POTENTIAL CASCADE EFFECTS OF COMPETITION ON BIOLOGICAL CONTROL OF INSECTS HERBIVORES

Data de subimissão: 25/09/2024 *Data de aceite: 10/01/2025*

Leandra de Oliveira Costa
Universidade Federal Rural de Pernambuco, Departamento de Agronomia
Recife-PE
http://lattes.cnpq.br/0416183661318756
https://orcid.org/0000-0002-6673-1071

Christian Sherley Araújo da Silva-Torres
Universidade Federal Rural de Pernambuco, Departamento de Agronomia
Recife-PE
https://lattes.cnpq.br/6987761145766931
https://orcid.org/0000-0002-2364-5421

ABSTRACT: In natural ecosystems, many insect species can interact in different ways. Herbivore insects can compete for host plants, shelter, mating, and oviposition sites. Additionally, natural enemies can compete for their herbivore prey (food) or host (development) in the same habitat. Therefore, competition can regulate the populations of herbivore insects, which can be important pests, and their respective natural enemies. Competition can affect the efficacy of biological control strategies. Competition for resources (prey/host) will reduce its access to at least one of the competing species. Also, competition can alter the behavior of natural enemies, such as foraging, predation, and parasitism rates, which in turn will affect pest populations. In some situations, competition between natural enemies may lead to pest resurgence, due to mutual interference of biocontrol agents and a lack of efficient pest control. In others, competition can have a synergistic effect in pest control, in which multiple natural enemy actions add up to a complimentary biological control, increasing its final effect on pest populations. The understanding and adequate management of competition effects in the habitat is essential to guarantee efficient and sustainable pest control.

KEYWORDS: Parasitoids, predators, population regulation, resource availability

INTRODUCTION

Competition in natural enemies

Plants constitute the first trophic level in nature, and their abundance can be regulated by abiotic (e.g., climate conditions, water availability, and soil properties) and biotic (e.g., pathogens, herbivores) factors. In turn, herbivore insects use host plants as food sources, shelter, sexual encounters, oviposition, and development sites (SCHOONHOVEN et al., 2005). Thus, insects that use the same plant as hosts will establish intrinsic relationships, sometimes complex ones, that are affected by biotic and abiotic factors (SCHOONHOVEN et al., 1998). Those interactions among herbivores can be either obligatory or facultative (SHARMA et al., 2021) and depend on the availability of resources and species involved. Interactions can vary in a gradient of positive to neutral to negative effects between species involved, such as mutualism (+,+), amensalism (0,-), commensalism (0,+), and competition (-,-) (ODUM; BARRETT, 2007, BRONSTEIN, 2015). Among these ecological interactions, the competition is characterized by the struggle between two or more organisms for the same resources within a habitat (FIELD; CALBERT, 1998, BATCHELOR et al., 2005, MAYFIELD; LEVINE 2010, ODE et al., 2022). Thus, one possible result of the competition is negative effects (e.g., reduction in fecundity and survival) for both organisms involved due to less availability sharing of resources. It is ubiquitous to have highly asymmetric competition in nature, in which one species involved suffers negative effects, whereas the other does not (PAINE, 1966, KRAAIJEVELD; GODFRAY, 1997, KAPLAN; DENNO, 2007, LAWTON; STRONG, 1981, JARRIGE et al., 2016).

Regarding the top-down effect on insect herbivore populations, natural enemies will keep their prey/host populations in check. It means that the third trophic level (e.g., predators, parasitoids, and pathogens) would help to regulate the population growth of insect herbivores through interactions of consumption (predation) or parasitism (PRICE et al., 1980). In turn, natural enemies compete for resources (e.g., prey/host and shelter). Therefore, they are subjected to similar effects of competition that lower trophic levels are.

Competition among natural enemies can occur within the species, also known as intraspecific, when individuals of the same species of predators (e.g., cannibalism) or parasitoids (e.g., superparasitism) compete for the same prey/host in the habitat (ODE et al., 2022). The possible outcome of intraspecific competition is the reduction of predation or parasitism effectiveness due to cannibalism, superparasitism, or resource depletion. In addition, competition can occur between natural enemy species, also known as interspecific competition for the same prey/host. The possible outcomes are competitive displacement/exclusion, in which one species becomes dominant in the habitat and displaces the other, or coexistence, where both species can coexist if they occupy different niches (HARVEY et al., 2013).

Regarding how the resource is shared/used by the competing species, natural enemy competition can be further classified as scramble competition and contest competition (STERCK et al., 1997, VAN SHAIK 1989). In the scramble (e.g., exploitation) competition scenario, the resource (prey/host) is accessible to all species competing (none monopolizes it). In other words, it occurs when different species of natural enemies exploit the same resource, which is finite and shared equally amongst the competitor species. It causes a reduction in the resource availability for all species involved. Competitors interact undirectly, responding to the levels of resources that were reduced by activities of the other competitors. The shared exploitation of prey/host could lead to a faster depletion of resources available, affecting the survival and reproduction of natural enemy species that depend on that resource. In extreme cases, all species involved would die because none would obtain the amount of resources it needs (PRASAD, 2022).

This type of competition is frequent in ecosystems where the resources are distributed more evenly and spread, reducing the frequency of direct interactions between competitors (DENNO et al., 1995; MA et al., 2009). Also, some species of exotic lady beetles can adapt to new habitats, compete with native species for local prey, and cause a reduction in prey availability, resulting in smaller populations of native lady beetle populations (EVANS et al., 2011). For instance, the lady beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) caused a reduction of biodiversity of different native species worldwide after introduction, such as in Michigan (USA) with the displacement of *Cycloneda munda* (Say), *Coleomegilla maculata* (DeGeer), *Brachiacantha ursina* (F.) e *Chilocorus stigma* (Say) (COLUNGA-GARCIA; GAGE, 1998; BAHLAI et al., 2015; ROY et al., 2016; CAMACHO-CERVANTES et al., 2017; ZAVIEZO et al., 2019).

In the contest (interference) competition between natural enemies, there is direct physical interaction between competitors to secure the resources. In this case, there will be a winner and a loser, and resources can be conquered totally or not at all (ODE et al., 2022). Each successful species obtains all the resources it requires for survival or reproduction. It is common when resources (prey/hosts) are stable in the habitat. In some parasitoid species, it is possible to find individuals that interact directly to get the host with aggressive behaviors towards other competitors, such as bites, stings, and kicks (HARDY et al., 2013). Female parasitoids of Mymaridae, Bethylidae, and Scelionidae show parental care and interference competition, in which females fight for and protect parasitized hosts. They may attack and kill competing females of the same (superparasitism) or different species (multiple parasitisms) that try to oviposit in the same host and guard the host until progeny emergence (HARDY; BLACKBURN, 1991; PÉREZ-LACHAUD et al., 2002; PÉREZ-LACHAUD et al., 2004).

Influence of natural enemies competition on community structure

Competition is considered one of the major biotic factors modulating distribution, abundance, and diversity in multispecies communities (BARABÁS et al., 2016). Its importance relies on the fact that competition (intra- and inter-) regulates niche size and occupancy, the evolution of life history traits, and functions in ecological communities. In such communities, natural enemies are fundamental regulators of prey/host populations through direct and indirect interactions (GUILLER et al., 2012; COURBAUD et al., 2012). As they compete for a shared resource, the intensity of selection pressure increases and some natural enemy species are favored against others (KAPLAN; DENNO, 2007; GAO; REITZ, 2017). In addition, the selection pressure among natural enemies may affect their behavior to avoid potential competition (KOIVISTO et al., 2016, MUELLER et al., 2016). For instance, predatory beetles of the genus *Pterostichus* (Coleoptera: Carabidae) avoid territories where ants *Formica polyctena* (Foerst.) (Hymenoptera: Formicidae) are present. Authors observed that beetles changed their walking path when attacked directly by the ants, increased their walking speed, and reduced the number and time of stops to avoid competition (REZNIKOVA; DOROSHEVA, 2004). Additionally, some species adapt to use varied resources or the same resource in different ways, which is known as niche partition (BONSALL et al., 2002, MESZÉNA et al., 2006, KALMYKOV; KALMYKOV, 2013). For instance, parasitoids that attack the same host can show behaviors to avoid competition, as follows: i) parasitize specific host developmental stages, ii) explore different microhabitats, and iii) temporal separation, in which parasitism can occur in different hours of the day (YAMAMOTO et al., 2007; FLEURY et al., 2009; HACKETT-JONES et al., 2009). This partition reduces the intensity of direct competition, allowing the coexistence of different natural enemy species in the multispecies community.

Competition between natural enemies can also affect the population dynamic of prey/hosts. When two different prey or host species share the same natural enemy, they can affect each other's presence by the population density of the natural enemy. This phenomenon is known as apparent competition, similar to competition for resources, and could lead to the exclusion of the prey or host species (HOLT, 1977; HOLT; LAWTON, 1993; HOLT et al., 1994). In the same way that two species of natural enemies could not coexist exploring exactly the same resource, it is expected that two host/prey species could not coexist if they share the natural enemy species in the same habitat. Moreover, competition displacement or exclusion is not exclusive of prey/hosts, parasitoids and predators can also be eliminated from the environment by displacement (BRODEUR; ROSENHEIM, 2000). This can result when one natural enemy species is more efficient in using resources than the other, depleting or using the resource completely to the detriment of the competitor. Therefore, competitive exclusion can reduce the diversity of natural enemies in the ecosystem, hence the population abundance and diversity of prey/hosts in the same habitat (HOLT; BONSALL, 2017).

Insect parasitoids develop in/on the host. Occasionally, parasitoids can feed on hosts (WAAGE; HASSELL, 1982; KIDD; JERVIS, 1991). For this reason, they are considered as eventual predators. In turn, parasitized hosts can be attacked by other predators of the same host (prey), known as intraguild predation (ROSENHEIM et al., 1995). This is a combination of predation and competition, as different natural enemy species competing for the same resource attack each other. In addition, when one host is attacked simultaneously by multiple parasitoid species, the developing larvae can attack and consume one another, with the survival of the best competitor under those circumstances. Some factors affecting the outcome of multiple parasitism competition are host developmental stage, age, and aggressive behavior of parasitoid larvae (HARVEY et al., 2013, THIERRY et al., 2022). Thus, the interactions between natural enemies (e.g. predator-predator, predator-parasitoid, parasitoid-parasitoid) can compromise the efficacy of biological control, as it may cause a reduction in parasitism or predation rate of the target pest species (POLIS et al., 1989; DIXON, 2000; HEMPTINNE et al., 2012, FRAGO, 2016).

TOP-DOWN AND BOTTOM-UP EFFECTS AS REGULATORS OF POPULATIONS

Besides competition, other interactions are major forces regulating the distribution and abundance of species in habitats. The top-down and bottom-up effects explain how different trophic levels (within the food chain) regulate insect herbivores, parasitoids, and predator populations (HUNTER; PRICE, 1992).

The top-down effect occurs when higher trophic levels exert pressure on lower levels. Generally, it involves predator-prey interactions exerted by natural enemies on herbivore populations through tri-trophic interactions, and it affects the structure and dynamics of organisms in the same ecosystem. The top-down effect is important to prevent herbivore population peaks, reaching threshold levels, and crop yield loss. Thus, predators and parasitoids have a role in maintaining ecological equilibrium in the habitats (COCO et al., 2022). In addition to the pressure exerted by the higher trophic levels on herbivore populations due to direct consumption, there is another possible way the *top-down* effect interferes with herbivore populations, also known as “trophic cascade”. It occurs when variations in population densities of higher trophic levels (natural enemy species) cause an indirect impact on herbivore populations (BRODIE et al., 2014; RIPPLE et al., 2016). For instance, one natural enemy species is excluded due to intraguild predation or invasion of an exotic species, and this can either increase or release pressure on herbivore populations below. Moreover, this cascades down on plant community composition and structure in the same ecosystem (KINDLMANN et al., 2011).

In contrast, the *bottom-up* effect refers to the impact of lower trophic levels (plant community) on higher trophic levels (herbivores and natural enemy populations). In this context, plants depend on abiotic factors such as water, light, and soil nutrients to grow and reproduce; hence, plant biomass will be available to sustain herbivore populations. When plant productivity increases, herbivore populations have more food available and can expand, and this can also relay to higher trophic levels, as more host/prey is available to predators and parasitoids (HAN et al., 2022). In ecosystems where plant community (abundance and diversity) availability is low, there is restriction in the population growth of higher trophic levels (herbivores and their natural enemies) due to lack of resources (HAN et al., 2020, BLUNDELL et al., 2020).

Resource nutritional quality is also an important factor of the *bottom-up* effect modulating community structure. For instance, low-nutrition value plants or rich in defense compounds (e. g. alkaloids, glucosinolates, terpenoids, and tannins) can have a direct impact and restrict herbivore population growth, regardless of the top-down pressure exerted by predators (MITHOFER; BOLAND 2012; HAN et al., 2022). In this sense, isoprene can reduce feeding by *Manduca sexta* (L.) but not by *Pieris rapae* (L.) and *Plutella xylostella* (L.). In contrast, *M. sexta* is not affected by nicotine in tobacco plants (LAOTHAWORNKITKUL et al., 2008; LOIVAMAKI et al., 2008). Thus, the effect of plant nutritional value will depend on the species of insect herbivores feeding on those plants. For herbivore species negatively affected by plant quality, this effect can relay up to higher trophic levels (predators and parasitoids) by reduction of prey/host available for natural enemies. In contrast, herbivore species adapted to toxic plant compounds may sequester plant toxins, and toxicity can be conveyed to higher levels, negatively affecting natural enemy populations, in turn, relaxing the pressure on herbivore populations (FÜRSTENBERG-HÄGG et al., 2013).

Finally, another important factor that can affect community structure is human agriculture activity. Farming promotes rapid habitat transformation due to human fragmentation of land to produce crops. In this case, humans are key agents disrupting the natural equilibrium in habitats, altering the abundance and distribution of plants, herbivores, and natural enemy species in the area, affecting the *top-down* and *bottom-up* effects (BANSE, 2007; HOPCRAFT et al., 2010; ESTES et al., 2011).

POSITIVE EFFECTS OF COMPETITION

Up until now, we have enumerated a list of possible negative effects of competition on community structure and biological control in previous sections. For instance, when there is multiple parasitism or superparasitism on the same host, we could have a reduction in the population of both parasitoid species. Therefore, the efficacy of either parasitoid species is compromised, leading to a reduction in pest control, and the pest population could reach levels higher than that subjected to suppression of only one parasitoid species (MAY; HASSELL, 1981; COMINS; HASSELL, 1996; BONSALL; HASSELL, 1999). In contrast, there are specific circumstances where competition interactions may have positive effects, suppressing herbivore populations, and species may coexist in the same habitat.

Different species can act together in a broad sense as population control agents. For instance, the occurrence of many natural enemies competing for the same resources in a crop field would, in theory, increase the number of prey consumed or hosts parasitized, which could reflect in more efficient and broad pest control. Even if one of the natural enemy species (predator or parasitoid) involved is less efficient, the presence of the other species could mitigate this limitation, securing the pressure upon the herbivore population and avoiding pest population threshold levels. But, for this to work, it depends on the species and life stages of the insects involved (LAW; ROSENHEIM, 2011; TAKIZAWA; SNYDER, 2011). An example of broad-sense pest control and the coexistence of different natural enemy species is in some brassica crops infested by the cabbage root fly *Delia radicum* (L.).Young larvae of *D. radicum* are parasitized by the specialist parasitoid *Trybliographa rapae* (Westw.), and pupae are preferred by the beetle *Aleochara bilineata* (Gyllenhal). Beetles can also attack eggs of the pest (READER; JONES, 1990). Thus, niche partitioning and multiple natural enemies contribute to this pest control in brassica crops.

Another potential positive point of competition is that it could favor natural selection and stimulate adaptation, which in turn can favor niche diversification, as noted in a previous section of this chapter. It would induce sympatric species to evolve and explore the same resources differently (ACKERMANN; DOEBELI, 2004). The evolution of adaptive traits would increase the efficacy in prey capture, host parasitism, and natural enemy survival under adverse conditions. Adaptations could involve changes in foraging behavior and physiology, leading to more specialized natural enemies over time. Niche diversification would reduce the intensity of direct competition and allow the coexistence of multiple natural enemies in the community (ROBINSON; PFENNING, 2013).

REFERÊNCIAS

ACKERMANN, M., DOEBELI, M. **Evolution of niche width and adaptive diversification.** Evolution, v. 58, p. 2599-2612, 2004.

BAHLAI, C.A., COLUNGA-GARCIA, M., GAGE, S.H., LANDIS, D.A. **The role of exotic ladybeetles in the decline of native ladybeetle populations: evidence from long-term monitoring.** Biological Invasions, v.17, p. 005-1024. 2015.

BANSE, K. **Do we live in a largely top-down regulated world? Journal of Biosciences,** v. 32, p. 791–796, 2007.

BARABÁS, G., J. MICHALSKA-SMITH, M., & ALLESINA, S. **The effect of intra-and interspecific competition on coexistence in multispecies communities.** The American Naturalist, v. 188, p. E1-E12, 2016.

BATCHELOR, T.P., HARDY, I.C., BARRERA, J.F., PÉREZ-LACHAUD, G. **Insect gladiators II: competitive interactions within and between bethylid parasitoid species of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae).** Biological Control, v. 33, p. 194-202, 2005.

BRODEUR, J., ROSENHEIM, J.A. **Intraguild interactions in aphid parasitoids.** Entomologia experimentalis et applicata, v. 97, p. 93-108, 2000.

BONSALL, M.B., HASSELL, M.P. **Parasitoid-mediated effects: apparent competition and the persistence of host–parasitoid assemblages.** Researches on Population Ecology, v. 41, p. 59-68, 1999.

BONSALL, M.A., HASSELL, M.P., and ASEFA, G. **Ecological trade-offs, resource partitioning, and coexistence in a host-parasitoid assemblage.** Ecology, v. 83, p. 925–934. 2002.

BRODIE, J.F., ASLAN, C.E., ROGERS, H.S., REDFORD, K.H., MARON, J.L., BRONSTEIN, J.L. et al. **Secondary extinctions of biodiversity.** Trends in Ecology & Evolution, v.29, p.664–672, 2014.

BRONSTEIN, J.L. **The study of mutualism**, p. 3-19. In J.L. Bronstein (eds.), Mutualism. New York, Oxford Univ. Press, 2015, 315p.

BLUNDELL, R., SCHMIDT, J.E., IGWE, A., CHEUNG, A.L., VANNETTE, R.L., GAUDIN, A.C., CASTEEL, C.L. **Organic management promotes natural pest control through altered plant resistance to insects.** Nature Plants v. 6, p. 483–91, 2020.

CAMACHO-CERVANTES, M., ORTEGA-ITURRIAGA, A., DEL-VAL, E. **From effective biocontrol agent to successful invader: the harlequin ladybird (*Harmonia axyridis*) as an example of good ideas that could go wrong.** PeerJ, v.*5*, p.3296, 2017.

COCO, A.M., YIP, E.C., KAPLAN, I., J.F. TOOKER. **More phylogenetically diverse polycultures inconsistently suppress insect herbivore populations.** Oecologia, v. 198, p. 1057–1072, 2022.

COLUNGA-GARCIA, M., GAGE, S.H. **Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape.** Environmental Entomology, v. 27, p. 1574-1580, 1998.

COMINS, H.A., HASSELL, M.P. **Persistence of multispecies host–parasitoid interactions in spatially distributed models with local dispersal.** Journal of theoretical Biology, v. 183, p. 19-28, 1996.

COURBAUD, B., VIEILLEDENT, G., KUNSTLER, G. **Intra-specific variability and the competition–colonisation trade-off: coexistence, abundance and stability patterns.** Theoretical Ecology, v. 5, p. 61-71, 2012.

DENNO R.F., MCCLURE M.S., OTT J.R. **Interspecific interactions in phytophagous insects: competition reexamined and resurrected**. Annu Rev Entomol v. 40, p. 297–331, 1995.

DIXON, A.F.G. **Insect predator-prey dynamics: ladybird beetles and biological control.** Cambridge University Press, 86p. 2000.

ESTES, J.A., J. TERBORGH, J.S. BRASHARES, M.E. POWER, J. BERGER, W.J. BOND, S.R. CARPENTER, T.E. ESSINGTON, R.D. HOLT, J.B.C. JACKSON. **Trophic downgrading of planet earth.** Science, v. 333, p. 301–306, 2011.

EVANS, E.W., SOARES, A.O., YASUDA, H. **Invasions by ladybugs, ladybirds, and other predatory beetles.** BioControl, v. 56, p. 597–611, 2011.

FRAGO, E. **Interactions between parasitoids and higher order natural enemies: intraguild predation and hyperparasitoids.** Current Opinion in Insect Science, v. 14, p. 81-86, 2016.

FIELD, S.A., CALBERT, G. **Patch defence in the parasitoid wasp *Trissolcus basalis*: when to begin fighting?**. Behaviour v. 135, p. 629–42, 1998.

FÜRSTENBERG-HÄGG, J., M. ZAGROBELNY, M., BAK, S. **Plant defense against insect herbivores.** International journal of molecular sciences, v. 14, p. 10242-10297, 2013.

GAO, Y.L., REITZ, S.R. **Emerging themes in our understanding of species displacements.** Annual Review of Entomology, v. 62, p. 165–183, 2017.

GILLER, P. **Community structure and the niche.** Springer Science & Business Media, 176p. 2012.

HARDY, I.C., BLACKBURN, T.M. **Brood guarding in a bethylid wasp.** Ecological Entomology, v. 16, p. 55-62, 1991.

HARDY, I.C.W., M. GOUBAULT & T.P. BATCHELOR. **Hymenopteran contests and agonistic behaviour.** p. 147-177. In I.C.W. Hardy & M. Briffa (eds.), Animal Contests. Cambridge University Press, 2013, 379p.

HARVEY, J.A., POELMAN, E.H., TANAKA, T. **Intrinsic inter- and intraspecific competition in parasitoid wasps.** Annual. Review of Entomology, v. 58, p. 333–51, 2013.

HARVEY, J.A., POELMAN, E.H., TANAKA, T. **Intrinsic inter-and intraspecific competition in parasitoid wasps.** Annual review of entomology, v. 58, p. 333-351, 2013.

HACKETT-JONES, E., COBBOLD, C., WHITE, A. **Coexistence of multiple parasitoids on a single host due to differences in parasitoid phenology**. Theoretical Ecology. v. 2, p. 19–31, 2009.

HAN, P., BECKER, C., LE BOT, J., LARBAT, R., LAVOIR, A. V., DESNEUX, N. **Plant nutrient supply alters the magnitude of indirect interactions between insect herbivores: From foliar chemistry to community dynamics.** Journal of Ecology, v. 108, p. 1497-1510, 2020.

HAN, P., LAVOIR, A.V., RODRIGUEZ-SAONA, C., DESNEUX, N. **Bottom-up forces in agroecosystems and their potential impact on arthropod pest management.** Annual Review of Entomology, v. 67, p. 239-259, 2022.

HEMPTINNE, J.L., MAGRO, A., SALADIN, C., DIXON, A.F.G. **Role of intraguild predation in aphidophagous guilds.** Journal of Applied Entomology, v. 136, p. 161-170, 2012.

HOLT, R.D., BONSALL, M.B. **Apparent competition**. Annual Review of Ecology, Evolution, and Systematics, v. 48, p. 447-471, 2017.

HOLT, R.D. **Predation, apparent competition, and the structure of prey communities.** Theoretical Population Biology, v. 12, p. 197–229, 1977.

• HOLT RD, LAWTON JH. **Apparent competition and enemy-free space in insect host-parasitoid communities.** Am Nat, v. 142, p. 623–645, 1993.

• HOLT, R.D., LAWTON, J.H. **The ecological consequences of shared natural enemies.** Annual Review of Ecology, Evolution, and Systematics, v. 25, p. 495–520, 1994.

HOPCRAFT, J.G.C., OLFF, H., SINCLAIR, A.R.E. 2010. **Herbivores, resources and risks: Alternating regulation along primary environmental gradients in savannas.** TREE, v. 25, p. 119–128, 2010.

HUNTER MD., PRICE PW. **Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities.** Ecology, v. 73, p.724–32, 1992.

JARRIGE A., KASSIS, A., SCHMOLL, T., GOUBAULT, M. **Recently mated males of a lek-mating insect intensify precopulatory mate guarding under male competition.** Animal Behaviour, v. 117, p. 21–34, 2016.

KAPLAN, I., DENNO, R.F. **Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory.** Ecology Letters, v. 10, p. 977–94, 2007.

KALMYKOV, L.V., KALMYKOV, V.L. **Verification and reformulation of the competitive exclusion principle**. Chaos Soliton Fract. v. 56, p.124–131, 2013

KIDD, N.A.C., JERVIS, M.A. **Host-feeding and oviposition strategies of parasitoids in relation to host stage.** Researches on Population Ecology, v. 33, p. 13-28, 1991.

KINDLMANN, P., AMEIXA, O.M., & DIXON, A.F. **Ecological effects of invasive alien species on native communities, with particular emphasis on the interactions between aphids and ladybirds**. BioControl, v. 56, p. 469-476, 2011.

KRAAIJEVELD, A.R., GODFRAY, H.C.J. **Trade-off between parasitoid resistance and larval competitive ability in *Drosophila melanogaster*.** Nature, v. 389, n. 6648, p. 278-280, 1997.

KOIVISTO, E., HOSET, K.S., LE TORTOREC, A.H., NORRDAHL, K., KORPIMAKI, E. **Mobility of a small mammalian predator changes according to the activity patterns of potential intraguild predators.** Journal Zoology, v. 298, p. 121-127, 2013.

LAOTHAWORNKITKUL, J., PAUL, N.D., VICKERS, C.E., POSSELL, M., TAYLOR, J.E., MULLINEAUX, P.M., HEWITT, C.N. **Isoprene emissions influence herbivore-feeding decisions.** Plant, cell & environment, v.31, p. 1410–1415, 2008.

LAWTON, J.H., STRONG Jr, D.R. **Community patterns and competition in folivorous insects.** The American Naturalist, v. 118, p. 317-338, 1981.

LAW, Y.H., ROSENHEIM, J.A. **Effects of combining an intraguild predator with a cannibalistic intermediate predator on a species-level trophic cascade.** Ecology, v. 92, p. 333-341, 2011.

LOIVAMAKI, M., MUMM, R., DICKE, M., SCHNITZLER, J.P. **Isoprene interferes with the attraction of body- guards by herbaceous plants. Proceedings of the National Academy of Sciences**, v. 105, p. 17430–17435, 2008.

MA J., LIN, J.T., CHEN, H.J., HU, X.N. **The potential role of interspecific competition in fruit fly invasions. J Environ Entomol** v. 31, p. 361–364, 2009.

MAY, R.M., HASSELL, M.P. **The dynamics of multiparasitoid-host interactions.** The American Naturalist, v. 117, p. 234-261, 1981.

MAYFIELD, M.M., LEVINE, J.M. **Opposing effects of competitive exclusion on the phylogenetic structure of communities.** Ecology Letters, v. 13, p. 1085-1093, 2010.

MESZÉNA, G., GYLLENBERG, M., PÁSZTOR, L., METZ, J.A.J. **Competitive exclusion and limiting similarity: a unified theory.** Theoretical Population Biology, v. 69, p. 68–87, 2006.

MITHÖFER, A., & BOLAND, W. **Plant defense against herbivores: chemical aspects.** Annual review of plant biology, v. 63(1), p.431-450, 2012.

MUELLER, A.K., CHAKAROV, N., HESEKER, H., KRUGER, O. **Intraguild predation leads to cascading effects on habitat choice, behaviour and reproductive performance.** J. Anim. Ecol., v. 85, p. 774-784, 2013.

ODE, P.J.,VYAS, D.K., HARVEY, J.A. **Extrinsic inter-and intraspecific competition in parasitoid wasps.** Annual Review of Entomology, v. 67, p. 305-328, 2022.

ODUM, E.P., BARRETT, G.W. **Fundamentos de ecologia.** São Paulo: Cengage Learning, 632p. 2007

PAINE, R.T. **Food web complexity and species diversity.** The American Naturalist, v. 100, p. 65-75, 1966.

PÉREZ-LACHAUD, G., HARDY ICW, LACHAUD J-P. **Insect gladiators: competitive interactions between three species of bethylid wasps attacking the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae).** Biological Control, v. 25, p. 231–38, 2002.

PÉREZ-LACHAUD G., BATCHELOR T.P., HARDY I.C.W. **Wasp eat wasp: facultative hyperparasitism and intra-guild predation by bethylid wasps.** Biological Control, v. 30, p. 149–55, 2004.

POLIS, G.A., MYERS, C.A., HOLT, R.D. **The ecology and evolution of intraguild predation: potential competitors that eat each other.** Annual review of ecology and systematics, v. 20, p. 297-330, 1989.

PRASAD, K.H. **Community Structure.** p. 125-161. In K.H. Prasad (eds.). Insect Ecology: Concepts to Management. Singapore: Springer Nature Singapore, 228p. 2022.

PRICE, P.W., BOUTON, C.E., GROSS, P., MCPHERON, B.A., THOMPSON, J.N., WEIS, A.E. **Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies.** Annual review of Ecology and Systematics, v. 11, p. 41-65, 1980.

READER, P.M., JONES, T.H. **Interactions between an eucoilid [Hymenoptera] and a staphylinid [Coleoptera] parasitoid of the cabbage root fly.** Entomophaga, v. 35, p. 241-246, 1990.

REZNIKOVA, Z.; DOROSHEVA, H. I**mpacts of red wood ants Formica polyctena on the spatial distribution and behavioural patterns of ground beetles (Carabidae).** Pedobiologia, v. 48, p.15-21, 2004.

RIPPLE, W.J., ESTES, J.A., SCHMITZ, O.J., CONSTANT, V., KAYLOR, M.J., LENZ, A., MOTLEY, J.L., SELF, K.E., TAYLOR, D.S., SHOW LESS. **What is a trophic cascade?** Trends in Ecology & Evolution, v. 31, p. 842–849, 2016.

ROBINSON, B.W., PFENNIG, D.W. **Inducible competitors and adaptive diversification.** Current Zoology, v. 59, p. 537-552, 2013.

ROSENHEIM, J.A., KAYA, H.K., EHLER, L.E., MAROIS, J.J., JAFFEE, B.A. **Intraguild predation among biological-control agents: theory and evidence.** Biological control, v. 5, p. 303-335, 1995.

ROY, H.E., BROWN, P.M.J., ADRIAENS, T., BERKVENS, N., BORGES, I., CLUSELLA-TRULLAS, S., COMONT, R.F., DE CLERCQ, P., ESCHEN, R., ESTOUP, A., EVANS, E.W., FACON, B., GARDINER, M.M., GIL, A., GREZ, A.A., GUILLEMAUD, T., HAELEWATERS, D., HERZ, A., HONEK, A., HOWE, A.G., HUI, C., HUTCHISON, W.D., KENIS, M., KOCH, R.L., KULFAN, J., HANDLEY, L.L., LOMBAERT, E., LOOMANS, A., LOSEY, J., LUKASHUK, A.O., MAES, D., MAGRO, A., MURRAY, K.M., MARTIN, G.S., MARTINKOVA, Z., MINNAAR, I.A., NEDVED, O., ORLOVA-BIENKOWSKAJA, M.J., OSAWA, N., RABITSCH, W., RAVN, H.P., RONDONI, G., RORKE, S.L., RYNDEVICH, S.K., SAETHRE, M.G., SLOGGETT, J.J., SOARES, A.O., STALS, R., TINSLEY, M.C., VANDEREYCKEN, A., VAN WIELINK, P., VIGLÁŠOVÁ, S., ZACH, P., ZAKHAROV, I.A., ZAVIEZO, T., ZHAO, Z. **The harlequin ladybird, *Harmonia axyridis*: global perspectives on invasion history and ecology.** Biological Invasions, v. 18, p. 997–1044, 2016.

SCHOONHOVEN, L.M., JERMY, T., VAN LOON, J.J.A. **Insects and plants: how to apply our knowledge.** p. 343–365. In L.M. Schoonhoven, T. Jermy & J.J.A. van Loon (eds.), Insect-plant biology: From physiology to evolution, Springer US, 1998, 409p.

SCHOONHOVEN, L.M., VAN LOON, J.J.A., DICKE, M. **Insect plant biology**, 2nd ed. Oxford University Press, 421p. 2005.

SHARMA, G., MALTHANKAR, P.A., MATHUR, V. **Insect–plant interactions: a multilayered relationship.** Annals of entomology, v. 114, p. 1-16, 2021.

STERCK, E.H.M., WATTS, D.P., VAN SCHAIK, C.P. **The evolution of female social relationships in nonhuman primates.** Behavioral Ecology and Sociobiology, v. 41, p. 291–309, 1997.

THIERRY, M., PARDIKES, N.A., ROSENBAUM, B., XIMÉNEZ-EMBÚN, M.G., HRČEK, J. **The presence of multiple parasitoids decreases host survival under warming, but parasitoid performance also decreases.** Proceedings of the Royal Society B, v. 289, p. 20220121, 2022.

TAKIZAWA, T., SNYDER, W.E. **Cannibalism and intraguild predation of eggs within a diverse predator assemblage.** Environmental Entomology, v. 40, p. 8-14, 2011.

VAN SHAIK, C.P.. **The ecology of social relationships amongst female primates.** In V. Standen, & R.A. Foley (eds.), Comparative Socioecology: The behavioural ecology of humans and other mammals (p. 195–218). Oxford: Blackwell, 1989.

WAAGE, J.K., HASSELL, M.P. **Parasitoids as biological control agents–a fundamental approach.** Parasitology, v. 84, p. 241-268, 1982.

YAMAMOTO, D., HENDERSON, R., CORLEY, L.S., IWABUCHI, K. **Intrinsic, inter-specific competition between egg, egg-larval, and larval parasitoids of plusiine loopers.** Ecological Entomology. v. 32, p. 221–228, 2007.

ZAVIEZO, T., SOARES, A.O., GREZ, A.A. **Interspecific exploitative competition between *Harmonia axyridis* and other coccinellids is stronger than intraspecific competition.** Biological Control, v. 131, p. 62-68. 2019.