and defense, respectively. This indicates that indirect effects mediated by plant biomass and plant traits can be important regulators of herbivore population size in equilibrium with herbivore coexistence. Our results could be generally applicable to plant–herbivore interactions with non-specific plant defense that is induced through both intra- and transgenerational responses.

Keywords Plant–herbivore interaction · Induced defense · Indirect effect · Population dynamics

Introduction

An ecological theory predicts that plant abundant in the terrestrial ecosystem is maintained by carnivore predation and/or disease of herbivores (HSS hypothesis, Hairston et al. (1960)), although a meta-analysis recently showed that terrestrial plant communities are controlled by top-down effects of herbivores, e.g., via reductions of plant biomass (Jia et al. 2018). Importantly, such top-down effects on plants possibly feed back to dynamics of herbivores. In plant–herbivore interactions on individual plants, two types of plant-mediated effects can alter competitive outcomes among herbivores. One effect

arises from a reduction in the host plant's biomass, resulting in exploitative resource competition. Based on current consensus, which regards exploitative competition as an indirect interaction (Abrams 1987; Kaplan and Denno 2007; Schmitz 2009; Wootton 1994), this is referred to as an indirect effect mediated by plant biomass. In plant–insect interaction, for example, it was reported that exploitative and interference competitions were equally frequent when all herbivore species were considered as a whole (Denno et al. 1995). Another indirect effect is caused by trait changes in plant individuals, referred to as an indirect effect mediated by plant traits. It is widely recognized that indirect effects mediated by traits are ubiquitous and play significant roles in the community dynamics that include various types of interactions, e.g., trophic and mutualistic interactions (Ohgushi 2012; Werner and Peacor 2003), and are typical in plant–herbivore interactions (reviewed by Kaplan and Denno 2007; Ohgushi 2005; Ohgushi 2007; Ohgushi 2012).

Although indirect interactions between herbivore species that are temporally or spatially separated have been investigated frequently (Kaplan and Denno 2007; Ohgushi 2005), they can also occur between spatiotemporally co-occurring species (e.g., Goudard and Loreau 2012), where bi-directional influences between herbivores causes more

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s12080-020-00479-2>) contains supplementary material, which is available to authorized users.

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complex interactions. Importantly, Kaplan and Denno (2007) indicated that defoliation intensity by leaf-chewing insects had no impact on the effect size of heterospecific competitors, although they suspected that even small amounts of herbivory damage can induce systemic defenses with important ecological effects. Therefore, resource competition could be concealed by effect of induced plant defense. Studies of trait-mediated indirect effects and density-mediated indirect effects, a concept analogous to the indirect effects mediated by biomass in a context of population dynamic model, have emphasized that the effects are difficult to distinguish from one another because the two effects jointly influence the dynamics (Anderson 1999; Preisser and Bolnick 2008; Rinehart et al. 2017; Wootton 2002). However, it is expected that partition of the two indirect effects will provide deeper understanding of the organization and maintenance of an ecological community by revealing mechanisms that determine herbivore densities.

Because of the difficulty in partitioning the two types of indirect effects, theoretical studies of trait-mediated indirect effects have usually dealt with the combined effects of density and trait-mediated indirect effects. Despite such limitations, those studies clarified the influences of trait change on the coexistence of interacting species (see below). Research has focused on the defensive traits in lower trophic species, which can be classified into specific and non-specific defenses that affect a single or multiple higher trophic species. Defenses can occur at different phases of the sequence of trophic interactions (Bateman et al. 2014), which may also influence the degree of defense specificity. Note that induced non-specific defenses generally associate with trait-mediated indirect effects via intensification of the defense level in response to attacks from multiple higher trophic species. As the quantitative response to attack intensity is a key factor in induced defenses in both plant–herbivore and prey–predator systems, it has been included in model frameworks. Note also that there are two types of models in those frameworks: non-fitness-based and fitness-based models (Yamamichi et al. 2019), which exclude and include an adaptive determination of the focal trait (i.e., a defense level), respectively.

The non-fitness-based models usually formulate a defensive response by an arbitrary increasing function of density of interacting species. Those are unlikely to include a justification with respect to fitness, by which results could depend on a choice of response function. On the other hand, the fitness-based models are expected to provide more general results because of a consistent framework orienting trait change based on a fitness landscape. The fitness-based models can be further classified into two approaches: the optimal trait and the fitness gradient approaches (Yamamichi et al. 2019). The optimal trait approach assumes that individuals of lower trophic species always adjust their defense levels optimally under the given attack pressure from higher trophic species

at each moment. Alternatively, the fitness gradient approach assumes that induced defenses gradually change along the local fitness gradient to increase individual fitness in response to a changing environment. Note that, the optimal trait approach can always access the highest of the local maxima, while the fitness gradient approach may drive the trait towards a local maximum that is not the global maximum in cases with multiple local fitness maxima, or even a fitness minimum under frequency-dependent selection (Yamamichi et al. 2019). However, when the system involves only a single fitness maximum without frequency dependence, it is expected that results are similar in the two approaches.

The optimal trait approach is adequate for studies of rapid defensive responses, e.g., a behavioral response of prey animal. Matsuda et al. (1993) explored the optimal defense strategy of a single species of prey against two predator species with considering specificity of defense; this was a pioneering study investigating trait-mediated (i.e., behavior-mediated) indirect interactions, which found “indirect mutualism” between two predators via a trade-off between two specific defenses. In order to focus on the fitness effects, they did not study the population dynamics of predators, thus the total effect of defenses on system dynamics remained unclear. Theoretically, Kimbrell et al. (2007) showed that in intraguild predation, the optimization of non-specific vigilance in the prey influences the stability of the dynamics, but they paid no attention to the roles of the two indirect effects mediated by density and traits (i.e., vigilance) on the population dynamics.

On the other hand, the fitness gradient approach is more applicable to responses over generations, e.g., the transgenerational induction of defenses in plants that are considered to result from epigenetic modification (Agrawal 2002; Holeski et al. 2012; Rasmann et al. 2012). van Velzen (2020) modeled one-prey, two-predator system with evolution of prey defense based on the fitness gradient approach, which indicated that evolution of prey defense promotes coexistence of those species. As the fitness gradient approach is conceptually analogous to rapid contemporary evolution, previous studies of defense evolution should also be reviewed here. Matsuda et al. (1996) analyzed the evolution of prey choice in predator species and both specific and non-specific defenses in prey species, in multiple predator, multiple prey systems, which showed that non-specific defenses were unlikely to contribute on community complexity alone in comparison to specific defenses. With specific defense, prey weaken defense against rare predator, which prevents predators from extinction, promoting community complexity. Some researchers focused on evolution of prey defenses in an intraguild predation system, considering evolution both specific and non-specific defenses in shared prey that are effective specifically against consumer and non-specifically against both omnivore and consumer. Ellner and Becks (2011) modeled evolution of defenses in intraguild predation,

showing that the rapid evolution of prey defenses tend to result in oscillation dynamics, modes of which were different from cases without the rapid evolution. Ikegawa et al. (2015) studied effects of evolution of both specific and non-specific defenses of shared prey on species coexistence in an intraguild predation system, showing that a combination of two types of defenses promotes both feasibility and stability of coexistence. These studies clarified the relationships between changes in species or genotypic interaction and community complexity (or coexistence), but did not reveal the role of density- and trait-mediated indirect effects on regulating the population dynamics.

Therefore, the previous studies using fitness-based models did not reveal the relationship between two types of indirect effects. In the present study, to clarify the roles of indirect effects mediated by biomass and trait on the regulation of herbivore densities, we explored a one-plant, two-herbivore system with non-specific induced plant defenses, in which two herbivores co-occur spatiotemporally, by taking the fitness gradient approach.

Mathematical model

We considered two species of herbivore (P and Q) sharing a single plant species (S), focusing on a plant population with overlapping generations within which herbivores can reproduce continuously. The densities of herbivores P and Q in the population are denoted by p and q , respectively, and the biomass of the plant population is defined as s . The basal foraging rates of herbivores P and Q per plant biomass are defined by u and v . The products of the foraging rates and translation efficiencies from foraged plant biomass to herbivore density are denoted by a and b for herbivores P and Q , by which the translation efficiencies are a/u and b/v , respectively. Additionally, the natural mortality rates of P and Q are represented by m_p and m_q . The density dynamics of the two herbivore species and the biomass of the plant population are formulated as

$$\frac{dp}{dt} = ae^{-\alpha x} sp - m_p p \quad (1a)$$

$$\frac{dq}{dt} = be^{-\beta x} sq - m_q q \quad (1b)$$

$$\frac{ds}{dt} = (r - cx)s - ue^{-\alpha x} sp - ve^{-\beta x} sq \quad (1c)$$

where r is the intrinsic biomass growth rate of the plant population and x is the average level of non-specific defense in the population. We consider that the defense level is constrained to be non-negative ($x \geq 0$) because of unrealities of negative defense level that results in greater herbivory than the original level of herbivore species, and in higher plant growth rate than

its intrinsic growth rate. It is assumed that the investment in defenses is approximately uniform among the population's plant individuals; therefore, x may be regarded as the average within the population. When the plant allocates resources to a defensive trait x , the foraging rates of P and Q decrease exponentially as $e^{-\alpha x}$ and $e^{-\beta x}$, respectively. The defense is accompanied by a cost (Strauss et al. 2002), which is assumed to affect the biomass growth as cx , which incorporates trade-offs between investments in defense and in growth.

We consider that changes in plant individuals' defense levels can be induced depending on the herbivory conditions; indeed, in various plant–herbivore systems, the level of induced response in plants is known to increase with herbivore density (Ramirez and Eubanks 2016; Shiojiri et al. 2010; Zheng et al. 2007). To construct a fitness-based model for the plant response, we defined individual plant fitness. Following the above formulation, $(1/s)(ds/dt)$ represents a population growth rate per unit of biomass. An individual's reproductive output may be proportional to the population growth rate per unit of biomass, as the average offspring production of an individual in terms of biomass is a product of the individual biomass and the population growth rate per unit of biomass. Therefore, $(1/s)(ds/dt)$ can be regarded as a proxy for the fitness of an individual with defense level x . Adopting an optimal trait approach (Yamamichi et al. 2019), the optimal defense level at any moment is derived by solving $(1/s)(ds/dt) = 0$ under the given herbivory conditions, although the equation cannot be solved explicitly in Eq. (1c). Instead, we adopted a fitness gradient approach (Yamamichi et al. 2019), assuming that the level of induced defense in the plant population gradually changes at a rate proportional to the individual fitness gradient. Thus, the dynamics of the average defense level would be

$$\frac{dx}{dt} = G \frac{\partial}{\partial x} \left(\frac{1}{s} \frac{ds}{dt} \right) = G(-c + u\alpha e^{-\alpha x} p + v\beta e^{-\beta x} q) \quad (1d)$$

where G is the plant's response speed (Holt and Barfield 2012).

If the defensive trait level in the plant is fixed (i.e., constitutive defense), this system is analogous to the Lotka–Volterra type one-prey, two-predator model, in which either of the predator species generally becomes extinct via competitive exclusion. Specifically, when the defense is absent, the herbivore species P and Q can persist exclusively under $a/m_p > b/m_q$ and $a/m_p < b/m_q$, respectively, which corresponds with Tilman's R^* rule (Tilman 1982). Accordingly, we refer to such species as “superior,” and to the other species as “subordinate.” For example, when $a/m_p < b/m_q$, Q is the superior, and P is the subordinate species.

The effects of defense cost c on equilibrium values can be eliminated by normalizing the defense level and its efficiencies as $\tilde{x} = cx$, $\tilde{\alpha} = \alpha/c$, and $\tilde{\beta} = \beta/c$, as in the following analysis.

Equilibrium in a system without herbivore species Q

First, we considered a case with a single herbivore (i.e., species P without Q). We analyze the dynamics of p , s , and x , ignoring those of q . If $1/\alpha \geq r$ (defense is less effective), a solution of \tilde{x} becomes negative. In this case, \tilde{x} is expected to be 0 due to a constraint of $\tilde{x} \geq 0$; therefore, an equilibrium could be

$$\left(p_1^*, s_1^*, \tilde{x}_1^* \right) = \left(\frac{r}{u}, \frac{m_p}{a}, 0 \right) \quad (2)$$

where asterisks mean equilibrium state. At this equilibrium, $1/\alpha \geq r$ coincides with a condition that a fitness gradient of \tilde{x} is negative or equal to 0 ($dx/dt \leq 0$ in Eq. (1d)), which assure a stability of $\tilde{x} = 0$ on Eq. (2). Therefore, we examine the local stability of $(p_1^*, s_1^*) = (r/u, m_p/a)$ on p - s space, excluding dynamics of defense Eq. (1d). In the absence of defenses (fixing \tilde{x} at 0), the system is analogous to a Lotka–Volterra type one-prey, one-predator system with a neutrally stable equilibrium, which represents continuous oscillation under a given initial condition around this equilibrium. It should be noticed that when the trajectory is distant from the equilibrium (e.g., $p_1^* \ll p$), the selection gradient of \tilde{x} can be positive ($dx/dt > 0$ in

Eq. (1d)), resulting in an increment of \tilde{x} . Indeed, simulations indicate that when the amplitude of oscillation is high, the defense level can be intermittently positively synchronized with high herbivore density. In the long run, however, the intermittent defense expression gradually reduces a level of the peak, eventually resulting in oscillations without defense expression (Fig. 1). On the other hand, when $1/\alpha < r$ (i.e., the defense is more effective), equilibrium may be reached,

$$\left(p_2^*, s_2^*, \tilde{x}_2^* \right) = \left(\frac{1}{\tilde{\alpha}u} e^{\tilde{\alpha}r-1}, \frac{m_p}{a} e^{\tilde{\alpha}r-1}, r - \frac{1}{\tilde{\alpha}} \right) \quad (3)$$

with the defense, which is always locally stable (Appendix 1).

Since the system is symmetric between two herbivores, equilibrium in a case without herbivore species P can be derived by the similar manner.

Equilibrium in a system with both species P and Q

Next, we analyzed the dynamics of a system involving both herbivore species P and Q . The system has an equilibrium where all variables are positive. The equilibrium is

$$\left(p_3^*, q_3^*, s_3^*, \tilde{x}_3^* \right) = \left(\frac{\tilde{\beta}}{u(\tilde{\alpha}-\tilde{\beta})} \left\{ \frac{1}{\tilde{\beta}} - \left(r - \frac{1}{\tilde{\alpha}-\tilde{\beta}} \log \left[\frac{am_q}{bm_p} \right] \right) \right\} \left(\frac{am_q}{bm_p} \right)^{\frac{\tilde{\alpha}}{\tilde{\alpha}-\tilde{\beta}}}, \right. \\ \left. \frac{\tilde{\alpha}}{v(\tilde{\alpha}-\tilde{\beta})} \left\{ \left(r - \frac{1}{\tilde{\alpha}-\tilde{\beta}} \log \left[\frac{am_q}{bm_p} \right] \right) - \frac{1}{\tilde{\alpha}} \right\} \left(\frac{am_q}{bm_p} \right)^{\frac{\tilde{\beta}}{\tilde{\alpha}-\tilde{\beta}}}, \left(\frac{am_q}{bm_p} \right)^{\frac{\tilde{\alpha}}{\tilde{\alpha}-\tilde{\beta}}}, \frac{1}{\tilde{\alpha}-\tilde{\beta}} \log \left[\frac{am_q}{bm_p} \right] \right) \quad (4)$$

which is feasible and stable only when

$$\tilde{\alpha} < \tilde{\beta}, am_q/bm_p < 1 \text{ and } \frac{1}{\tilde{\alpha}^c} > r - \frac{1}{\tilde{\alpha}-\tilde{\beta}^c} \log \left[\frac{am_q}{bm_p} \right] > \frac{1}{\tilde{\beta}^c} \quad (5a)$$

or

$$\tilde{\alpha} > \tilde{\beta}, am_q/bm_p > 1 \text{ and } \frac{1}{\tilde{\alpha}^c} < r - \frac{1}{\tilde{\alpha}-\tilde{\beta}^c} \log \left[\frac{am_q}{bm_p} \right] < \frac{1}{\tilde{\beta}^c} \quad (5b)$$

(Appendix 2). It should be noted that conditions (5a) and (5b) correspond to cases where the superior species are Q and P , respectively (i.e., $a/m_p < b/m_q$ and $a/m_p > b/m_q$). Remarkably, Eq. (5) corresponds to the unfeasibility/instability conditions of the equilibria (and neutrally stable orbits) with either herbivore alone (P or Q) (Appendix 2). Notably, the result suggests that when two herbivores coexist, plants generally express some levels of induced defense, i.e., $\tilde{x}_3^* > 0$. Eq. (4) indicates that, a cost of defense (c) does not

affect equilibrium levels of plant biomass (s) and induced defense (x) (note that $\tilde{x} = cx$, $\tilde{\alpha} = \alpha/c$, and $\tilde{\beta} = \beta/c$). This is consistent with result of van Velzen (2020) that analyzed defense evolution of prey species by simulations in one-prey, two-predator systems, where prey density and defense are constant independently of defense cost in cases of stable coexistence.

Results

Generally, a Lotka–Volterra-type one-prey two-predator system leads to the extinction of either predator species by competitive exclusion through the shared resource (i.e., R^* rule). This is also true for a constitutive defense with a fixed level because it only decreases the predation rate by a constant amount and can be regarded as a single component of the

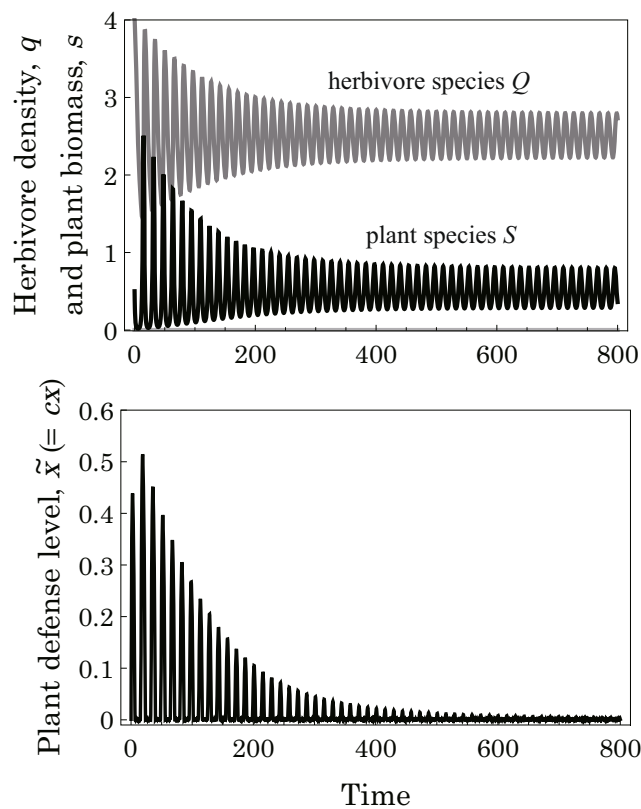


Fig. 1 An example of simulation. In this case, an equilibrium state is coexistence of herbivore species *P* and plant without defense, which is neutrally stable (see Eq. (2)). If an initial density of herbivore *P* significantly differs from equilibrium value, plant could express induced defense intermittently. After some period, induced defense disappears, resulting in oscillation of herbivore density and plant biomass without defense. Parameters are $a=0.2$, $b=1$, $m_p=m_q=0.1$, $c=1$, $u=v=0.8$, $r=2$, and $G=1$, $\alpha=0.45$ and $\beta=0.25$

parameters. However, non-specific induced defenses can facilitate the stable coexistence of two herbivores (Eqs. (4) and (5)). This is possible only when plant individuals flexibly alter their induced defense levels in response to instantaneous herbivory pressure.

The above analysis indicates that the feasibilities and stabilities of equilibria depend on four parameters: r (an intrinsic biomass growth rate of the plant population), $\tilde{\alpha}$ and $\tilde{\beta}$ (normalized defense efficiencies of species *P* and *Q*), and am_q/bm_p (a and b are products of foraging rates and translation efficiencies from plant biomass to herbivore density, whereas m_p and m_q are natural mortality rates of species *P* and *Q*). The parameter dependences of the equilibria are summarized in Fig. 2, where species *Q* and *P* are assumed to be the superior and subordinate species, respectively (i.e., $am_q/bm_p < 1$). As shown in Fig. 2, the coexistence of two herbivores tends to occur when the subordinate herbivore *P* is more tolerant to plant defenses ($\tilde{\alpha} < \tilde{\beta}$) with either relatively high or low $\tilde{\alpha}$ (the dark gray region in Fig. 2). However, when $\tilde{\alpha}$ is intermediate within such a region, the subordinate herbivore can

persist to the exclusion of the superior herbivore (the light gray region in Fig. 2), where the coexisting equilibrium is unstable. If the herbivore *P* is significantly tolerant ($\tilde{\alpha} \ll \tilde{\beta}$), a suppression of the herbivory *P* is costly. In this case, the plant defense mainly targets the susceptible *Q*, the superior herbivore, by which the equilibrium defense level becomes relatively low (see Eq. (4)), resulting in their coexistence. Furthermore, when $\tilde{\alpha}$ becomes large and relatively approaches $\tilde{\beta}$, both herbivore species *P* and *Q* are similarly tolerant to plant defense, which could reduce a difference in effect of plant defense between herbivores, resulting in their coexistence in a narrow parameter region.

We can graphically derive and represent the resulting equilibria of the ecological system along environmental gradients by illustrating zero net growth isocline, i.e., ZNGI (Chase and Leibold 2003). For cases that are indicated by circles in the middle panel of Fig. 2, ZNGIs are plotted in Fig. 3. In this figure, each curve bounds regions, above and below which a herbivore species decreases and increases its density, respectively. An intersection of two curves can be a candidate of coexisting equilibrium of two herbivore species, although its stability is not ensured because of an ignorance of dynamics of biomass and defense of plant in these plots. Black and gray discs represent equilibrium values of biomass and defense of plant in the absence of herbivore species *Q* and *P*, respectively. If the black disc locates below the gray curve, it means that herbivore *Q* can increase in the equilibrium with plant and herbivore *P*. On the other hand, if the gray disc is below the black curve, herbivore *P* can increase in the equilibrium with plant and herbivore *Q*. According to Fig. 3, there are no coexisting equilibrium in panels (d), (g), and (h), where herbivore *Q* can increase in the equilibrium with plant and herbivore *P*. On ZNGI plot, the stability of equilibrium state was often examined by illustrating “impact vectors” and “supply point.” It should be noticed that such an approach is possible in linear systems where an external input of resource or nutrient limits system growth. The analyzed model does not satisfy those conditions because of nonlinear dynamics of defense x and a divergence of plant biomass s in the absence of herbivores. Therefore, the stability of equilibrium cannot be discussed by such an approach in the considered system.

We compared equilibria (2), (3), and (4) to examine the differences in variables between single herbivore conditions with either herbivore and with coexistence of two herbivores under condition (5a), where herbivores *P* and *Q* are the subordinate and superior species, respectively. First, we compared the conditions with subordinate herbivore *P* alone and those with coexistence. As is shown in Appendix 3, where coexistence with *Q* occurs, the subordinate herbivore’s density p^* becomes smaller, whereas the plant defense \tilde{x}^* and the plant biomass s^* are increased (see Table 1). It is remarkable

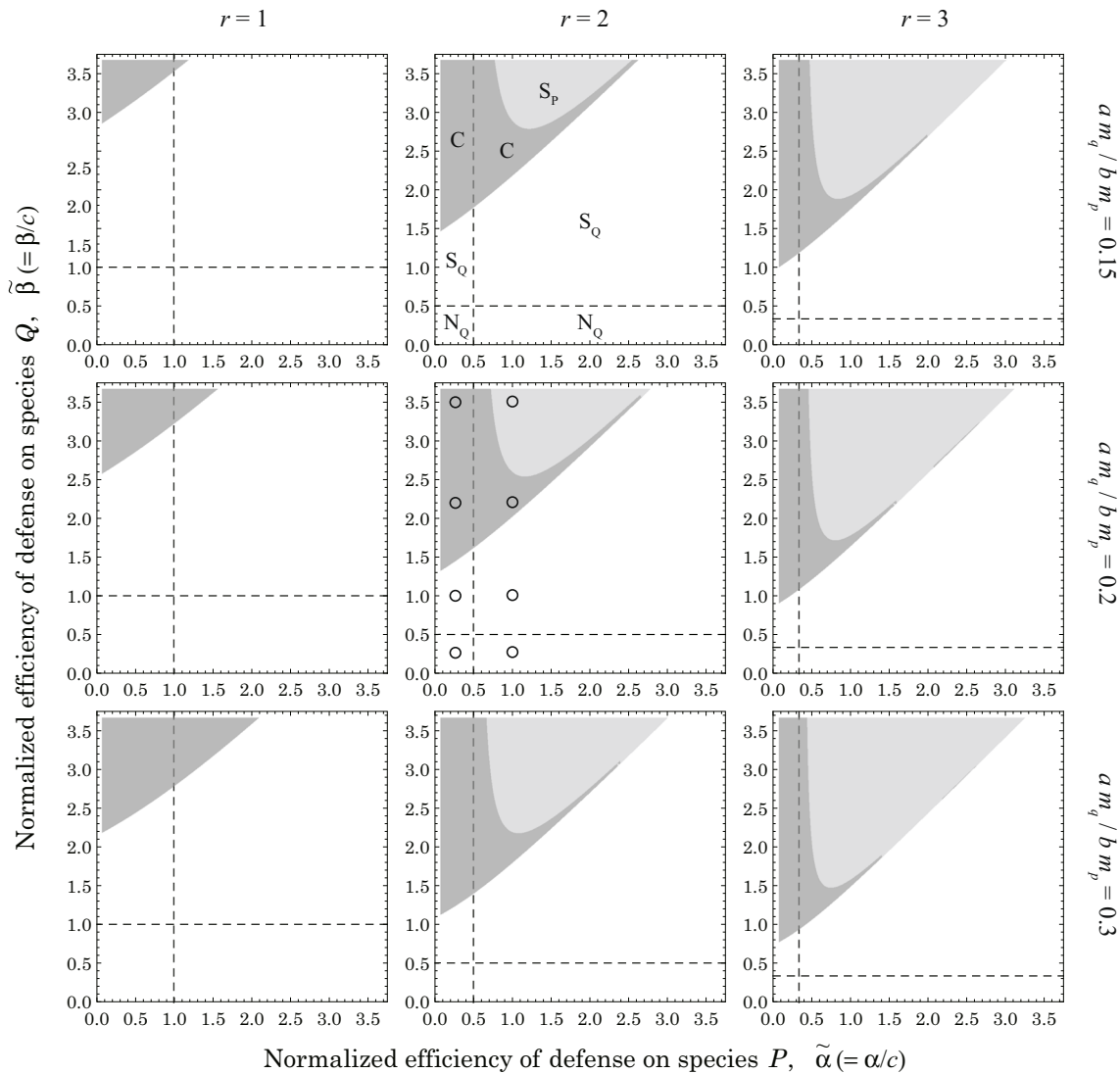


Fig. 2 Analytical results of parameter dependences of equilibrium state with superior species Q and subordinate species P . In the white region, species Q ultimately excludes species P by competitive exclusion, leading either to stable equilibrium with plant defense (S_Q) or a neutrally stable state without defense (N_Q , i.e., $\tilde{\beta} < 1/r$). In the light gray region, species P remains stably with plant defense (S_P). In the dark gray region, species P and Q coexist stably with plant defense (C). Where $\tilde{\alpha} < 1/r$ (vertical dashed lines), a co-occurrence of plant and species P can be a neutrally

stable equilibrium without plant defense, in the absence of species Q . On the other hand, if $\tilde{\beta} < 1/r$ (dashed lines), a co-occurrence of plant and species Q can be a neutrally stable equilibrium without plant defense, in the absence of species P . In those cases, oscillation is possible with arbitrary closed orbits. Circles on the mid-panel indicate parameter sets whose dynamics are plotted in Figs. 3, 4, and 5. Common parameters are $b = 1$, and $m_p = m_q = 0.1$, whereas $a = 0.15, 0.2$ and 0.3 in top, middle and bottom panels, respectively

that the subordinate herbivore’s density decreases despite the increment in resources. From this, it can be concluded that the subordinate species is suppressed by increased defense levels; that is, the indirect effect mediated by plant defenses tends to regulate the subordinate species’ density. The equilibrium (2) was neutrally stable with potentially closed orbits, where the temporal average of each orbit over a given period is known to correspond to the equilibrium value (Volterra 1928). Therefore, the analytical results of the equilibrium can also capture trends in the system’s average properties. Those trends are also shown by ZNGIs in Fig. 3, in which panels (a), (b), and (f) involve stable coexistence equilibrium of two

herbivore species (see also Fig. 2). In comparison between the equilibrium with coexistence and that with one herbivore species only, we can confirm the change of plant defense and plant biomass after introduction of another herbivore species, which is consistent to analytical results.

We also confirmed these results using simulations based on Eq. (1), introducing a superior herbivore Q into a system of the subordinate herbivore P and plants, as illustrated in Fig. 4 with identical conditions with those at circles in the middle panel of Fig. 2. In the simulations, when a plant defense level becomes negative, we replace it by a slightly positive value (i.e., $x = 0.001$). This treatment operationally ensures x to stay near 0

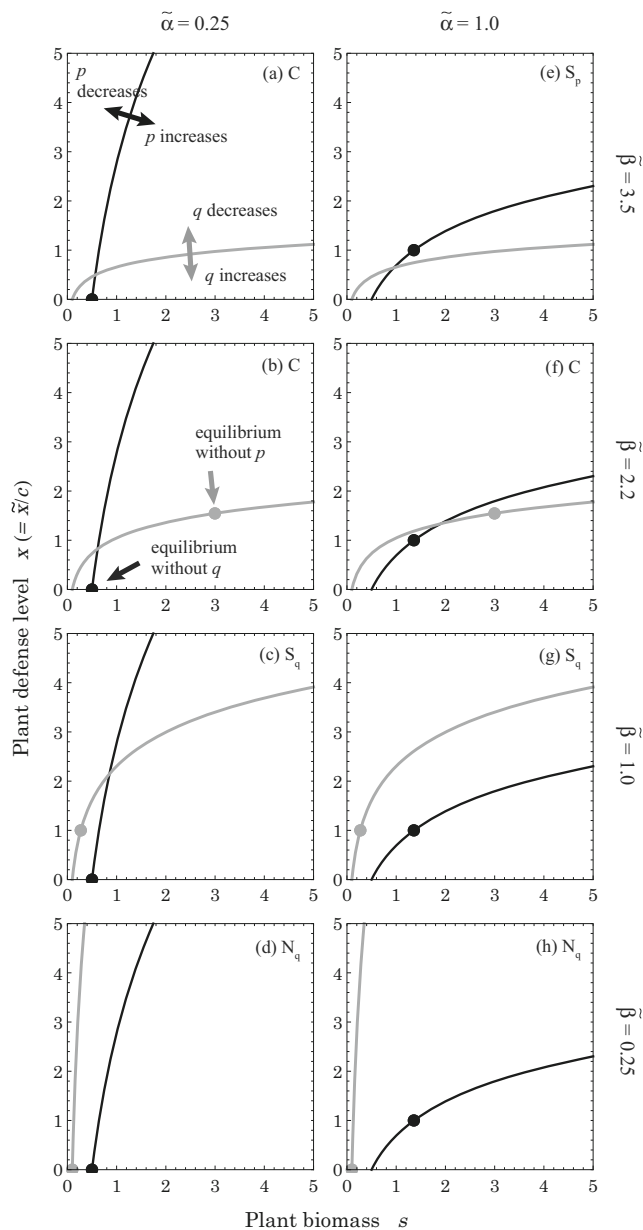


Fig. 3 Zero net growth isoclines (ZNGI) of two herbivore species under the parameter sets that are indicated by the circles in Fig. 2. Each curve bounds regions, above and below which a herbivore species decreases and increases, respectively. Black and gray discs represent equilibrium values of biomass and defense of plant in the absence of herbivore species *Q* and *P*, respectively. Common parameters are as in the middle panel of Fig. 2, i.e., $a = 0.2$, $b = 1$, $r = 2$, and $m_p = m_q = 0.1$, and additional parameter is $c = 1$

under a negative selection gradient (i.e., a decreasing trend), and enable x to increase from 0 under a positive selection gradient (i.e., a switch to increasing trend) (see Eq. (1d)). Figure 4 shows that, before the introduction of species *Q*, the dynamics reached a stable equilibrium when $\tilde{\alpha} > 1/r$, but oscillated around a neutrally stable equilibrium when $\tilde{\alpha} \leq 1/r$. After the introduction of *Q*, the dynamic was significantly altered, except in the scenario shown in Fig. 4(e), resulting

Table 1 Differences in the densities of herbivores, biomass, and defense levels of plants between cases with a single herbivore species and with coexistence of two herbivore species, where species *P* and *Q* are subordinate and superior herbivores, respectively

	<i>P</i> and <i>Q</i> in comparison to <i>P</i> alone	<i>P</i> and <i>Q</i> in comparison to <i>Q</i> alone
<i>P</i> (subordinate)	Decrease	–
<i>Q</i> (superior)	–	Decrease
<i>S</i>	Increase	Decrease
\tilde{x}	Increase	Decrease

in either the extinction of the subordinate species *P* or stable coexistence. This figure shows that coexistence with superior species causes a decline in the density of the subordinate species (p), accompanied by incremental changes in both plant biomass (s) and plant defense levels (\tilde{x}) (Fig. 4(a), (b), and (f)).

In the presented analysis, we analytically prove that coexisting equilibria with plant defense are always locally stable (see Appendix 2). However, it should be remarked that when a response speed G is small, simulations tend to represent oscillation around equilibrium despite of its stability. In addition, a magnitude of oscillation depends on initial condition even with a unique parameter set, likewise a neutral stability. With small G values, a real part of maximum eigenvalue is negative, although its absolute value becomes small. In this case, dynamics around the equilibrium is sensitive to an error in numerical calculation, which may result in unexpected oscillations.

Next, we compared conditions with the superior herbivore *Q* alone and conditions with both herbivores *P* and *Q*. According to Appendix 3, under coexistence with *P*, the superior herbivore’s density q^* , the plant defense level \tilde{x}^* , and the plant biomass s^* decreased (see Table 1). This trend may be consistent with the suppression of a superior species via resource depression; that is, the indirect effect mediated by plant biomass tends to regulate the superior species’ density. This trend is confirmed by simulations, which is shown in Fig. 5.

Discussion

In the presented study, we indicate that indirect effects mediated by plant traits and plant biomass are important regulators of herbivore population size in equilibrium with herbivore coexistence, by using a fitness gradient approach. When the fitness function is simple (i.e., having neither multiple maxima nor frequency dependence), both optimal trait and fitness gradient approaches are expected to result in similar consequences (Yamamichi et al. 2019). Since our model satisfies this condition, the results may be generally applicable to both intra- and transgenerational responses in non-specific plant

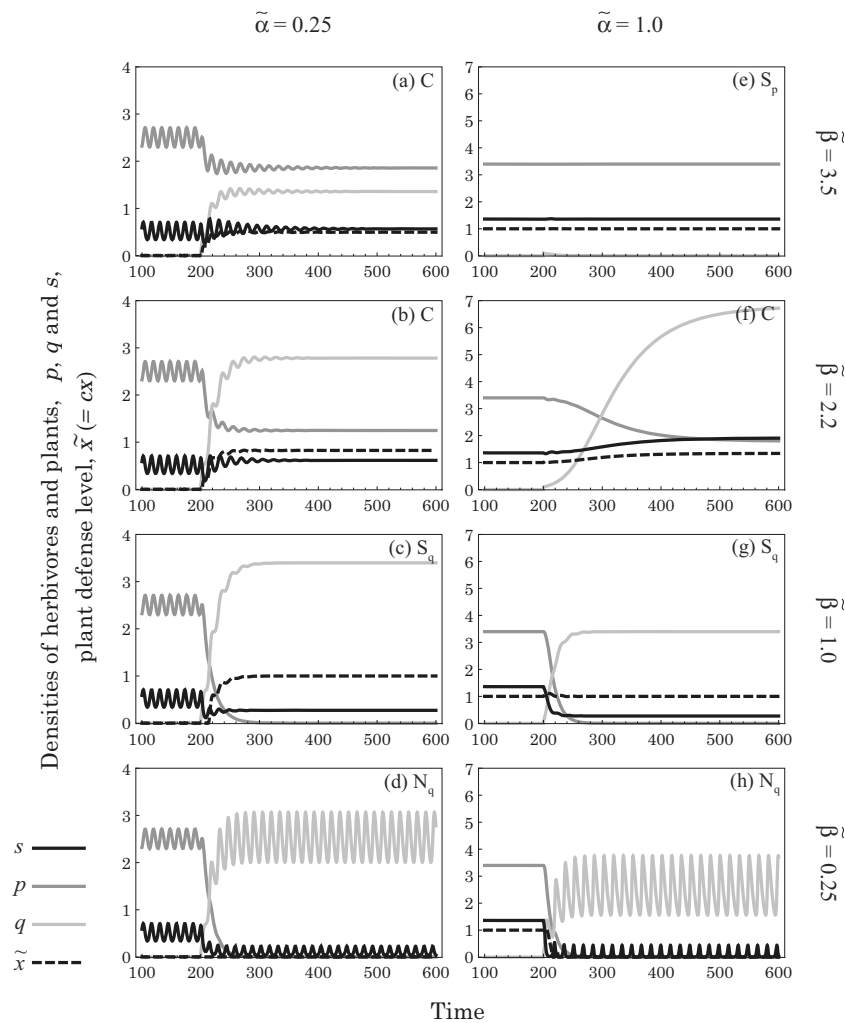


Fig. 4 Examples of simulations using the parameter sets that are indicated by the circles in Fig. 2. Superior species Q (q) invades a system that initially included plant (s) and subordinate species P (p) only. Under the given parameter values, the equilibrium without species Q is neutrally stable at $\tilde{\alpha} = 0.25$ without plant defenses, but stable at $\tilde{\alpha} = 1.0$ with plant defenses. At 200 time steps, the superior species Q is subsequently introduced with $q = 0.1$. The neutral stability of equilibrium results in oscillating dynamics. The letters on the panels, C, S_p , S_q , and N_q , represent the categories of the equilibrium after introduction (see Fig.

2). Common parameters are as in the middle panel of Fig. 2, i.e., $a = 0.2$, $b = 1$, $r = 2$, and $m_p = m_q = 0.1$, and additional parameters are $c = 1$, $u = v = 0.8$ and $G = 1$. The initial conditions of (a)–(d) are equilibrium value except for p , i.e., $(p, s, x) = (r/u - 0.2, m_p/a, 0)$, where p is smaller than equilibrium value by 0.2. On the other hand, the initial conditions of (e)–(f) are equilibrium values, i.e., $(p, s, x) = ((1/\tilde{\alpha}u)e^{\tilde{\alpha}r-1}, (m_p/a)e^{\tilde{\alpha}r-1}, r-1/\tilde{\alpha})$

defenses. In addition, it has been known that in a plant species, multiple insects often induce an identical plant defensive substance (secondary metabolite, enzyme, etc.) with toxic and/or repellent effects (Chen 2008), which suggested that induced plant defenses can be non-specific against multiple herbivores in many cases. Thus, the results of presented analysis are expected to be applicable to a wide range of plant–herbivore systems.

Reciprocal dominance of the two types of plant-mediated indirect effects

It has been pointed out that density- and trait-mediated indirect effects are not easily distinguished from one another

(Anderson 1999; Preisser and Bolnick 2008; Rinehart et al. 2017; Wootton 2002). In the present study, focusing on the indirect effects mediated by plant biomass and non-specific induced defenses, we revealed that, where two herbivore species coexist on a single host plant, the densities of competitively superior and subordinate herbivores are regulated by negative indirect effects mediated by plant biomass and plant defenses, respectively. This suggests that when herbivores coexist in a single host plant population, two types of indirect effect are generally at play in the system and apparently regulate the respective densities of each herbivore.

The analysis shows that, to facilitate the coexistence of two herbivore species, the subordinate species must be less susceptible to the plant’s defenses (see Eq. (5)). It appears

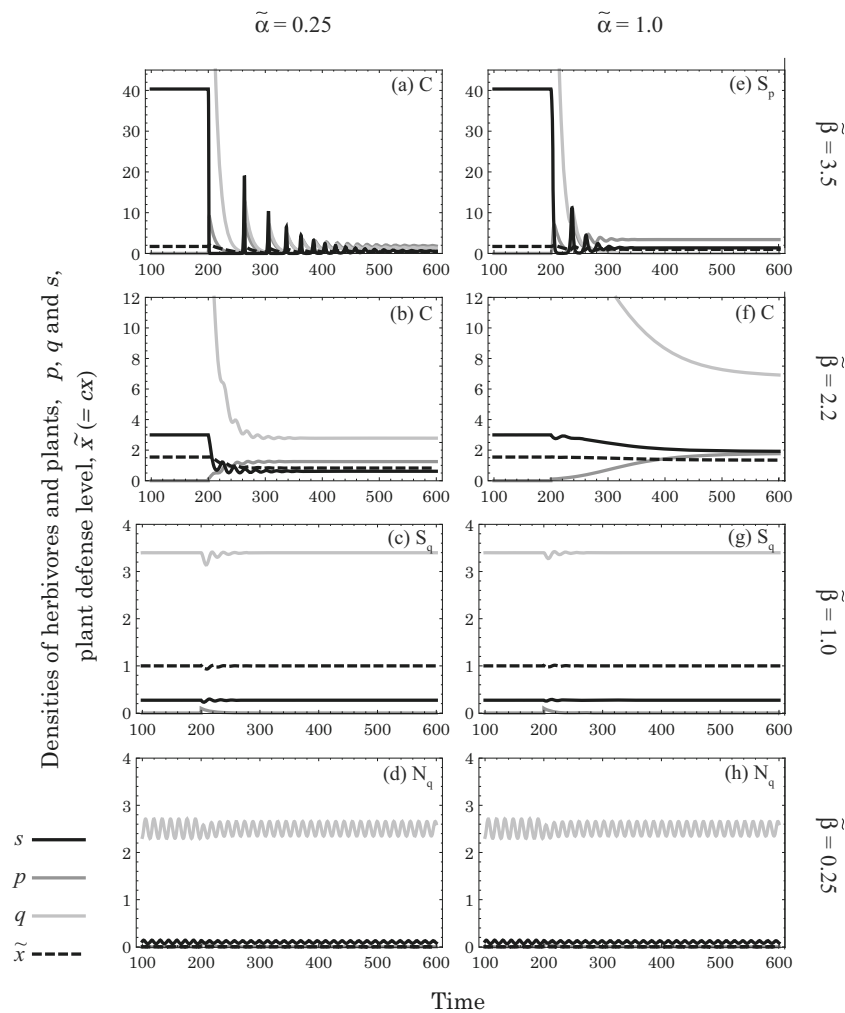


Fig. 5 Examples of simulations with the parameter sets indicated by circles in Fig. 2. Subordinate species P (p) invades a system initially included the plant (s) and the superior herbivore Q (q) only. Under the given parameter values, the equilibrium without species P is neutrally stable at $\tilde{\beta} = 0.25$ without plant defenses, but stable at $\tilde{\beta} > 0.5$ with plant defenses. The neutral stability of the equilibrium results in oscillating dynamics. At 200 time steps, the subordinate species P is subsequently introduced with $p = 0.1$. The letters on the panels, C, S_p , S_q , and N_q , represent the categories of the equilibrium

after introduction (see Fig. 2). Common parameters are as in the middle panel of Fig. 2, i.e., $a = 0.2$, $b = 1$, $r = 2$, and $m_p = m_q = 0.1$, and additional parameters are $c = 1$, $u = v = 0.8$ and $G = 1$. The initial conditions of (a)–(c) and (e)–(g) are equilibrium values, i.e., $(q, s, x) = \left(\left(\frac{1}{\tilde{\beta}v} \right) e^{\tilde{\beta}r-1}, \left(\frac{m_q}{b} \right) e^{\tilde{\beta}r-1}, r-1/\tilde{\beta} \right)$. On the other hand, the initial conditions of (d) and (h) are equilibrium value except for q , i.e., $(q, s, x) = (r/v - 0.2, m_q/b, 0)$, where q is smaller than equilibrium value by 0.2

paradoxical that the subordinate herbivore, with lower susceptibility to the defense, tends to be regulated by the indirect effect that is mediated by induced defenses. This results from the plant’s response to the superior herbivore. A plant originally develops relatively low defense levels against the subordinate species with lower susceptibility due to the inefficiency of the defense. In response to the presence of an exploitatively superior species that has higher susceptibility, it is advantageous for plants to develop intensified defenses. The intensified induced defense negatively affects the subordinate species and reduces its density. Conversely, in comparison to the sole presence of the superior species, the coexistence of two herbivores is accompanied by a lower defense level. In this case, the intrusion of a tolerant subordinate herbivore

causes a decline of defense level of the plant due to a decreasing advantage of defenses, causing a dominance of the indirect effect mediated by plant biomass. Consequently, both types of indirect effect may be simultaneously instrumental in regulating the density or biomass of interacting species sharing a common resource at a similar trophic level.

Coexistence of two herbivores under non-specific induced plant defenses

Plants’ non-specific induced defenses can facilitate the coexistence of two herbivores that are exclusive of one another in the absence of the defense. Matsuda et al. (1996) studied the effects of the evolution of specific and non-specific defenses

on community complexity in multiple predator, multiple prey systems using computer simulations, and demonstrated that the effects of non-specific defenses were minor in both two-predator, two-prey and ten-predator, ten-prey systems. Adopting the analogous model scheme, we focused on the effects of non-specific defenses in a one-plant two-herbivore system, which clearly illustrates the promotional effects of plants' non-specific inducible defenses on the coexistence of herbivores, and analytically determines the conditions for coexistence. Matsuda et al. (1996) analyzed evolution of prey choice in predator species and both specific and non-specific defenses in prey species, in multiple predator, multiple prey systems. They examined structures of established food webs in simulations with randomly choosing basal growth rates of predators that are analogous to our parameters a and b . They concluded that non-specific defenses were unlikely to contribute to community complexity alone, which may be inconsistent to our result. One reason of the inconsistency might be the evolution of prey choice in the presence of multiple prey species, which are not included in our analysis due to considering a single host plant species only. In addition to this, in our analysis, Fig. 2 indicates that a possibility of coexistence of herbivores also significantly depends on other parameters than a and b , which may suggest that promotional effects of non-specific defenses on species coexistence are difficult to be detected by varying the basal growth rates of predators only.

Significantly, the coexistence of two herbivores is possible only when the superior species is more susceptible to plant defenses than the subordinate species is, that is, when $\tilde{\alpha} < \tilde{\beta}$ (or $\tilde{\alpha} > \tilde{\beta}$) under $a/m_p < b/m_q$ (or $a/m_p > b/m_q$) (see condition (5)). In this case, the negative effect of the plant's induced defense can negate the advantage held by the superior species in resource competition, resulting in a balance between the two herbivores' population growth rates. This implies that plants' non-specific induced defenses can "rescue" the subordinate herbivorous species from extinction. However, for the coexistence of more than two species of herbivore, it may become necessary to consider multiple phenotypic traits of plants, as in Anderson et al. (2009).

Future directions

The past two decades have seen significant advances in our understanding of the role played by indirect effects in structuring biotic communities (Ohgushi et al. 2012). At this point, therefore, it is appropriate to integrate density- and trait-mediated indirect effects and to assess how they interact with one another over long timescales. It may not be easy to test experimentally results of the present analysis because the model focuses on equilibrium state of herbivore densities and plant biomass, which could be achieved through long-term transgenerational dynamics. If presence-absence status

of herbivore species varies regionally, our predictions could be tested by comparing equilibrium states between regions with and without herbivore species. However, in such a regional comparison, we have to pay attention to a reason of variation of species distribution. An adequate comparison requires an identical environmental condition among regions; therefore, the presence and absence of species must be determined by chance, e.g., via a difference in invasion processes.

The integration of different types of indirect effects can yield profound insights and more precise predictions that are unlikely to be derived from investigations of a single type of indirect effect. We believe that expansion of the temporal scale can enrich our conceptual perspectives on indirect effects across a wide range of ecosystems, including prey-predator systems.

Acknowledgments We thank the members of the Centre for Ecological Research for their comments and encouragement. We wish to thank two anonymous reviewers for their helpful comments and suggestions.

Funding information This research was supported financially by JSPS KAKENHI Grant Numbers 19K06851. This research was partly supported by the International Research Unit of Advanced Future Studies at Kyoto University.

Appendix 1. Local stability of equilibrium in a system without herbivore species Q

At the equilibrium (3) with $x^* > 0$, a characteristic polynomial of dynamic equation (1a), (1c), and (1d) is

$$\lambda^3 + Gc^2\tilde{\alpha}\lambda^2 + \left(\frac{m_p}{\tilde{\alpha}} + Gc^2m_p\tilde{\alpha}\right)\lambda + Gc^2m_p = 0 \quad (\text{A1})$$

Since all coefficients are positive, the real parts of all possible solutions of λ are negative when

$$Gc^2\tilde{\alpha}\left(\frac{m_p}{\tilde{\alpha}} + Gc^2m_p\tilde{\alpha}\right) - Gc^2m_p = G^2c^2\tilde{\alpha}^2m_p > 0 \quad (\text{A2})$$

from the Routh–Hurwitz stability criterion. The condition holds explicitly; therefore, the equilibrium is always locally stable.

Appendix 2. Local stability of equilibrium in a system with both species P and Q

Equilibrium with a single herbivore species P

- (i) In the absence of the plant's induced defenses, $x^* = 0$.

In this case, we examine the stability of equilibrium

$$(p_1^*, q_1^*, s_1^*, \tilde{x}_1^*) = \left(\frac{r}{u}, 0, \frac{m_p}{a}, 0\right) \tag{B1}$$

with full dynamics Eqs. (1a–d) (see Eq. (2)). The stability of equilibrium (B1) is relatively difficult to consider directly because the defense level $x^* = 0$ is a boundary equilibrium at which dx/dt should be negative, rather than 0, corresponding to $1/\alpha \sim \geq r$. We analyzed the stability of equilibrium (B1), ignoring dynamics of x with under $1/\alpha \sim \geq r$. According to the eigenvalues of the system without dynamics of x , it is neutrally stable when $am_q / bm_p > 1$.

When the equilibrium (B1) is neutrally stable, numerous oscillating orbits may arise around the equilibrium. We may also consider the orbits' stability following Volterra's (1928) analysis. For a periodic solution with period T , Eq. (1) can yield

$$\frac{1}{p} \frac{dp}{dt} = \frac{d \log p}{dt} = as - m_p \log p(T) - \log p(0) = a \int_0^T s(t) dt - m_p T = 0 \tag{B2a}$$

and

$$\bar{s} = \frac{1}{T} \int_0^T s(t) dt = \frac{m_p}{a}, \text{ and } \bar{p} = \frac{1}{T} \int_0^T p(t) dt = \frac{r}{u}. \tag{B2b}$$

Thus,

$$\log q(T) - \log q(0) = b \int_0^T s(t) dt - m_q T > 0, \text{ if } \bar{s} = \frac{m_p}{a} > \frac{m_q}{b} \tag{B2c}$$

and $q(t)$ increases along the periodic orbit over the period T . Therefore, any planar periodic orbit repels if the planar

equilibrium repels.

(ii) In the presence of the plant's induced defenses, $x^* > 0$.

In this case, we examine the stability of equilibrium

$$(p_2^*, q_2^*, s_2^*, \tilde{x}_2^*) = \left(\frac{1}{\tilde{\alpha}u} e^{\tilde{\alpha}r-1}, 0, \frac{m_p}{a} e^{\tilde{\alpha}r-1}, r - \frac{1}{\tilde{\alpha}}\right) \tag{B3}$$

with full dynamics Eq. (1a-d) (see Eq. (3)). This is feasible only when $1/\alpha \sim < r$, which is necessary for $x^* > 0$. The system has four eigenvalues at equilibrium, although three of these are identical to the eigenvalues of equilibrium without the dynamics of q (i.e., equilibrium (3)). The remaining eigenvalue determines the stability of equilibrium (B3) against an invasion of Q . When it is positive, species Q may increase at the equilibrium. The stability condition of Eq. (B3) is

$$\tilde{\alpha} < \tilde{\beta} \text{ and } \frac{1}{\alpha \sim} < r - \frac{1}{\alpha \sim - \tilde{\beta} \sim} \log \left[\frac{am_q}{bm_p} \right] \tag{B4a}$$

or

$$\tilde{\alpha} > \tilde{\beta} \text{ and } \frac{1}{\tilde{\alpha}} > r - \frac{1}{\tilde{\alpha} - \tilde{\beta}} \log \left[\frac{am_q}{bm_p} \right]. \tag{B4b}$$

Equilibrium with two herbivore species P and Q

A characteristic polynomial of the system at equilibrium (4) is

$$\lambda^4 + G \frac{1}{2} c^2 \{ \tilde{\alpha}(1+B) + \tilde{\beta}(1-A) \} \lambda^3 + \frac{1}{\tilde{\alpha} - \tilde{\beta}} \left\{ m_q \left(1 + Gc^2 \tilde{\beta}^2 \right) A + m_p \left(1 + Gc^2 \tilde{\alpha}^2 \right) B \right\} \lambda^2 + \frac{1}{2} \frac{G}{\tilde{\alpha} - \tilde{\beta}} c^2 \{ \tilde{\alpha}(1+B) + \tilde{\beta}(1-A) \} (m_q A + m_p B) \lambda + Gc^2 m_p m_q A B = 0 \tag{B5a}$$

where

$$A = \tilde{\alpha} \left\{ \left(r - \frac{1}{\tilde{\alpha} - \tilde{\beta}} \log \left[\frac{am_q}{bm_p} \right] \right) - \frac{1}{\tilde{\alpha}} \right\} \tag{B5b}$$

$$B = \tilde{\beta} \left\{ \frac{1}{\tilde{\beta}} - \left(r - \frac{1}{\tilde{\alpha} - \tilde{\beta}} \log \left[\frac{am_q}{bm_p} \right] \right) \right\} \tag{B5c}$$

According to the feasibility of equilibrium (4), $A < 0$ and $B < 0$ under $\tilde{\alpha} < \tilde{\beta}$, whereas $A > 0$ and $B > 0$ under $\tilde{\alpha} > \tilde{\beta}$. Applying the Routh–Hurwitz stability criterion, the equilibrium is stable if

$$\frac{1}{2} Gc^2 \{ \tilde{\alpha}(1+B) + \tilde{\beta}(1-A) \} > 0, \quad \frac{1}{\tilde{\alpha} - \tilde{\beta}} Gc^2 (m_q A \tilde{\beta}^2 + m_p B \tilde{\alpha}^2) > 0 \quad \frac{1}{2} Gc^2 \frac{\{ \tilde{\alpha}(1+B) + \tilde{\beta}(1-A) \} (m_q A \tilde{\beta} + m_p B \tilde{\alpha})^2}{(\tilde{\alpha} - \tilde{\beta}) (m_q A \tilde{\beta}^2 + m_p B \tilde{\alpha}^2)} > 0 \quad \text{and } Gc^2 A B m_p m_q > 0 \tag{B6}$$

which can hold under $\tilde{\alpha}(1+B) + \tilde{\beta}(1-A) > 0$. Combining the feasibility and stability conditions, we obtain condition (5).

Coexistence of two herbivores P and Q , and existence of either P or Q alone

In this section, we show that the stability and feasibility conditions of coexisting equilibria with both herbivores P and Q never overlap those of equilibria with either P or Q alone.

(i) a case with $1/\alpha^* \geq r$ and $1/\beta^* \geq r$

In this case, one of two equilibria is feasible and stable depending on am_q / bm_p , where either herbivore species can remain alone in the plant colony without defenses. It should be noted that condition (5) cannot hold with $1/\alpha^* \geq r$ and $1/\beta^* \geq r$ simultaneously, implying that the coexistence of the two herbivores P and Q is impossible in this case.

(ii) a case with $1/\alpha^* < r$ and $1/\beta^* \geq r$ (by which $\alpha^* > \beta^*$)

In this case, both equilibria may be feasible (i.e., the equilibrium with herbivore species P alone in the presence of plant defenses and that with herbivore Q alone in the absence of plant defenses). These equilibria may be unstable in the case of violation of condition (B4b) and $am_q / bm_p > 1$, respectively. (Notably, it can be shown that these two equilibria never stabilize simultaneously under $1/\alpha^* < r$). A combination of these instability conditions coincides with condition (5b). That is, a feasibility/stability condition of equilibrium with both P and Q corresponds with the unfeasibility/instability conditions of equilibria with either herbivore alone. Considering a symmetric relationship between the two species, we can also show a similar proof for a case where $1/\alpha^* \geq r$ and $1/\beta^* < r$.

(iii) a case with $1/\alpha^* < r$ and $1/\beta^* < r$

In this case, both equilibria with either herbivore species P or Q alone in the presence of plant defenses may be simultaneously feasible (notably, it can be shown that these two equilibria never stabilize simultaneously under $1/\alpha^* < r$ and $1/\beta^* < r$). Considering a symmetrical relationship between the two species, these equilibria destabilize simultaneously when

$$\tilde{\alpha} < \tilde{\beta} \text{ and } \frac{1}{\tilde{\alpha}} > r - \frac{1}{\tilde{\alpha} - \tilde{\beta}} \log \left[\frac{am_q}{bm_p} \right] > \frac{1}{\tilde{\beta}} \quad (\text{B7a})$$

or

$$\tilde{\alpha} > \tilde{\beta} \text{ and } \frac{1}{\tilde{\alpha}} < r - \frac{1}{\tilde{\alpha} - \tilde{\beta}} \log \left[\frac{am_q}{bm_p} \right] < \frac{1}{\tilde{\beta}} \quad (\text{B7b})$$

based on Eq. (B4). When this condition is combined with $1/\alpha^* < r$ and $1/\beta^* < r$, it can coincide with condition (5). This indicates that the feasibility/stability conditions of equilibrium with both P and Q corresponds with the unfeasibility/instability conditions of both equilibria with either P or Q alone.

Appendix 3. Comparison of variables between a state with P alone and with the coexistence of P and Q

Case 1: P and Q are subordinate and superior species, respectively, as in condition (5a)

(i) a case where $r < 1/\tilde{\alpha}$

When $r \leq 1/\tilde{\alpha}$, a state with infestation of P only is not accompanied by any plant defense ($x = 0$, see Eq. (2)). In this case, the difference in plant biomass between infestation by P only and by both P and Q is

$$s_3^* - s_1^* = \frac{m_p}{a} \left(\frac{am_q}{bm_p} \right)^{\frac{\tilde{\alpha}}{\tilde{\alpha} - \tilde{\beta}}} - \frac{m_p}{a} = \frac{m_p}{a} \left\{ \left(\frac{am_q}{bm_p} \right)^{\frac{\tilde{\alpha}}{\tilde{\alpha} - \tilde{\beta}}} - 1 \right\} \quad (\text{C1})$$

which is positive under condition (5a). Therefore, the plant biomass increases with the coexistence of herbivores P and Q (i.e., $s_3^* > s_1^*$) under $r < 1/\tilde{\alpha}$.

However, a change in the density of herbivore P between the state with P only and its coexistence with herbivore Q is

$$\begin{aligned} p_3^* - p_1^* &= \frac{\tilde{\beta}}{u(\tilde{\alpha} - \tilde{\beta})} \left\{ \frac{1}{\tilde{\beta}} - \left(r - \frac{1}{\tilde{\alpha} - \tilde{\beta}} \log \left[\frac{am_q}{bm_p} \right] \right) \right\} \left(\frac{am_q}{bm_p} \right)^{\frac{\tilde{\alpha}}{\tilde{\alpha} - \tilde{\beta}}} - \frac{r}{u} \quad (\text{C2}) \\ &= \frac{\tilde{\beta}}{u(\tilde{\alpha} - \tilde{\beta})} \left\{ \frac{1}{\tilde{\beta}} - \left(r - \frac{1}{\tilde{\alpha} - \tilde{\beta}} \log[k] \right) \right\} k^{\frac{\tilde{\alpha}}{\tilde{\alpha} - \tilde{\beta}}} - \frac{r}{u} \end{aligned}$$

where $k = am_q / bm_p$. A differentiation of Eq. (C2) with respect to k is

$$\frac{\partial}{\partial k} (p_3^* - p_1^*) = \frac{1}{u(\tilde{\alpha} - \tilde{\beta})^3} k^{\frac{\tilde{\alpha}}{\tilde{\alpha} - \tilde{\beta}}} \left[(\tilde{\alpha} - \tilde{\beta}) \left\{ -r\tilde{\alpha}\tilde{\beta} + (\tilde{\alpha} + \tilde{\beta}) \right\} + \tilde{\alpha}\tilde{\beta} \log[k] \right] \quad (\text{C3})$$

Here,

$$F = (\tilde{\alpha} - \tilde{\beta}) \left\{ -r\tilde{\alpha}\tilde{\beta} + (\tilde{\alpha} + \tilde{\beta}) \right\} + \tilde{\alpha}\tilde{\beta} \log[k] \quad (\text{C4})$$

is an increasing function of k . When $k < 1$, under condition (5a), Eq. (C4) is maximized as $\tilde{\alpha}\tilde{\beta}(\tilde{\alpha} - \tilde{\beta}) (1/\tilde{\beta} + 1/\tilde{\alpha} - r)$ at $k = 1$, which is negative under condition (5a). Accordingly, Eq. (C3) is always positive because $(\tilde{\alpha} - \tilde{\beta})^3 < 0$ in condition (5a). Since Eq. (C3) is positive, Eq. (C2) is an increasing function of k , which is maximized as

$$\frac{\tilde{\alpha}}{u(\tilde{\alpha} - \tilde{\beta})} \left(\frac{1}{\tilde{\alpha}} - r \right) \quad (\text{C5})$$

at $k = 1$, which is negative under $r < 1/\tilde{\alpha}$ and condition (5a). Where $p_3^* - p_1^*$ is negative, the density of the subordinate herbivore P is generally decreased as a result of coexistence with the superior herbivore Q ($p_3^* < p_1^*$), where $r < 1/\tilde{\alpha}$.

In the coexistence equilibrium, the plant generally develops some level of induced defense (see Eq. (6)). Therefore, the plant’s defense increases where there is coexistence with the superior herbivore Q ($\tilde{x}_3^* > \tilde{x}_1^*$).

(ii) a case where $r \geq 1/\tilde{\alpha}$

When $r \geq 1/\tilde{\alpha}$, conditions with infestation of P only are accompanied by some level of plant defense ($x > 0$, see Eq. (3)). In this case, the difference in plant biomass between conditions of infestation by P only and that with coexistence of both P and Q is

$$s_3^* - s_2^* = \frac{m_p}{a} \left(\frac{am_q}{bm_p} \right)^{\frac{\tilde{\alpha}}{\tilde{\alpha}-\tilde{\beta}}} - \frac{m_p}{a} e^{\tilde{\alpha}r-1} \\ = \frac{m_p}{a} \left\{ \exp \left[\frac{\tilde{\alpha}}{\tilde{\alpha}-\tilde{\beta}} \log \left[\frac{am_q}{bm_p} \right] \right] - \exp \left[\tilde{\alpha} \left(r - \frac{1}{\tilde{\alpha}} \right) \right] \right\} \tag{C6}$$

This is positive under condition (5a); therefore, the plant biomass increases where there is coexistence of herbivores P and Q (i.e., $s_3^* > s_1^*$).

However, the difference in the density of herbivore P between conditions with P only and coexistence of herbivores P and Q is

$$p_3^* - p_2^* = \frac{\tilde{\beta}}{u(\tilde{\alpha}-\tilde{\beta})} \left\{ \frac{1}{\tilde{\beta}} - \left(r - \frac{1}{\tilde{\alpha}-\tilde{\beta}} \log \left[\frac{am_q}{bm_p} \right] \right) \right\} \left(\frac{am_q}{bm_p} \right)^{\frac{\tilde{\alpha}}{\tilde{\alpha}-\tilde{\beta}}} - \frac{1}{\tilde{\alpha}u} e^{\tilde{\alpha}r-1} \tag{C7} \\ = \frac{\tilde{\beta}}{u(\tilde{\alpha}-\tilde{\beta})} \left\{ \frac{1}{\tilde{\beta}} - \left(r - \frac{1}{\tilde{\alpha}-\tilde{\beta}} \log[k] \right) \right\} k^{\frac{\tilde{\alpha}}{\tilde{\alpha}-\tilde{\beta}}} - \frac{1}{\tilde{\alpha}u} e^{\tilde{\alpha}r-1}$$

where $k = am_q / bm_p$. The differentiation of Eq. (C7) with respect to k is

$$\frac{\partial}{\partial k} (p_3^* - p_2^*) = \frac{1}{u(\tilde{\alpha}-\tilde{\beta})^3} k^{\frac{\tilde{\alpha}}{\tilde{\alpha}-\tilde{\beta}}} \left[(\tilde{\alpha}-\tilde{\beta}) \left\{ -r\tilde{\alpha}\tilde{\beta} + (\tilde{\alpha} + \tilde{\beta}) \right\} + \tilde{\alpha}\tilde{\beta} \log[k] \right] \tag{C8}$$

Here,

$$F = (\tilde{\alpha}-\tilde{\beta}) \left\{ -r\tilde{\alpha}\tilde{\beta} + (\tilde{\alpha} + \tilde{\beta}) \right\} + \tilde{\alpha}\tilde{\beta} \log[k] \tag{C9}$$

is an increasing function of $\log[k]$. Due to $\log[k] < (\tilde{\alpha}-\tilde{\beta}) (r-1/\tilde{\alpha})$, under condition (5a) and $r \geq 1/\tilde{\alpha}$, Eq. (C9) is maximized as $\tilde{\alpha}(\tilde{\alpha}-\tilde{\beta})$ at $\log[k] = (\tilde{\alpha}-\tilde{\beta}) (r-1/\tilde{\alpha})$, which is negative under condition (5a). Since $(\tilde{\alpha}-\tilde{\beta})^3$ is also negative

under condition (5a), Eq. (C8) is always positive. This indicates that Eq. (C7) is an increasing function, which is maximized as 0 at $k = \exp \left[(\tilde{\alpha}-\tilde{\beta}) (r-1/\tilde{\alpha}) \right]$, suggesting that Eq. (C7) is negative. Where $p_3^* - p_2^*$ is negative, the density of the subordinate herbivore P is generally decreased as a result of its coexistence with the superior herbivore Q ($p_3^* < p_2^*$).

The change in the plant defense \tilde{x} between conditions where subordinate herbivore P alone is present and conditions where it coexists with superior herbivore Q is expressed as

$$\tilde{x}_3^* - \tilde{x}_2^* = \frac{1}{\tilde{\alpha}-\tilde{\beta}} \log \left[\frac{am_q}{bm_p} \right] - \left(r - \frac{1}{\tilde{\alpha}} \right) \tag{C10}$$

which is positive under condition (5a). Where $x_3^* - x_2^*$ is positive, the plant defense increases in response to P ’s coexistence with superior herbivore Q ($\tilde{x}_3^* > \tilde{x}_2^*$).

Case 2: P and Q are the superior and subordinate species, respectively, as in condition (5b)

(i) a case where $r < 1/\tilde{\alpha}$

Since condition (5b) is inconsistent with $r < 1/\tilde{\alpha}$, the coexistence of superior species P and subordinate species Q is impossible where $r < 1/\tilde{\alpha}$. Therefore, this case may be ignored.

(ii) a case where $r \geq 1/\tilde{\alpha}$

In this case, conditions with the infestation of P only are accompanied by some level of plant defense ($x > 0$, see Eq. (3)). The difference in plant biomass between the infestation of P only and that of both P and Q is

$$s_3^* - s_2^* = \frac{m_p}{a} \left(\frac{am_q}{bm_p} \right)^{\frac{\tilde{\alpha}}{\tilde{\alpha}-\tilde{\beta}}} - \frac{m_p}{a} e^{\tilde{\alpha}r-1} \\ = \frac{m_p}{a} \left\{ \exp \left[\frac{\tilde{\alpha}}{\tilde{\alpha}-\tilde{\beta}} \log \left[\frac{am_q}{bm_p} \right] \right] - \exp \left[\tilde{\alpha} \left(r - \frac{1}{\tilde{\alpha}} \right) \right] \right\} \tag{C11}$$

This is negative under condition (5b); therefore, plant biomass decreases where herbivores P and Q there coexist after an additional infestation of subordinate herbivore Q (i.e., $s_3^* < s_2^*$).

On the other hand, a change of density of herbivore P between the state with P only and the coexistence with herbivore Q is

$$p_3^* - p_2^* = \frac{\tilde{\beta}}{u(\tilde{\alpha}-\tilde{\beta})} \left\{ \frac{1}{\tilde{\beta}} - \left(r - \frac{1}{\tilde{\alpha}-\tilde{\beta}} \log \left[\frac{am_q}{bm_p} \right] \right) \right\} \left(\frac{am_q}{bm_p} \right)^{\frac{\tilde{\alpha}}{\tilde{\alpha}-\tilde{\beta}}} - \frac{1}{\tilde{\alpha}u} e^{\tilde{\alpha}r-1} \tag{C12} \\ = \frac{\tilde{\beta}}{u(\tilde{\alpha}-\tilde{\beta})} \left\{ \frac{1}{\tilde{\beta}} - \left(r - \frac{1}{\tilde{\alpha}-\tilde{\beta}} \log[k] \right) \right\} k^{\frac{\tilde{\alpha}}{\tilde{\alpha}-\tilde{\beta}}} - \frac{1}{\tilde{\alpha}u} e^{\tilde{\alpha}r-1}$$

where $k = am_q / bm_p$. A differentiation of Eq. (C12) with respect to k is

$$\frac{\partial}{\partial k} (p_3^* - p_1^*) = \frac{1}{u(\tilde{\alpha} - \tilde{\beta})^3} k^{\tilde{\alpha} - \tilde{\beta}} \left[(\tilde{\alpha} - \tilde{\beta}) \left\{ -r\tilde{\alpha}\tilde{\beta} + (\tilde{\alpha} + \tilde{\beta}) \right\} + \tilde{\alpha}\tilde{\beta} \log[k] \right] \quad (\text{C13})$$

Here,

$$F = (\tilde{\alpha} - \tilde{\beta}) \left\{ -r\tilde{\alpha}\tilde{\beta} + (\tilde{\alpha} + \tilde{\beta}) \right\} + \tilde{\alpha}\tilde{\beta} \log[k] \quad (\text{C14})$$

is an increasing function of $\log[k]$. Due to $(\tilde{\alpha} - \tilde{\beta}) (r - 1/\tilde{\beta}) < \log[k] < (\tilde{\alpha} - \tilde{\beta}) (r - 1/\tilde{\alpha})$ under condition (5b), Eq. (C14) is minimized as $\tilde{\beta}(\tilde{\alpha} - \tilde{\beta})$ at $\log[k] = (\tilde{\alpha} - \tilde{\beta}) (r - 1/\tilde{\beta})$, which is positive under condition (5b). Accordingly, Eq. (C13) is always positive because $(\tilde{\alpha} - \tilde{\beta})^3 > 0$ under condition (5b). This indicates that Eq. (C12) is an increasing function, which is maximized as 0 at $k = \exp \left[(\tilde{\alpha} - \tilde{\beta}) (r - 1/\tilde{\alpha}) \right]$, suggesting that Eq. (C12) is negative. Where $p_3^* - p_2^*$ is negative, the density of the superior herbivore P is generally decreased as a result of its coexistence with the subordinate herbivore Q ($p_3^* < p_2^*$).

The change in plant defense \tilde{x} between conditions where there is presence of the superior herbivore P alone and those where there it coexists with the subordinate herbivore Q is

$$\tilde{x}_3^* - \tilde{x}_2^* = \frac{1}{\tilde{\alpha} - \tilde{\beta}} \log \left[\frac{am_q}{bm_p} \right] - \left(r - \frac{1}{\tilde{\alpha}} \right) \quad (\text{C15})$$

which is negative under condition (5b). Where $x_3^* - x_2^*$ is negative, the plant defense decreases in response to coexistence with the subordinate herbivore Q ($\tilde{x}_3^* < \tilde{x}_2^*$).

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