FLÁVIA MARIA DARCIE MARQUITTI

**PARASITAS DE INTERAÇÕES E A COEVOLUÇÃO
DE MUTUALISMOS**

**INTERACTION PARASITES AND THE
COEVOLUTION OF MUTUALISMS**

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Orientador: Prof. Dr. Paulo Roberto
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*Dedico esta tese com
todo meu amor para
Mã, Pá, Li, Bi e Luiz.
E ao meu orientador,
Miúdo, com muito carinho.*

“...at the borders of interdisciplinarity, progress occurs.

*Whenever the languages of two disciplines meet,
two cultures interact, and something new happens.”*

Martin A. Nowak

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Resumo

Mutualismos são interações em que os parceiros se exploram reciprocamente com benefícios líquidos para ambos os indivíduos que interagem. Sistemas mutualistas multi-específicos podem ser descritos como redes de interação, tais como aquelas formadas por sistemas de polinização, dispersão de sementes, estações de limpeza em ambientes recifais, formigas defensoras de plantas, mimetismo mülleriano e bactérias fixadoras de nitrogênio em raízes de plantas. As interações mutualísticas estão sujeitas à trapaça por indivíduos que, por meio de algum comportamento, alcançam o benefício oferecido pelo parceiro sem oferecer nada ou oferecer muito pouco em troca. No entanto, interações mutualísticas persistem apesar da existência de trapaceiros. Neste trabalho, mostro que os parasitas de interações mutualísticas, os trapaceiros, aumentam a resiliência das redes mutualísticas às perturbações mais rapidamente em redes aninhadas, redes tipicamente encontradas em mutualismos ricos em espécies. Portanto os efeitos combinados de trapaceiros, estrutura e dinâmica das redes mutualísticas podem ter implicações para a forma como a biodiversidade é mantida. Em seguida, estudo as condições em que flores tubulares, que sofrem maiores danos ao interagirem com ladrões de néctar, conseguem coexistir com flores planares, polinizadores e pilhadores por meio de efeitos indiretos da trapaça em seu sucesso reprodutivo. O roubo do néctar pode aumentar o sucesso de uma planta se as interações com pilhadores gerarem maior quantidade de polinização cruzada, aumentando assim o sucesso reprodutivo das plantas que interagem com ambos os visitantes florais. Tal resultado sugere uma nova fonte de manutenção da cooperação e da diversidade de estratégias por meio de efeitos não lineares das interações entre diferentes estratégias. Finalmente, estudo como as interações locais promovem a prevalência de mímicos (trapaceiros) em uma certa população na ausência de seus modelos. Mostro que presas que interagem localmente podem favorecer a predominância de mímicos e predadores que os evitam após algumas gerações e que uma distribuição não aleatória de indivíduos no espaço pode reforçar ainda mais este efeito inesperado de alopatria de modelo e mímico.

Abstract

Mutualisms are interactions in which organisms of different species exploit each other with net benefits for both interacting individuals. Multispecific mutualistic system can be depicted as interaction networks, such as those formed by plant-pollinator interactions, dispersal systems, species interacting in cleaning stations in reef environments, protective ants in plants, müllerian mimicry, and nitrogen fixing bacteria on the roots of plants. Mutualistic interaction is subject to cheating by individuals who, by means of a diversity of behavioral strategies, achieve the benefit provided by the partner offering nothing or few in return. However, the mutualistic interactions persist despite the existence of cheaters. In this work I show that the parasites of mutualistic interactions increase the resilience of mutualistic networks to disturbances in nested networks, typically found in species-rich mutualisms. Therefore the joint effect of cheating, structure and dynamics of mutualistic networks have implications for how biodiversity is maintained. I subsequently study the conditions under which tubular flowers, which suffer stronger damages when interacting with nectar robbers, can coexist with planar flowers, pollinators, and robbers through indirect effects of cheating on their reproductive success. The theft of nectar may increase the success of a plant if its interactions with robbers generate higher degrees of cross-pollination, thus increasing the reproductive success of plants that interact with both floral visitors. This study suggests a new source of continued cooperation and diversity strategies through non-linear effects of the interactions between different strategies. Finally, I study how local interactions can promote the prevalence of mimic (the cheaters) in a given population in the absence of their models. I found that prey interacting locally may favor the predominance of mimic preys and avoid predators that, after a few generations and under a non-random distribution of individuals in space, can further strengthen this unexpected effect allopatry of the mimic and its model.

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1 — Introdução

1.1 Interações mutualísticas

Este trabalho tem como tema principal a evolução de estratégias que se aproveitam das interações entre outras espécies, resultando um maior sucesso, seja ele reprodutivo ou em sobrevivência. Portanto, a base deste trabalho trata de interações entre indivíduos de diferentes espécies. Uma das interações interespecíficas mais interessantes do ponto de vista evolutivo são aquelas em que indivíduos de espécies diferentes se beneficiam reciprocamente ao interagir, chamadas de interações mutualísticas, ou variações tais como simbiose (Boucher, 1988; Bronstein, 1994). Utilizo aqui a palavra mutualismo para me referir às interações em que ambos os indivíduos envolvidos recebem algum benefício líquido, seja na forma de “serviço” ou de “recompensa” (Bronstein et al., 2004).

Ainda que o benefício mútuo resulte em um benefício líquido para ambos os parceiros mutualísticos, alguns custos estão associados à essa interação. Aquele indivíduo que trapaceia o parceiro pode conseguir, em geral, um maior benefício líquido por evitar os custos da interação mutualística, como por exemplo, gerar o benefício em troca (Yu, 2001; Bronstein, 2001). Desta forma, podemos dizer que a interação mutualística está sujeita à trapaça por indivíduos que, por meio de algum comportamento, alcançam o benefício oferecido pelo parceiro sem oferecer nada em troca.

Este comportamento de trapaça reduz o sucesso, em reprodução ou sobrevivência, entre os organismos que mantêm a reciprocidade de benefícios. Portanto podemos esperar que os trapaceiros, ou ainda, os parasitas de interações, levem o mutualismo à extinção (Yu, 2001; Bronstein, 2001). Do ponto de vista evolutivo, muitos estudos procuram entender como a trapaça é limitada e as interações de mutualismo persistem em sistemas biológicos (Herre et al., 1999; Sachs et al., 2004; Sachs & Simms, 2006; Nowak, 2006).

1.2 Mutualismos e seus trapaceiros

A seguir, exemplifico alguns tipos de interações mutualísticas e seus diferentes trapaceiros associados. Classifico o mutualismo de acordo com o benefício recebido: transporte, proteção e nutrição (Bronstein et al., 2004).

1.2.1 Mutualismo de transporte

O mutualismo de transporte compreende as interações em que um dos parceiros oferece algum tipo de *commodity*, como por exemplo recurso alimentar, em troca de transporte, como o transporte de gametas (Bronstein et al., 2004). Este tipo de mutualismo compreende interações entre polinizadores e plantas e dispersores de sementes e plantas. Interações entre polinizadores e plantas são aquelas em que o visitante floral (como abelhas, beija flores, morcegos) visitam a flor em estágio reprodutivo em busca de néctar, pólen ou óleos e nesta ação passam a carregar os grãos de pólen em alguma parte de seu corpo. Estes grãos de pólen poderão fecundar a parte feminina de outra flor da mesma espécie, efetuando assim a reprodução das plantas (Bronstein, 1994).

Muitas flores dependem da polinização cruzada, isto é de gametas de flores de outros indivíduos de plantas, como ocorre com plantas dióicas que possuem flores com apenas um dos sexos em um mesmo indivíduo (Bawa, 1980; Frankel & Galun, 2012). Flores de *Yucca*, mesmo não sendo dióicas e serem auto-compatíveis, apresentam sementes duas vezes mais viáveis quando a polinização é cruzada e efetuada por mariposas da família Prodoxidae do que quando autopolinizadas (Pellmyr et al., 1997; Pellmyr, 2003). Por outro lado, as mariposas que polinizam essas plantas são altamente dependentes da flor para ovipor seus ovos (Pellmyr, 2003).

A dispersão de sementes também pode ser um fator determinante no sucesso reprodutivo de uma planta. Quanto maior a distância que a semente germina em relação a outras sementes e à planta mãe mais se diminui o efeito competitivo por nutrientes do solo e de ataques por inimigos naturais, resultando em maior sobrevivência das plântulas (Janzen, 1970; Cain et al., 2000). Desta forma, sementes que são carregadas por animais para outras localizações podem ter maiores chances de sobreviver e chegar à fase adulta (Galetti, 2002). Plantas que investem em frutos carnosos passam a atrair animais frugívoros que efetuam o transporte de suas sementes. Em casos extremos, algumas sementes só germinam após passarem pelo trato digestivo de um animal que dispersa seus frutos, onde a dormência da semente é quebrada (Traveset et al., 2008).

No entanto, como descrito anteriormente, as interações de mutualismo de transporte estão sujeitas aos parasitas de interações. Plantas que oferecem recursos, como néctar, podem ser visitadas de forma ilegítima por pilhadores de néctar (ou ladrões de néctar). Estes animais visitam a flor através de um orifício feito na parte basal da corola ou ainda através de pequenas aberturas entre as pétalas, por onde retiram o recurso sem tocar nas partes reprodutivas dessas flores (Irwin & Brody, 1998; Maloof, 2001; Irwin et al., 2010). Em outros casos, o visitante entra legitimamente pela flor, porém por desacoplamento morfológico acessa o recurso sem tocar nas partes reprodutivas da flores (Irwin et al.,

2001). É o que ocorre com formigas do gênero *Formica* que são muito pequenas em relação às flores de *Polemonium viscosu* e diminuem significativamente a quantidade de sementes nessas plantas (Galen, 1999). Os efeitos dos pilhadores de néctar podem influenciar o comportamento dos polinizadores, como em flores de *Ipomopsis aggregata* (Polemoniaceae), cuja marca deixada pela abelha que rouba o néctar é um sinal que os beija-flores, polinizadores desta flor, identificam e passam a evitá-las, reduzindo ainda mais a capacidade reprodutiva da planta (Irwin & Brody, 1998).

Animais frugívoros podem se comportar como predadores de sementes (Schupp et al., 2010). Ao invés de ingerirem o frutos e dispersarem a semente para longe da planta mãe, animais chamados de consumidores de polpa, como o chapim *Parus* spp (Paridae) e algumas espécies de tentilhões *Fringilla* spp (Fringillidae), retiram o fruto da árvore, consomem a polpa e deixam a semente ainda no pedúnculo ou próximo à planta mãe (Schupp et al., 2010).

Pilhadores e ladrões de néctar, flores com baixa concentração de néctar e consumidores de polpa quebram a interação mutualística e passam a ter um efeito negativo ou de menor benefício sobre seus parceiros. Desta forma, a trapaça é dependente da interação entre um par de indivíduos de diferentes espécies que cooperam entre si e geram benefícios mútuos. Na ausência da interação de mutualismo entre plantas e polinizadores ou da interação entre dispersores de sementes e plantas, não há como uma outra espécie se aproveitar de recursos sem custos (Bronstein, 2001). Além disso, os trapaceiros se limitam pela própria falta de recursos (alimentícios ou reprodutivos) que sua alta frequência pode gerar.

1.2.2 Mutualismo de proteção

O mutualismo de proteção é caracterizado por parceiros que fornecem proteção física ou contra inimigos naturais e que em retorno recebem alimento ou proteção recíproca. Um caso especial de proteção é o inquilinismo, como o que ocorre entre formigas e mirmecófitas. Neste tipo de interação as formigas vivem dentro da planta ou sobre suas folhas e protegem a planta contra o ataque de herbívoros (Bronstein, 1998).

No entanto algumas formigas utilizam-se dos recursos fornecidos pela planta, como o néctar, e não respondem aos ataques de herbívoros (Bronstein, 1998). Algumas formigas são capazes de castrar a planta hospedeira, protegendo apenas as folhas jovens das quais retiram o néctar das domácias e destroem folhas mais antigas e flores, reduzindo a capacidade de reprodução dessas plantas a quase zero (Yu & Pierce, 1998). Por outro lado, as plantas podem responder à trapaça dos indivíduos dessas espécies por aborto das estruturas produtoras de recursos (Izzo & Vasconcelos, 2002).

Outro tipo de interação por proteção ocorrem em ambientes recifais, em estações de limpeza, onde pequenos peixes e crustáceos atuam como limpadores de ectoparasitas e tecidos necrosados de peixes, tartarugas e até tubarões que são clientes nessas estações. A remoção dos tecidos e parasitas são fonte de alimento para os limpadores (Grutter, 1995). Peixes da espécie *Labroides dimidiatus* são limpadores que ocorrem comumente

em recifes tropicais do Indo-Pacífico. A maior eficiência deste limpador ocorre quando um par de indivíduos atua conjuntamente do que apenas um indivíduo efetua a limpeza em estações da Grande barreira de Corais, na Austrália (Bshary et al., 2008). Quando apenas um indivíduo de *Labroides dimidiatus* executa a limpeza de um cliente, maiores são as chances que este limpador irá trapacear e comer muco e tecido saudável de seu cliente (Bshary et al., 2008). Por outro lado, o cliente pode aproveitar-se da tranquilidade de estações de limpeza e aproveitar o momento de limpeza para se alimentar de alguns peixes limpadores (Côté, 2000).

O mimetismo é, em geral, um outro tipo de interação de proteção (Ruxton et al., 2004). O mimetismo é caracterizado por espécies modelo e mimética, sendo a última similar ao modelo. Um exemplo clássico é o aposematismo de algumas espécies de borboletas e cobras. Em geral, cobras e insetos que apresentam uma coloração ou comportamentos conspicuos apresentam também algum tipo de nocividade aos seus predadores (Ruxton et al., 2004; Pfennig & Mullen, 2010). Então a sinalização em coloração ou comportamento passa a ser reconhecida por predadores que reconhecem como alerta de algum perigo, e por aprendizagem, passam a evitar os padrões (Ruxton et al., 2004). O perigo pode ser, por exemplo, a presença de algum veneno ou apenas a impalatabilidade daquela presa. Mímicos dessas espécies modelo nocivas (chamados de mímicos Batesianos) se assemelham em cor ou comportamento ao modelo aposemático, e portanto podem ser classificados como trapaceiros (Pfennig & Mullen, 2010).

No entanto, em alguns casos, o mimetismo pode não estar relacionado à proteção. O mimestismo agressivo caracteriza-se por um mímico que se assemelha a um modelo não perigoso e por isso não é evitado por potenciais presas ou hospedeiros, propiciando aos mímicos maiores taxas de predação ou parasitismo (Cheney, 2010). O mimetismo pode também estar relacionado à reprodução (Dafni, 1984; Galetti, 2002), como as orquídeas *Disa ferruginea* que não possuem recursos florais para seus visitantes, mas que mimetizam flores de *Kniphofia uvaria* que oferecem recursos, como nectar, e desta forma conseguem atrair borboletas polinizadoras (Johnson, 1994). Em alguns casos, orquídeas do gênero *Ophrys* se assemelham visualmente e por odor aos próprios polinizadores e desta forma atraem machos que, por pseudocópulas com a flor mimética, aumentam as chances de polinização desta flor (Schiestl et al., 1999). Em todos os casos de mimetismo, o mimético se comporta como um trapaceiro ao sinal honesto, seja de perigo, de não-perigo ou ainda um sinal honesto de recurso.

Plantas que apresentam frutos não carnosos que se assemelham em cor ou forma a frutos carnosos também podem ser consideradas plantas trapaceiras, já que a confusão feita pelos dispersores de sementes pode lhes garantir a dispersão da semente, oferecendo ao animal pouco ou nenhum recurso energético, como a polpa (Galetti, 2002). Este é o caso de sementes de plantas do gênero *Ormosia* (Fabaceae), que são similares a frutos que contêm tecidos nutritivos como arilos (e.g. *Trichilia* sp (Meliaceae)). As sementes de *Ormosia* não apresentam tecidos nutritivos associados e têm suas sementes expelidas sem danos nas fezes de aves e portanto dispersas (Galetti, 2002). As aves podem ser

prejudicadas por gastarem energia no consumo de alimentos pouco nutritivos. Plantas de *Ormosia* são beneficiadas por terem suas sementes levadas para longe, possivelmente aumentando as chances de germinação e sobrevivência da prole (Foster & Delay, 1998).

1.2.3 Mutualismo de nutrição

Este tipo de mutualismo é aquele geralmente associado ao tipo simbiótico, em que as espécies envolvidas na interação estão intimamente ligadas e trocam componentes nutricionais essenciais para seus parceiros e que eles não podem produzir ou tem baixa eficiência em adquirir sem a interação (Denison, 2000). Como exemplo temos as bactérias fixadoras de nitrogênio associadas às raízes de diversas leguminosas e também os fungos denominados micorrizas. Em ambos os casos, a planta fornece açúcares produzidos pela fotossíntese aos seus parceiros. As bactérias fixam o nitrogênio do solo, fornecendo às raízes dessas plantas um dos elementos limitantes ao crescimento das plantas (Ågren et al., 2012).

A maior dificuldade em identificar um trapaceiro da interação é quantificar as trocas de recursos entre os parceiros e a partir de qual limiar a planta ou seu hospedeiro associado (bactéria ou fungo) estão tendo um benefício líquido muito maior que o gerado ao parceiro (Bronstein et al., 2004). No entanto, estudos experimentais vêm demonstrando a incapacidade de algumas linhagens de bactérias associadas às raízes de leguminosas em fixar nitrogênio (Oono et al., 2011). Estas linhagens de bactérias utilizam-se dos recursos oferecidos pelas plantas, porém não provêm o nitrogênio que as linhagens mutualistas provêm.

1.3 Coevolução em mutualismos

Muitas espécies dependem de seus parceiros mutualistas para defesa, como formigas que protegem plantas que possuem nectários extra-florais; alimentação, como aves frugívoras que se alimentam de frutos carnosos de angiospermas e espalham suas sementes; e também na reprodução, como polinizadores que efetuam a fecundação cruzada de plantas e obtêm néctar delas (Diaz-Castelazo et al., 2004; Jordano, 2000; Olesen & Jordano, 2002). Esse tipo de interação é comum nos mais variados tipos de ambiente, fazendo com que a conservação de mutualismos seja importante para manutenção da diversidade de espécies (Thompson, 2005).

Por essas interações beneficiarem ambos os indivíduos das espécies envolvidas, é comum observar a evolução de características, morfológicas e comportamentais, que maximizam o benefício da interação. O processo de evolução recíproca é chamado de coevolução e é determinado localmente como resultado das pressões seletivas associadas às interações entre indivíduos de populações locais (Thompson, 1994). Em algumas populações a coevolução entre mutualistas pode existir (*hotspots*) e em outras não, ou ser muito fraca (*coldspots*), formando mosaicos geográficos de coevolução (Gomulkiewicz et al., 2000). Estudos teóricos utilizando modelos matemáticos indicam como a presença

de interação mutualística entre espécies influencia, em especial, suas características fenotípicas ao longo do tempo (Nuismer et al., 1999; Gomulkiewicz et al., 2000; Nuismer et al., 2000,0). Quando consideradas somente duas espécies em uma comunidade e nenhum evento migratório, os alelos que beneficiam a interação em cada espécie, levando à maximização da aptidão dos indivíduos das espécies envolvidas, foram fixados ao longo do tempo (Nuismer et al., 1999).

Quadro 1.1 — Dependência de frequência.

Como a trapaça surge quando organismos conseguem explorar os benefícios de interações de cooperação (aqui mutualismos), podemos esperar que a trapaça se espalhe e invada as populações e comunidades interagentes. Desta forma, a trapaça apresentaria um equilíbrio estável de mutualistas e trapaceiros, ou seria um transiente em que a trapaça está evoluindo e extinguirá o mutualismo entre indivíduos. Portanto, a aptidão da trapaça é um fator-chave para se entender sua persistência e evolução dependente da frequência, de modo que a aptidão relativa da trapaça $\left(\frac{\text{aptidão trapaceiro}}{\text{aptidão mutualista}}\right)$ diminui à medida que os trapaceiros se tornam mais comum no sistema. Quando a dependência de frequência negativa leva a aptidão relativa da trapaça para um valor abaixo ao do mutualista, podemos encontrar um equilíbrio estável, em que mutualistas e trapaceiros coexistem (A). No entanto, se a aptidão relativa da trapaça não se torna menor que a dos mutualistas, o mutualismo é extinto (B).

Ao menos três fatores podem levar à aptidão do trapaceiro ser negativamente dependente da frequência: (i) quando os trapaceiros são detectáveis (por predadores em casos de mimetismo Batesiano, por exemplo), mas menos detectados em baixas frequências; (ii) quando a trapaça tem impacto negativo sobre o próprio crescimento (como a escassez de flores se todos os visitantes florais atuarem como pilhadores de néctar); (iii) quando os mutualistas tem um efeito (direto ou indireto) positivo entre si, resultando em dependência negativa dos trapaceiros. ■

Este quadro é baseado no Quadro 2 de Ghoul et al. (2014)

É importante observar que os parasitas de interações mutualísticas (os trapaceiros) exploram uma mesma característica que um cooperador (o parceiro mutualístico), porém fazendo pressão seletiva oposta à do mutualista sobre a característica principal da interação, *e.g.* o pilhador explora o néctar que a planta oferece como recompensa ao polinizador legítimo. Alguns estudos demonstram que a presença desses parasitas de interações pode alterar o comportamento dos mutualistas verdadeiros (Irwin & Brody, 1998; Maloof, 2001). Portanto a trapaça deve ser um comportamento auto-limitante, em que sua alta frequência resulta em uma pior aptidão para o indivíduo que a adota. Veja no Quadro 1.1 como a trapaça pode ser dependente de frequência. A dependência de frequência pode determinar como mutualismo e trapaça coexistem ou se excluem ao longo do tempo evolutivo.

1.4 Redes mutualísticas

Muitos modelos foram elaborados para entender a coevolução, considerando pares de espécies e, em poucos casos, três espécies (Nuismer & Doebeli, 2004). Estudos atuais de mutualismos não-obrigatórios, que ocorrem quando os indivíduos das espécies que interagem não dependem totalmente da presença do parceiro para sua existência, têm demonstrado que muitas espécies interagem por meio desse tipo de interação formando redes (Jordano et al., 2003). Em geral, independente se a interação mutualística é de polinização, dispersão de sementes, limpeza entre peixes ou ainda entre formigas e plantas com nectários extra-florais, o padrão das interações encontrado é aninhado (Bascompte et al., 2003; Guimarães et al., 2006, 2007).

A estrutura de redes mutualísticas é caracterizada por poucas espécies centrais (aquelas que possuem muitas interações) que interagem bastante entre si e com espécies periféricas (aquelas que possuem poucas interações), muitas espécies periféricas interagindo principalmente com as espécies centrais e raramente interagindo com as espécies também periféricas. Além disso, essas redes geralmente formam somente um grupo coeso de interações, sem se notar grupos de espécies que interagem mais entre si do que com outras espécies na rede (Jordano et al. (2003), Lewinsohn et al. (2006), mas veja Olesen et al. (2007)). Muitos estudos caracterizaram padrões em diversas redes de interações mutualísticas (Olesen & Jordano, 2002; Bascompte et al., 2003; Jordano et al., 2003; Olesen et al., 2007), porém poucos deles trataram como seria a dinâmica coevolutiva que os padrões estruturais dessas redes poderiam gerar (Guimarães et al., 2007a).

Essas redes mutualísticas devem ser constituídas por espécies que respondem às mudanças fenotípicas, e até genotípicas, de outras espécies da rede. O que se espera da coevolução em redes mutualísticas é que ela resulte em uma complementaridade das características que maximizem a probabilidade da interação ocorrer e convergência das características entre as espécies de um mesmo conjunto (Guimarães et al., 2007a; Santamaría & Rodríguez-Gironés, 2007). A estrutura da rede de interação deve ser importante em como o processo coevolutivo ocorre entre as espécies e, em especial, quais

espécies influenciam as mudanças coevolutivas com maior intensidade (Thompson, 2005; Guimarães et al., 2007a; Olesen et al., 2007). Apesar de muitos sistemas de interações mutualísticas serem compostos por indivíduos que cooperam entre si, gerando benefício mútuo, nem sempre os indivíduos cooperam com seus parceiros (como os trapaceiros) (Genini et al., 2010).

A presença de trapaceiros em redes de coevolução mutualística deve influenciar no resultado que se espera da evolução da característica explorada ou do comportamento de todas as espécies. Ainda, a exploração por um indivíduo de uma espécie em rede depende que interações mutualísticas estejam ocorrendo entre outros indivíduos. Portanto a evolução de indivíduos ou espécies exploradoras está intrinsecamente ligada à interação mutualística e este fato deve influenciar como redes de interação evoluem e se estruturam. Nos capítulos a seguir mostro os resultados de análise de estabilidade em redes que consideram a presença de espécies trapaceadoras (Capítulo 2), como espécies trapaceadas podem coexistir com seus trapaceiros por meio de uma punição indireta aos seus cooperadores (mutualistas) (Capítulo 3), em seguida trato de como o espaço e as interações locais podem ser importantes na manutenção da cooperação e como os trapaceiros podem coexistir com seus explorados em condições locais (Capítulo 4). Por fim, finalizo esta teste de doutorado com as conclusões gerais obtidas dos resultados dos trabalhos desenvolvidos ao longo destes quatro anos (Capítulo 5).

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2 — Stability of mutualistic networks

The role of exploiters on the stability of mutualistic networks

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Abstract

The network organization of interactions among species may affect biodiversity maintenance. Theory predicts that species-rich mutualisms form unstable networks and understanding how these interactions persist is an ecological unsolved problem. Previous works suggest that mutualisms can be stabilized by antagonistic interactions. An overlooked aspect of mutualistic networks is that not all component species recorded are truly mutualistic partners. Some of these species are cheaters, in which individuals use the resources provided by a partner without returning any benefit in return. Cheating is therefore antagonistic interactions and it is hypothesized that antagonisms may stabilize species-rich assemblages. We hypothesize that stabilization of species-rich mutualisms may be achieved by these antagonistic lifestyles. Here, we combine the empirical organization of 48 mutualistic networks comprising disparate mutualisms with qualitative stability analysis to suggest that cheaters may facilitate stabilization of species-rich mutualisms. We simulated different proportions of cheaters in each empirical network in two different ways: species cheating on all its interactions and cheating only on some interactions. For a subset of our dataset (8 networks) we have the cheaters identified and we used the empirical frequency of interactions in the field as a proxy to the effect of a species over its partners. In all cases, cheaters improve the resilience of mutualistic networks. However, the impact of cheaters on stability depends on the network organization, being stronger in nested networks formed by free-living mutualists than in modular networks that are typical of intimate interactions, such those between myrmecophytes and their protective ants. We hypothesize that one possible solution for the apparently paradoxical stability of species-rich mutualisms is the overlooked diversity of cheating interactions these mutualisms maintain.

Introduction

Mutualisms are ecological interactions in which partners do reciprocal exploitation with net benefits for both interacting individuals (Bronstein et al., 2004). These interactions usually form networks of interacting species (Bascompte et al., 2003; Bascompte & Jordano, 2007), such as the interactions between plants and their pollinators (Olesen et al., 2008; Kaiser-Bunbury et al., 2010), or protective ants (Guimarães et al., 2006b; Rico-Gray et al., 2012). These networks can vary from few species interacting among themselves very intimately, like in the interactions between myrmecophytes and their protective ants, to species-rich free-living mutualistic interactions such as the seed dispersal by vertebrates (Guimarães et al., 2007; Fontaine et al., 2011). Theory predicts the structure of mutualistic networks affects evolutionary dynamics (Guimarães et al., 2008), species extinctions (Kaiser-Bunbury et al., 2011), and persistence of interacting populations (Bastolla et al., 2009; Thébaud & Fontaine, 2010; Allesina & Tang, 2012; Mougi & Kondoh, 2012; Rohr et al., 2014). Thus, the structure and dynamics of mutualistic networks have implications on how biodiversity is maintained. Understanding how species persist and coexist despite constant changes and perturbations is an open field for the study of species-rich networks.

Recent studies have linked aspects of network structure to biodiversity maintenance and stability of ecological networks (Thébaud & Fontaine, 2010; Allesina & Tang, 2012; Mougi & Kondoh, 2012; Rohr et al., 2014). For example, the stability of local assemblages of mutualistic partners is affected by patterns usually observed in mutualistic networks, such as interaction asymmetries and nestedness. Interaction asymmetries occur when interacting partners differ in their mutual degree of dependence, and asymmetrical networks are likely to facilitate the maintenance of diversity (Bascompte et al., 2006). Nestedness is characterized by the pattern formed when the more specialized species (species that establish few interactions) interact with proper subsets of those species interacting with the more generalized species (species that establish many interactions). There is an intense debate about the importance of nestedness to the stability of ecological networks (Bastolla et al., 2009; Thébaud & Fontaine, 2010; Allesina & Tang, 2012; Rohr et al., 2014).

Theory based on generalized Lotka-Volterra models predicts that higher nestedness degrees minimize the effects of competition allowing higher diversity (Bastolla et al., 2009) and nestedness has also as important effect on species persistence in numerical simulations (Thébaud & Fontaine, 2010). Mathematically, the nested structure of networks maximizes the range of conditions that allow the coexistence of many species in stable solutions (Rohr et al., 2014). However, nested networks are, in theory, less prone to be resilient, i.e., to return to equilibrium after a local perturbation, when compared to theoretical unstructured mutualistic networks (Allesina & Tang, 2012). In contrast, qualitative stability analysis predicts that antagonistic interactions may stabilize ecological networks (Allesina & Tang, 2012) and the combinations of antagonism with some proportions

of mutualistic interactions are theoretically stable in ecological communities (Mougi & Kondoh, 2012). An overlooked aspect in this debate is that mutualisms indeed fuel the emergence of antagonistic lifestyles associated with mutualisms.

Most analyses of the consequences of mutualistic interactions to community persistence rely on the assumption that all component species of empirical networks are mutualistic partners. Nevertheless, we know this assumption is not supported by the natural history of mutualistic assemblages (Maloof & Inouye, 2000; Irwin et al., 2001; Genini et al., 2010). In all mutualisms, from cleaning interactions between fish in coral reefs (Bshary, 2002) to pollination (Irwin & Brody, 1998), from the interactions between plants and protective ant (Izzo & Vasconcelos, 2002) to seed dispersal by vertebrates (Galetti, 2002), there are exploiters species that explore the mutualisms without providing any benefit (Bronstein, 2001). Therefore, some of the interactions within these networks are made by species that explore their interacting partners without providing any resources or services. These are actually antagonistic interactions, where one species has the benefit, but the other species is prejudiced by the interaction. However, they are a very special type of antagonistic interaction because these exploitative lifestyles are a direct, evolutionary result of mutualisms (Irwin & Brody, 1998; Maloof, 2001; Irwin et al., 2010).

Exploiters of mutualisms exploit mutualistic interactions in multiple ways. Species cheating on pollination interactions often use a non-legitimate way to visit the flower and rob the nectar, avoiding contact with the reproductive structures of the flowers (Irwin & Brody, 1998; Genini et al., 2010). Some fruit-eating birds also cheat fruiting plants by damaging the seeds or by consuming the pulp, dropping out the seeds without dispersing them (Jordano, 1983; Heleno et al., 2011). The contrary also occurs and some plants produce conspicuous seeds without any reward that are dispersed by deceived naïve birds searching for arillated seeds (Galetti, 2002). In ant-plants mutualisms, some ant species often use the extra-floral nectar or live inside myrmecophyte trees without protecting the plant against herbivory (Izzo & Vasconcelos, 2002; Raine et al., 2004). Antagonistic interactions, therefore, are implicitly included in many mutualistic networks through the cheating behavior of exploiters.

The prevalence of cheating in supposedly mutualistic systems can be impressive. For instance, up to 70% of flowers of *Pavonia dasypetala* (Malvaceae) can have signals of robbery by the bumblebee *Trigona ferricauda* (Meliponini) in flower shrubs (Roubik, 1982). In pollination networks, up to 75% of animal species can act as exploiters of the mutualism with all their partners or at least with some of them (Genini et al., 2010). Cheating thus may play an important role on the ecological dynamics of mutualistic networks (Bronstein, 2001), as it does on the stability of models of pairwise interactions (Pellmyr & Huth, 1994). In three species models, the exploiter of the mutualism is also likely to promote the stability of mutualistic interactions (Ferriere et al., 2002; Morris et al., 2003). The question now is if and how cheaters affect the resilience of networks formed by dozens of species with disparate structural patterns observed in mutualisms.

In this study, we investigated the effect of cheating on the stability mutualistic assemblages, such as pollination, seed dispersal, and ant-plant mutualisms, by combining mathematical modeling and the empirical information on mutualistic networks. Specifically, we generated theoretical networks using the same organization of natural mutualistic networks and used numerical simulations to estimate community stability in the presence of mutualism exploiters assuming two scenarios: (i) species presenting the cheating behavior in all their interactions and (ii) species presenting the cheating behavior only when interacting with a certain subset of their partners. We expected that the presence of the mutualism exploiters in the networks would promote stability, as observed for antagonistic networks in the presence of mutualism (Roubik, 1982). However, because network structure markedly varies across different types of mutualisms (Guimarães et al., 2007) we also expected to observe different effects of cheating on the different types of mutualistic interactions. Next, we investigated the importance of the network structure when considering cheating on mutualistic networks by exploring the relationship among stability, network structure, and the type of mutualism. Finally, for a small subset of our dataset in which we have strong, empirical information on which species are cheaters, we checked how the stability changes when we consider real frequencies of interactions as the effect of a species over its partners and the real exploiters observed on these networks.

Material and methods

Dataset and matrix representation

To study the effect of cheating in mutualistic networks, we used a set of 48 mutualistic networks, available online in the Interaction Web Database website (www.nceas.ucsb.edu/interactionweb) and from published papers (Guimarães et al., 2007; Genini et al., 2010). Our dataset encompassed 10 networks depicting ant-plant protection mutualisms, 7 networks of fruiting plants and fruit-eating vertebrates and 31 networks of flowering plants and their pollinators. An interaction network, composed of A animal species and P plant species, can be represented by its matrix form, $M_{P \times A}$. The interaction between the plant i and the animal j is represented in the $m_{i,j}$ element of this matrix. If the plant i and the animal j interact, then $m_{i,j} > 0$, otherwise $m_{i,j} = 0$.

The community matrix and stability analysis

To explore how cheaters affect the stability of mutualistic networks, we define a $N_{S \times S}$ matrix (hereafter community matrix), where $S = P + A$. The matrix N describes the effect species j (column) has on species i (row) around the equilibrium point of an unspecified dynamical system describing the density of the species through time (May, 1972; Allesina & Tang, 2012). In $N_{S \times S}$ matrix, if species in the row i has interactions with the species in column j , then $n_{i,j} > 0$, otherwise $n_{i,j} = 0$. Thus N and M are linked and we used the M matrix, obtained from observed empirical data, to generate

the community matrix, N . We kept the structure of the observed matrix M to compose the community matrix N . Therefore, for $i \neq j$ $n_{i,j} > 0$ and $n_{j,i} > 0$ if $m_{i,j-P} > 0$; otherwise $n_{i,j} > 0$.

For each of the 48 mutualistic networks, we simulated 1,000 community matrices (N), keeping the same structure of interactions from the observed network (M). We set the effect of each interaction between pairs of animal-plant as a number from a continuous uniform distribution between 0 and 1 – $U(0,1)$. Besides the interactions observed between animals and plants, we considered only the intra-specific competition effect, and then $n_{i,i} = -1$, for any diver i , $i \in \{1, \dots, S\}$. We divided the elements of each row i , but the element of the diagonal $n_{i,i}$, by $\sum_{j, i \neq j} n_{i,j}$. So, the effects of each mutualistic partner are just a fraction of the effects of intraspecific competition. Because our work focuses on mutualistic interactions, we have not considered inter-specific competition, therefore $n_{i,j} = 0$, $i \in \{1, \dots, A\}$, $j \in \{1, \dots, A\}$, $i \neq j$. Moreover, $n_{i,j} = 0$, $i \in \{A + 1, \dots, S\}$, $j \in \{A + 1, \dots, S\}$, $i \neq j$.

Exploiters and network structure

Although cheating behavior of plants over animals exists (e.g., mimetic fruits) most of recorded cheating behavior in literature is performed by animals. Therefore, we focused on the cheating effect only of animals over plants. We implemented two different scenarios to simulate how animals cheat on plants. In the first scenario (scenario (i)) fraction of species behave as cheaters on all their interactions. Examples of this kind of cheater are the bees *Trigona ferricauda* and *T. fulviventrtris*, which act as primary nectar robbers (Irwin et al., 2010). Thus, for a given animal k cheating its partner, we multiplied all the elements ($n_{i,k}, i \in 1, \dots, S$) in its column by -1. In the second scenario (scenario (ii)) species behave as cheaters only when interacting with subset of their partners. One example of this kind of cheater is the red-rumped agouti (*Dasyprocta leporina*), an important seed disperser of some large-seeded plants but that also prey upon seeds (Guimarães et al., 2006a). For this case, we multiplied only a subset of the matrix elements by -1. To explore how the proportion of cheaters can affect the stability on these networks, we systematically varied the proportions of cheaters on both scenarios. The proportions were: 5%, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90%, and 100% of species in the first scenario, and the same proportions for interactions in the second scenario. We randomly defined the species and the cheating interactions to simulate the cheating behavior.

We calculated the real part of the first eigenvalue – λ – of the respective community matrices N as a proxy for community stability (May, 1972). We compared the real part of the eigenvalue for each simulated cheating network ($\text{Re}(\lambda_{Ch})$) to the value of the original network (without cheating – $\text{Re}(\lambda_{NoCh})$). To make this comparison, we established the *stability acquirement* using the following equation:

$$\Lambda_i = \text{Re}(\lambda_{NoCh}) - \text{Re}(\lambda_{Ch_i}) \quad (2.1)$$

Then, positive values of Λ_i indicate the network has increased its stability with the existence of cheating behavior, and the opposite for the negative values of Λ_i . For each level of cheating behavior in each network, we calculated the Λ_i average value $-\overline{\Lambda_i}$. We had 11 average values for each network, showing the variation in stability as we increased the proportion of cheater species or cheating on some interactions. Thus, for each network we determined the rate of stability acquirement as a function of cheating proportion by the slope coefficient of the linear regression (rate of $\overline{\Lambda_i}$).

We evaluated the effect of the network structure on how stability changes with the cheating increment. We defined the network structure using four features: (1) connectance, (2) nestedness, (3) modularity, and (4) nestedness controlled by the network connectance. Connectance is the proportion of realized interactions in relation to the total number of possible interactions. Nestedness is the degree of interaction subsets on the network. Modularity measures the interaction density between and among groups of species. We measured the nestedness degree using the NODF metric (Almeida-Neto et al., 2008), transforming it to a 0–1 scale. For modularity, we used the Q metric (Newman & Girvan, 2004), calculated using the simulated annealing optimization method (Kirkpatrick et al., 1983), through the software MODULAR (Marquitti et al., 2014). Because nestedness is strongly associated with connectance (Almeida-Neto et al., 2008), we controlled nestedness by the connectance using the residuals of a linear regression between both variables, hereafter residual nestedness. Because connectance may have a negative effect on modularity, we controlled modularity by the connectance using the residuals of a linear regression between both variables, hereafter residual modularity. We performed linear regressions of the rate of stability acquirement (rate of $\overline{\Lambda_i}$) as a function of each structure feature separately.

From the dataset analyzed, we have 8 networks (6 of ant-plant and 2 of pollination networks) where exploiter species were identified and the estimated frequency of interactions between animals and plants estimated from field observations. We used this estimated values of frequencies as a proxy to the effect each species causes over their partners and the identities of cheaters to calculate the acquirement of stability. For each exploiter or each interaction exploited, we considered the negative value for the estimated effect. Then, we compared them to networks in which cheaters were simulated to see if the empirical distributions of cheating interactions lead to higher or lower stability than expected by assuming cheating is randomly distributed in the network.

Results

First of all we evaluated how the networks varied in their structure properties (see Table 2.1). The ant-plant protection networks were the smaller on average, with few animals and plants and also few interactions (11 ± 6 animals, 8 ± 3 plants, and 16 ± 12 interactions). In contrast, the pollinator plant networks were richer in average, with five times the number of animals, three times the number of plants, and ten times the number

of interactions observed in ant-plant protection networks (51 ± 33 animals, 26 ± 25 plants, and 151 ± 156 interactions). The seed dispersal-plant networks were similar in number of interactions and plant species than plant-pollinator networks but with half of the number of animal species (25 ± 28 animals, 27 ± 20 plants, and 161 ± 141 interactions). The dispersal-plant networks present the highest degree of nestedness ($NODF = 0.55 \pm 0.16$) and the lowest modularity value among the mutualistic networks ($Q = 0.27 \pm 0.05$). The ant-plant networks present the opposite structural pattern: the lowest nestedness ($NODF = 0.11 \pm 0.17$) and the highest modularity degrees ($Q = 0.71 \pm 0.18$). The pollination networks have intermediary values in both metrics ($Q = 0.45 \pm 0.13$ and $NODF = 0.31 \pm 0.16$). Therefore, these three sets of mutualistic interactions represent disparate network organizations. We then investigate how the presence of mutualism exploiters alter the stability of networks and how this stabilization effect is affected by the network organization.

We first evaluated how the stability of networks changed in consequence of the presence of mutualism exploiters. The networks increased the stability in consequence of the increasing frequency of cheating (Figures 2.1 and 2.2). Our approach allows us to standardize the maximum stability acquirement to 1. In all simulations, all networks reach around the maximum value of stability acquirement after a certain amount of cheating interactions were introduced. Hence the unknown factor is the rate in which stability is achieved with the increase in the number of cheating interactions. The rate of stability acquirement varied between scenarios, being usually higher when species are at the same time both cheaters and legitimate mutualistic partners, *i.e.*, the species present the cheating behavior only with a subset of its partners (scenario 2, 31 of 48 networks, Table 2.2).

The networks differ on how fast they increase in stability. However, we observed correlations between the rate of stability acquirement and the metrics only in the scenario in which species simultaneously establish mutualistic and cheating interactions (scenario 2, Table 2.3). High degrees of connectance and nestedness of the mutualistic interactions are positively related to the rate of stability acquirement, which happened with most of the pollination and seed-dispersal systems (Figures 2.2A and 2.2B). However, after controlling for the effects of connectance on nestedness, nestedness show no relationship with stability acquirement in the presence of exploiters (Figure 2.2C). On the other hand, the modularity of these networks has a negative effect on how fast stability increases in consequence of cheating, *i.e.* the most modular networks reach the maximum of stability acquirement only in very exploited networks (Figure 2.2D). It also happened when we controlled the effect of connectance on modularity (Figure 2.2E).

The empirical networks we had information about cheating had species acting as cheaters in all of their interactions and species only cheating on some of their interactions. We compared the real networks to the scenario in which exploiter species present the cheating behavior only with a subset of their partners (scenario (ii)). On Table 2.4 are the proportions of interactions that are made by animal exploiters on the real networks.

Table 2.1: Data references and network structure metrics.

Network	Reference	Type	A	P	E	C	K_A	K_P	NODF	Q	N_M
davidson&fisher-1991	IWDB	ANT	16	8	19	0.15	1.19	2.38	0.04	0.22	2
davidson-et.al-1989	IWDB	ANT	4	6	13	0.54	3.25	2.17	0.59	0.78	7
fonseca&Ganade-1996	IWDB	ANT	25	16	48	0.12	1.92	3.00	0.14	0.68	7
mtcCOLpen	[1]	ANT	6	5	7	0.23	1.17	1.40	0.08	0.69	4
mtcDIM10	[1]	ANT	8	9	9	0.13	1.13	1.00	0.00	0.86	8
mtcDIM100	[1]	ANT	9	7	11	0.17	1.22	1.57	0.07	0.78	5
mtcFLO	[1]	ANT	13	8	17	0.16	1.31	2.13	0.11	0.69	5
mtcPA10	[1]	ANT	8	7	9	0.16	1.13	1.29	0.00	0.79	6
mtcPacamp	[1]	ANT	12	9	16	0.15	1.33	1.78	0.05	0.78	6
mtcPOW	[1]	ANT	10	8	12	0.15	1.20	1.50	0.04	0.78	6
beehler-1983	IWDB	FRU	9	31	119	0.43	13.22	3.84	0.68	0.21	4
poulin-et.al-1999Mic	IWDB	FRU	19	4	33	0.43	1.74	8.25	0.48	0.33	3
poulin-et.al-1999Psc	IWDB	FRU	11	13	53	0.37	4.82	4.08	0.74	0.25	3
schleuning-et.al-2010	IWDB	FRU	88	33	419	0.14	4.76	12.70	0.35	0.30	5
snow&snow-1971	IWDB	FRU	14	65	249	0.27	17.79	3.83	0.43	0.28	4
snow&snow-1988	IWDB	FRU	19	29	211	0.38	11.11	7.28	0.72	0.20	4
sorensen-1981	IWDB	FRU	14	11	46	0.30	3.29	4.18	0.46	0.32	4
arroyo1	IWDB	POL	101	87	376	0.04	3.72	4.32	0.15	0.51	9
arroyo2	IWDB	POL	64	42	192	0.07	3.00	4.57	0.16	0.52	8
arroyo3	IWDB	POL	28	41	91	0.08	3.25	2.22	0.19	0.59	5
barret&helenurm-1987	IWDB	POL	102	12	167	0.14	1.64	13.92	0.31	0.47	5
bezerra-et.al-2009	IWDB	POL	13	13	71	0.42	5.46	5.46	0.85	0.20	4
dupont-et.al-2003	IWDB	POL	38	11	108	0.26	2.84	9.82	0.37	0.35	4
elberling&olesen-1999	IWDB	POL	118	23	238	0.09	2.02	10.35	0.15	0.50	8
hocking-1968	IWDB	POL	86	29	184	0.07	2.14	6.34	0.27	0.48	7
inouye-1988	IWDB	POL	91	42	281	0.07	3.09	6.69	0.17	0.44	7
kaiser-bunbury-control-2009	IWDB	POL	100	58	534	0.09	5.34	9.21	0.34	0.30	6
kaiser-bunbury-restored-2009	IWDB	POL	135	73	744	0.08	5.51	10.19	0.26	0.31	6
mcmullen-1993	IWDB	POL	54	105	204	0.04	3.78	1.94	0.25	0.57	10
medan-et.al-2002-LD	IWDB	POL	45	21	83	0.09	1.84	3.95	0.18	0.61	7
medan-et.al-2002-RB	IWDB	POL	72	23	125	0.08	1.74	5.43	0.23	0.57	9
mosquin-1967	IWDB	POL	18	11	38	0.19	2.11	3.45	0.32	0.45	6
motten-1982	IWDB	POL	44	13	143	0.25	3.25	11.00	0.51	0.30	6
olesen-aigrettes	IWDB	POL	13	14	52	0.29	4.00	3.71	0.52	0.33	4
olesen-flores	IWDB	POL	12	10	30	0.25	2.50	3.00	0.36	0.44	4
ollerton-et.al-2003	IWDB	POL	56	9	103	0.20	1.84	11.44	0.35	0.43	6
ramirez-1992	IWDB	POL	53	28	109	0.07	2.06	3.89	0.11	0.59	11
santos-2010	IWDB	POL	25	51	190	0.15	7.60	3.73	0.46	0.31	7
schemske-et.al-1978	IWDB	POL	32	7	59	0.26	1.84	8.43	0.53	0.34	5
small-1976	IWDB	POL	34	13	141	0.32	4.15	10.85	0.41	0.26	4
vazquez-ArroyoGoye-2002	IWDB	POL	29	10	43	0.15	1.48	4.30	0.30	0.53	6
vazquez-CerroLopez-2002	IWDB	POL	33	9	45	0.15	1.36	5.00	0.19	0.61	6
vazquez-LlaoLlao-2002	IWDB	POL	29	10	42	0.14	1.45	4.20	0.26	0.57	6
vazquez-Mascardi(c)-2002	IWDB	POL	26	8	36	0.17	1.38	4.50	0.23	0.54	6
vazquez-Quetihue(nc)-2002	IWDB	POL	24	7	31	0.18	1.29	4.43	0.22	0.54	5
vazquez-Safariland-2002	IWDB	POL	27	9	39	0.16	1.44	4.33	0.25	0.55	6
bignoniaceae	[2]	POL	57	10	75	0.13	7.50	1.32	0.11	0.64	7
malpighiaceae	[2]	POL	29	12	117	0.34	9.75	4.03	0.59	0.24	5

IWDB: Interaction Web Database; [1]: Guimarães et al. (2007); [2]: Genini et al. (2010)

ANT: ant-plant protection; FRU: seed dispersal-plant; POL: pollinator-plant

A: number of animal species; P: number of plant species; E: number of interactions; C: connectance; K_A : average degree of animals; K_P : average degree of plants; NODF: nestedness; Q: modularity; N_M : number of modules

Figure 2.3 shows the results for the real networks compared to the theoretical averages for each level of cheaters on the networks. Most of the ant-plant theoretical networks do not present any acquirement of stability. Only in the presence of many cheaters, the ant-plant networks change their stability. In contrast, both pollination networks show an increment on stability even on lower proportions of cheaters in the theoretical cases.

Table 2.2: Rate of stability acquirement.

Network	scenario (i)			scenario (ii)		
	$\bar{\Lambda}$	F value	p	$\bar{\Lambda}$	F value	p
davidson&fisher-1991	0.91	38.71	<0.001	0.92	332.21	<0.001
davidson-et.al-1989	0.42	3.11	0.110	0.77	22.60	<0.01
fonseca&ganade-1996	0.80	13.60	<0.01	0.76	20.78	<0.01
mtcCOLpen	1.03	41.46	<0.001	0.77	15.48	<0.01
mtcDIM10	0.47	3.12	0.110	0.54	4.53	0.06
mtcDIM100	0.95	23.88	<0.001	0.81	19.25	<0.01
mtcFLO	0.89	11.53	<0.01	0.78	16.57	<0.01
mtcPA10	1.05	24.83	<0.001	0.72	9.85	<0.05
mtcPAcamp	0.83	13.65	<0.01	0.74	14.20	<0.01
mtcPOW	1.11	26.71	<0.001	0.77	13.30	<0.01
beehler-1983	0.82	92.04	<0.001	0.95	365.68	<0.001
poulin-et.al-1999Mic	1.02	139.47	<0.001	1.04	3136.27	<0.001
poulin-et.al-1999Psc	0.67	68.06	<0.001	0.86	837.87	<0.001
schleuning-et.al-2010	0.73	57.48	<0.001	0.82	145.92	<0.001
snow&snow-1971	0.74	60.00	<0.001	0.94	1039.21	<0.001
snow&snow-1988	0.59	82.43	<0.001	0.87	194.16	<0.001
sorensen-1981	0.79	119.53	<0.001	0.80	480.01	<0.001
arroyo1	0.52	4.86	<0.1	0.67	13.02	<0.01
arroyo2	0.72	27.78	<0.001	0.75	23.63	<0.001
arroyo3	0.66	18.72	<0.01	0.75	38.76	<0.001
barret&helenurm-1987	1.18	95.77	<0.001	0.95	67.97	<0.001
bezerra-et.al-2009	0.78	302.01	<0.001	0.88	284.10	<0.001
dupont-et.al-2003	0.85	349.29	<0.001	0.91	1803.77	<0.001
elberling&olesen-1999	0.86	103.47	<0.001	0.85	77.98	<0.001
hocking-1968	0.62	14.38	<0.01	0.79	29.80	<0.001
inouye-1988	0.44	3.13	0.110	0.75	23.81	<0.001
kaiser-bunbury-control-2009	0.64	21.93	<0.01	0.78	111.37	<0.001
kaiser-bunbury-restored-2009	0.70	48.61	<0.001	0.74	63.95	<0.001
mcmullen-1993	0.59	10.08	<0.05	0.69	15.74	<0.01
medan-et.al-2002-LD	0.67	18.43	<0.01	0.76	29.16	<0.001
medan-et.al-2002-RB	0.74	7.71	<0.05	0.72	23.46	<0.001
mosquin-1967	0.67	14.68	<0.01	0.85	41.67	<0.001
motten-1982	1.02	419.45	<0.001	0.90	2888.25	<0.001
olesen-aigrettes	0.87	90.01	<0.001	0.85	1871.87	<0.001
olesen-flores	0.80	88.55	<0.001	0.80	116.42	<0.001
ollerton-et.al-2003	0.93	283.05	<0.001	0.98	742.80	<0.001
ramirez-1992	0.64	18.09	<0.01	0.64	14.97	<0.01
santos-2010	0.52	9.44	<0.05	0.84	331.32	<0.001
schemske-et.al-1978	1.04	118.34	<0.001	0.96	867.79	<0.001
small-1976	1.01	259.13	<0.001	0.92	1465.73	<0.001
vazquez-ArroyoGoye-2002	1.22	26.68	<0.001	0.83	22.37	<0.01
vazquez-CerroLopez-2002	1.10	44.46	<0.001	0.94	43.81	<0.001
vazquez-LlaoLlao-2002	0.55	7.43	<0.05	0.84	50.61	<0.001
vazquez-Mascardi(c)-2002	0.47	3.11	0.110	0.88	30.65	<0.001
vazquez-Quetihue(nc)-2002	0.57	7.29	<0.05	0.93	79.67	<0.001
vazquez-Safariland-2002	0.74	16.65	<0.01	0.87	44.64	<0.001
bignoniaceae	0.98	19.42	<0.01	1.01	49.08	<0.001
malpighiaceae	0.77	143.30	<0.001	0.90	661.74	<0.001

Figure 2.1: Stability acquirement ($\bar{\lambda}$) as a function of the proportion of exploiter animals. In the scenario (i) (A) the exploiter species present the cheating behavior in all their interactions. In the scenario (ii) (B) the exploiter species present the cheating behavior only with a subset of their partners.

Table 2.3: Rate of stability acquirement.

Metric	scenario (i)			scenario (ii)		
	Slope	F value	p	Slope	F value	p
Connectance	0.18	0.50	0.48	0.41	13.92	<0.001
NODF	-0.08	0.32	0.57	0.22	12.36	<0.01
residual NODF	-0.40	3.26	0.08	0.11	0.90	0.35
Q	0.01	0.00	0.96	-0.28	17.47	<0.001
residual Q	0.06	0.13	0.72	-0.21	7.02	<0.05

NODF: nestedness; Q: modularity; the residual metrics are from the linear regression of the metric with the connectance.

However, in all cases the stability acquirement is lower than the predicted by simulations assuming cheating interactions are randomly distributed among species (scenario 2).

Discussion

Stability in networks has been debated since May (1972, 1974) published the first studies challenging the view that complexity necessarily promotes stability and showing that complexity can be destabilizing in theoretical ecological communities. However,

Figure 2.2: Rate of stability acquirement (rate of $\bar{\Lambda}$) as a function of features of the network structure for both scenarios. In (a) is the regression of the rate of $\bar{\Lambda}$ with the Connectance, in (B) with the nestedness (here measured by the NODF metric), in (C) the residuals of Nestedness (NODF) with the Connectance, in (D) the Modularity (here measured by Q), and in (E) the residuals of Modularity (Q) with the Connectance. The colors of interaction types are the same used on Figure 2.1.

Figure 2.3: Stability acquirement in real and simulated networks. The first two plots are pollination networks and the last six plots are ant-plant protection networks. We used the simulated points from scenario (ii).

Table 2.4: Proportion of cheating interactions of the real networks.

Network	Interaction type	Proportion of exploited interactions
bignoniaceae	POL	75%
malpighiaceae	POL	23%
mtcColpen	ANT	20%
mtcDIM10.	ANT	10%
mtcDIM100	ANT	10%
mtcFLO	ANT	45%
mtcPAcamp	ANT	30%
mtcPOW	ANT	30%

ANT: ant-plant protection; POL: pollinator-plant

subsequent studies have shown that the nonrandom structure of these ecological networks can be the key to explain why so many species coexist in real communities (Bascompte & Jordano, 2007; Bastolla et al., 2009; Thébault & Fontaine, 2010; Allesina & Tang, 2012). In the present study, we focused on mutualistic networks. Even though many researchers have proposed that mutualistic communities are unstable (Levin & Anderson, 1970; Waser, 1978; Kunin & Iwasa, 1996), in fact mutualistic interactions have been persisting for millions of years (Pellmyr & Leebens-Mack, 1999). Furthermore, many pairwise interaction studies explain the evolutionary origin of exploiters of the mutualism and the unexpected stability of mutualistic interactions subject to cheating behavior of the partners (Ferriere et al., 2002; Morris et al., 2003). We studied how the cheating behavior in mutualistic networks could contribute to their stability. Matched to the presence of cheating, we also studied how the network structure can interact with the frequency of this behavior, promoting stability on mutualistic networks.

Our results identify three central points about how stability takes place in mutualistic networks. First, we have shown that the presence of exploiters, cheating in some of its interactions, increase stability in mutualistic networks. Indeed, we know that in real communities, the proportion of exploiters can be higher than the truly mutualistic partners. In pollination networks, it is reported that up to 75% of the interactions are of species cheating their partners in some way (Genini et al., 2010). Considering mixed cases, in which some species cheat all their partners and some cheat only in a few interactions, we could expect communities to be very stable. We also show that the more cheating behavior the network has, the more stable it will be. In fact, we noticed that all networks present a positive rate of acquirement in their stability as cheating proportion increased (see Figure 2.1A and 2.1B). We hypothesize that evolutionary processes based on mutualisms affect community persistence in two distinct ways. While on the one hand selection favoring mutualisms may destabilize communities, on the other hand the very existence of mutualistic interactions favors the evolution of these exploiters leading to an increase of the stabilizing effects of antagonistic interactions (Foster & Kokko, 2006). Mutualistic networks would be actually networks that mix antagonists and mutualists, a scenario that promotes stability (Mougi & Kondoh, 2012). Thus,

we hypothesize this special sort of antagonistic interaction, which emerges from the mutualisms, and exists only in the presence of the mutualism, are capable to maintain the mutualistic interactions in stable situations.

Second, we show that the structure of mutualistic interactions seems to be a key ingredient to the stability increment. Highly connected networks acquire stability in the presence of cheaters faster than the modular networks do. From theoretical studies on networks, we expect the modularity as a byproduct of reciprocal specialization and convergence of trait (Espinosa-Soto & Wagner, 2010; Donatti et al., 2011). In fact, when the mutualism is more specialized, the network of interactions presents a modular structure (Guimarães et al., 2007). For instance the interactions between myrmecophytes and their protective ants present very modular networks likely as a consequence of their specialization on some partners because of the high degree of association between partners. Another consequence of the specialization and the intimate association between the ant and their mutualistic plant is the strongly agonistic behavior against traitors (exploiters), for instance, through retaliation (Izzo & Vasconcelos, 2002). Although plants defend strongly against traitor ants, and because of its modular structural configuration do not increase the rate of stability raise in the presence of exploiters, theoretical studies predict that mutualistic networks with modular structure are more stable than the nested ones in the absence of exploiters (Allesina & Tang, 2012).

Third, we show that some of the real networks increase their stability in the presence of real exploiters, considering the frequency of interactions as a proxy to the effect between pairs of species. However, the stability acquirement is lower than expected by simulated networks with same structure and randomly assigned exploitative interactions. The effects also depend on species density in the equilibrium and on the nonlinearities of the interactions among species. Moreover, the proxy of the interaction strength may not be the best representations of the real impact of one species over its partners. Even though, the proxy in the empirical networks shows the same pattern of the simulated networks: the ant plant networks, which are more modular, have no stability acquirement in the presence of the few exploiters they have. The ant-plant networks considered in this analysis have lower number of species and also each species present lower number of partners than the pollination networks (see Table 2.1). On the other hand, the ants of the analyzed dataset spend almost the whole life inside their partner (Rico-Gray & Oliveira, 2007), while the pollination systems are characterized by pollinators establishing many interactions during their lifetime (Waser, 2006). Therefore, cheating is more prone to occur in pollination systems and then the stability acquirement can maintain the exploiters on the system (the present study and Foster & Kokko (2006)).

In conclusion, we found differences on stability of mutualistic networks just taking into account the presence of exploiters. The differences observed here are related to the network structure which in turn is a consequence of the mutualism type and the specialization the species evolve when establish the mutualism with their partners. Future studies focusing on the difference of exploiters on different sorts of mutualism, the

cost they cause to their partners, and the defenses their partners evolve in response to them will help us to understand the effects of cheating on the network organization and dynamics. Further, these studies will shed light on why so many mutualistic partners are still interacting despite the existence of the cheating behavior. We believe the cost caused by cheating behavior is low enough to not avoid the coexistence of many species that do not defend themselves against this behavior.

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3 — Cheating promoting coexistence

Cheating as coexistence promoter of cheated species

Manuscript in collaboration with Degang Wu, Luis A. Martinez-Vaquero, Massimo Stella, Alberto Antonioni, Claudius Graebner, and Blaž Krese.

Abstract

Mutualisms are interactions between individuals of different species that exploit each other, resulting in net benefits for both of them. However, sometimes one of the partners can overexploit the other, shifting the net outcome of the interaction and reducing the fitness of overexploited individuals. Examples of lifestyles that explore mutualisms include nectar robbers and nectar thieves which act as cheaters of plant-pollination interactions. These species explore floral resources such as pollen and nectar but do not pollinate flowers or make it marginally. Nevertheless, the indirect effects of cheaters may lead to unpredictable consequences for plant-pollinator interactions. In some localities, plants with flowers with tubular corolla suffer high levels of robbery and larceny. By destroying flowers or reducing nectar, cheating may lead legitimate pollinators to move longer distances among flowers. Because long-distance pollination events favor cross-pollination, cheaters may indirectly benefit the plants with tubular flowers they explored. To explore how the direct negative effects and the indirect potentially positive effects of cheaters may affect the evolution of plants and pollinators, we developed a game-theoretic mean field analytical model of two populations (plants and floral visitors) presenting two strategies each (shallow and tubular flowers, pollinators and cheaters). Our analytical results confirm coexistence of the two types of flowers and visitors and we characterize the synergetic effect of cheaters and pollinators in tubular flowers. We show that even when tubular flowers receive a lower fitness payoff when interacting with cheaters, they can coexist in high frequencies if the synergetic effect is positive. We suggest that the indirect effects of cheaters may not only increase the fitness of the explored plants under some scenarios but also favor the maintenance of intra-population phenotypic diversity in interacting species.

Introduction

Mutualisms are those interactions in which one individual exploits its partner resulting in net benefits for both interacting individuals (Bronstein, 1994). Species as myrmecophytes are dependent on the defense provided by the protective ants they host (Rico-Gray & Oliveira, 2007). Fleshy-fruited plants provide feeding resources to the animals that disperse the seeds (Jordano, 2000); and many angiosperms attract pollinators with nectar, oil, and pollen, increasing the chances of sexual reproduction among plants (Bawa, 1990). The existence of mutualism allowed the evolution of partners that overexploit the other shifting the net outcome of the interaction and reducing the fitness of overexploited individuals (Irwin & Brody, 1998; Maloof, 2001; Irwin et al., 2001,0). In pollination systems nectar robbers, which are a classical example of cheaters, reach the nectaries without pollinating the flower (Inouye, 1980; Irwin et al., 2010).

The presence of exploiter of the mutualism can affect the behavior of legitimate pollinators (Irwin & Brody, 1998). For example, the bumblebee (*Bombus occidentalis*) robs the nectar of *Ipomopsis aggregata* (Polemoniaceae), making a hole at the base of the corolla of the flower, allowing easy access to the nectar on the basal nectaries (Irwin & Brody, 1998). Because of this behavior the bumblebee does not touch the reproductive parts of the flower and also leaves the flower with no nectar for the next visitor. Some hummingbird species, which are the legitimate pollinators of *I. aggregata*, usually avoid flowers with a hole on the basal corolla (Irwin & Brody, 1998). This example shows how the harm caused by the exploiter directly reflects on other species using the same individual plant as resource.

Besides the strong evidences that cheaters can cause damages to flowers or decrease the plant fitness (Traveset et al., 1998; Irwin & Brody, 1998,9; Navarro, 1999; Lara & Ornelas, 2001; Navarro & Medel, 2009; Padyšáková et al., 2013), there are also evidences that cheaters can affect positively their partners, even though not pollinating. One of the potential benefits of the interaction of cheaters to cheated plants is based in decreased amount of reward provided by plants to the pollinators (Stout et al., 2000; Singh et al., 2014). As a consequence of lower reward per floral visit, the legitimate pollinator must travel further in order to visit more flowers and collect enough reward (pollen or nectar). When the legitimate pollinator travels longer and visits more flowers, it carries the pollen of plants distant from each other (Pyke, 1982; Zimmerman & Cook, 1985; Arizmendi et al., 1996; Maloof & Inouye, 2000; Stout et al., 2000; Zhang et al., 2009; Singh et al., 2014). By this process, the crossing-pollination rate increases, which may result in higher fitness, especially to auto-incompatible plant species (Singh et al., 2014).

Thus, not only the direct payoff gained from the interaction with the partners can be important to the coexistence of different types of flower visitors – cheaters and legitimate pollinators – and flowers, that naturally vary in their likelihood of being attacked by cheaters. The synergetic effect that cheaters and pollinators play over plants may allow the coexistence of the exploited and the explorer and may explain why even in high

frequencies of cheaters, we still observe the overexploited types of flowers. In this work, we are interested to understand how a pollination system may present coexistence of different types of flowers in the presence of cheaters and in which conditions different kinds of visitors and plants may evolve. To explore this problem, we use a mean field approach using game theory in two populations (plants and flower visitors) presenting two strategies (types) each (tubular and shallow flower plants, and pollinators and cheaters).

Analytical model

Natural history motivation

Cheaters may lead to considerable damage in plants they visited. As a consequence plants can avoid the cheating attack using different strategies (Irwin et al., 2004), such as deterring exploiter with chemical defences (Stephenson, 1982; Euler & Baldwin, 1996), escaping in time or space (Morris, 1996; Irwin et al., 2001), and also by physical barriers (Lara & Ornelas, 2001; Coombs & Peter, 2009). In this context, the structure of flowers may play an important role over the attacks by flower-visitor (Navarro, 1999; Lara & Ornelas, 2001; Urcelay et al., 2006; Coombs & Peter, 2009; Navarro & Medel, 2009). Plants with a shallow flower structure (as short tube length) are less prone to be robbed or at least they suffer less harm caused by cheaters than the plants with flowers of tubular structure (Lara & Ornelas, 2001; Coombs & Peter, 2009; Navarro & Medel, 2009). Flowers with a deep floral tubes are usually more specialized in attracting and fitting their pollinators and, as a consequence, they get a higher rate of pollination success (Nilsson, 1988; Fenster, 1991; Alexandersson & Johnson, 2002; Stang et al., 2006; Muchhala & Thomson, 2009; Anderson et al., 2014). However, when a non-specialist visitor tries to get a reward from this kind of flower, the larceny can be an easier and maybe the only way to reach it (Soberón & Martínez del Río, 1985; Lara & Ornelas, 2001; Urcelay et al., 2006; Coombs & Peter, 2009; Navarro & Medel, 2009; Singh et al., 2014). In this study we used tubular and shallow flowers as examples of flowers more and less vulnerable to the damages caused by cheaters, respectively.

The model

We introduce and discuss a baseline model for the evolution of a pollination system in which the frequency of pollinators (A_1) and cheaters (A_2) coevolve with the frequency of shallow (P_1) and tubular (P_2) flowering plants as a consequence of the payoffs each individual receives interacting with individuals of the other species (Table 3.1). We used a mean-field approximation, assuming spatial structure in populations do not lead to deviations of well-mixed dynamics. These interactions represent the pollination events generated by pollinators visiting plants or the cheating events due to cheaters exploring visiting plants. An individual also receives payoff when interacting with individuals of its own species (Table 3.2). These interactions represent competitive interactions for

resource use, in which resources here are in addition to the individuals of other species. All interactions involving these four strategies – the two kinds of flower visitors and the two kinds of plants – can be modeled as a game with two-populations (A , animal visitor; and P , flowering plants) and two-strategies each (A_1 and A_2 , P_1 and P_2). The payoff matrices of this game can be expressed as:

Table 3.1: Payoff matrices for the interactions between individuals of different populations. All parameters, but γ and σ , are restricted to be positive.

$$\Pi_{AP} = \begin{array}{cc} & \mathbf{P}_1 & \mathbf{P}_2 \\ \mathbf{A}_1 & \alpha & \beta \\ \mathbf{A}_2 & \alpha + \gamma & \beta + \gamma \end{array} \quad \Pi_{PA} = \begin{array}{cc} & \mathbf{A}_1 & \mathbf{A}_2 \\ \mathbf{P}_1 & \epsilon & \epsilon - \phi \\ \mathbf{P}_2 & \epsilon + \frac{\sigma}{2}(1-a) & \epsilon - \phi - \delta + \frac{\sigma}{2}a \end{array}$$

Table 3.2: Payoff matrices for the interactions between individuals of the same population.

$$\Pi_{AA} = \begin{array}{cc} & \mathbf{A}_1 & \mathbf{A}_2 \\ \mathbf{A}_1 & -\rho_A & 0 \\ \mathbf{A}_2 & 0 & -\rho_A \end{array} \quad \Pi_{PP} = \begin{array}{cc} & \mathbf{P}_1 & \mathbf{P}_2 \\ \mathbf{P}_1 & -\rho_P & 0 \\ \mathbf{P}_2 & 0 & -\rho_P \end{array}$$

where the value in each cell stands for the payoff that an individual of the strategy in the row gets when interacting with an individual of the strategy in the column. The parameters (α , β , δ , ϵ , ϕ , ρ_A , and ρ_P) assume positive values. The parameters γ and σ assume either positive or negative values.

The flower visitors have the benefit (α and β) when interacting with each type of flower, because they can consume the offered resource (e.g. nectar). However, cheating can have a cost because it requires a time investment in constructing the hole or the slit (Irwin et al., 2010) and also to escape from other plant protections. Thus, when cheater visits flowers, they can have a lower profit if compared with a pollinator, because we assume they have costs ($\gamma < 0$) associated with the cheating, as making the hole in the flower or even the incapability of using all the resource offered when the visit is through an illegitimate way. Nevertheless, if cheater is more efficient on removing the resource from the flower even having an associated cost with this action when compared with a pollinator, it results in a higher payoff to the cheater ($\gamma < 0$).

The two types of flowers only have benefit (ϵ), *i.e.* reproduction, when interacting with pollinators. We assume for simplicity that the pollinator is equally efficient when visiting either flowers. The two types of flowers lose the benefit and the resources invested to visitor's attraction when interacting with cheaters ($-\phi$), who cheat the flower stealing nectar (or other flower resources) and do not effectuate the pollination to the visited flower. We consider the gradient varying from purely nectar robbers ($\epsilon = \phi$), to the scenario in which cheaters are actually poor pollinators ($\epsilon > \phi$), as nectar thieves. We

assume that flowers vary in their vulnerability to the damage caused by the cheaters, in such a way that tubular flowers have a stronger negative effect ($-(\phi+\delta)$) when interacting with the cheater than shallow flowers due to the higher damage cheater can perform in their reproductive structures. Finally, we also considered the effect of the types of flower on themselves (ρ_P) and flower visitors on themselves (ρ_A). We did not include the effect of one type of flower over the other, and one type of visitor over the other.

We then modify the baseline model to study the potential synergetic effects of the different types of visitor of the tubular flowers. The synergy can result in a positive side-effect ($\sigma > 0$) to the tubular flowers if, for instance, the presence of cheaters in the environment increases the cross pollination made by the pollinators. In contrast, the synergy can be negative if, for instance, the potential pollinators avoid flowers visited by cheaters. Differently of the payoffs set before, the synergetic effect depends on the two types of flower visitors.

The payoffs set on the matrices above will determine the fitness that individuals of each strategy reaches when interacting with individuals of its own and of the other population. Then, the fitness of individuals of each strategy compared with the average population will determine the coevolutionary dynamics and the equilibria of the system. The fitness of each strategy depends not only on the payoff values but also on the frequencies that each strategy occurs on each population. Let a_1 be the frequency of pollinators, and a_2 the frequency of cheaters. If $a_1 = a$, then $a_2 = 1 - a$. Similarly to the flowering plant frequencies, we have $p_1 = p$ and $p_2 = 1 - p$. Finally, let $\vec{a} = \begin{bmatrix} a \\ 1-a \end{bmatrix}$ and $\vec{p} = \begin{bmatrix} p \\ 1-p \end{bmatrix}$, then we can define the fitness functions of each strategy as:

$$\vec{w}_A = \Pi_{AP}\vec{p} + \Pi_{AA}\vec{a} \quad (3.1)$$

$$\vec{w}_P = \Pi_{PA}\vec{a} + \Pi_{PP}\vec{p} \quad (3.2)$$

We analyzed the strategy frequencies in the equilibrium and we studied the conditions in which the tubular flowers – plants that are vulnerable to cheaters – can invade the flowers population even if suffering disadvantage. The strategies in each population coevolve as a function of the fitness of each strategy compared with the average of the population, resulting in the replicator equations defined below (Nowak, 2006):

$$\dot{a} = a(1-a)(w_{A_1} - w_{A_2}) \quad (3.3)$$

$$\dot{p} = p(1-p)(w_{P_1} - w_{P_2}) \quad (3.4)$$

Cheating can have a cost because it requires a time investment in constructing the hole or the slit (Irwin et al., 2010) and also to escape from other plant protections. Thus, it must compensate for the cheater to cheat the plant from which flowers it can not get the reward by the legitimate way (*i.e.*, as pollinators) (Lara & Ornelas, 2001; Urcelay et al., 2006; Coombs & Peter, 2009; Navarro & Medel, 2009). Even though, cheaters can be faster when visiting a flower, saving energy and resulting in higher payoff

than pollinators can get when visiting flowers. In order to analyze the effects of the parameters of the populations of plants and visitors, we explored five distinct situations:

- i. when no costs and no extra benefits occur between strategies in the same population ($\gamma = \delta = \sigma = 0$);
- ii. how the cost or benefit of cheating action, γ , affects the visitor population ($\gamma \neq 0$ and $\delta = \sigma = 0$);
- iii. how the extra cost tubular flowers pay when robbed, δ , affects plant population ($\delta \neq 0$ and $\gamma = \sigma = 0$);
- iv. how γ and δ affect both populations ($\gamma \neq 0$, $\delta \neq 0$, and $\sigma = 0$);
- v. how γ , δ , and the synergetic effect of flower visitors, σ , affect both populations ($\gamma \neq 0$, $\delta \neq 0$, and $\sigma \neq 0$).

Results

Model (i): No extra costs/benefits

If pollinators and cheaters receive exactly the same benefit when interacting with the flowers, and when the two types of flowers have the same benefit when interacting with pollinators and the same cost when interacting with the cheater, then the equilibrium is characterized by nine fixed points: $(p,a)=\{(0,0), (0,1), (1,1), (1,0), (0.5,0.5), (0.5,1), (0.5,0), (1,0.5), (1,0.5)\}$. Depending on the signal of ρ_A and ρ_P , the fixed points change their stability, as summarized on Table 3.3. The visualization of the fixed points can be observed by the gradient of the of the replicator equations (Figure 3.1). The gradient goes from the unstable fixed points to the stable fixed points. The magnitudes of ρ_A and ρ_P just change the velocity the gradient moves from/to the fixed points. All the other parameters have no influence in the coexistence study.

For the next analysis, we considered that the intra population effects were negative ($\rho_A > 0$ and $\rho_P > 0$) because each strategy can have a strong effect over itself as a result of intra-competition for other resources than the ones directly analyzed here. In

Table 3.3: Fixed points and stability of Model (i)

(p, a)	$\rho_A < 0$ and $\rho_P < 0$	$\rho_A > 0$ and $\rho_P < 0$	$\rho_A < 0$ and $\rho_P > 0$	$\rho_A > 0$ and $\rho_P > 0$
(0, 0)	Stable Node	Saddle Node	Saddle Node	Unstable Node
(0, 1)	Stable Node	Saddle Node	Saddle Node	Unstable Node
(1, 0)	Stable Node	Saddle Node	Saddle Node	Unstable Node
(1, 1)	Stable Node	Saddle Node	Saddle Node	Unstable Node
(0.5, 0.5)	Unstable Node	Saddle Node	Saddle Node	Stable Node
(0.5, 0)	Saddle Node	Unstable Node	Stable Node	Saddle Node
(0.5, 1)	Saddle Node	Unstable Node	Stable Node	Saddle Node
(0, 0.5)	Saddle Node	Stable Node	Unstable Node	Saddle Node
(1, 0.5)	Saddle Node	Stable Node	Unstable Node	Saddle Node

Figure 3.1: (A) $\rho_A < 0$ and $\rho_P < 0$, the stable fixed points are in the corners; (B) $\rho_A > 0$ and $\rho_P < 0$, the stable fixed points occur for $a = 0.5$; (C) $\rho_A < 0$ and $\rho_P > 0$, the stable fixed points occur for $p = 0.5$; (D) $\rho_A > 0$ and $\rho_P > 0$, the stable fixed points occur when the types of flowers and visitors are in equal frequencies.

this situation, the coexistence of the two types of flowers (here when $p = 0.5$) and two types of visitors (here when $a = 0.5$) is a stable situation. We are interested, in the next models, on how the different payoff parameters can affect the $(0.5, 0.5)$ equilibrium, resulting in dominance by one of the types, *i.e.* frequency higher than 0.5. Numerical evidence indicates that the cases with $\rho_A < 0$ or $\rho_P < 0$ do not give rise to a coexistence stable fixed point of both plants and animals, and are not going to be investigated further in the following.

Model (ii): The γ effect

To study the γ effect, we just added this payoff to the Model (i), using the stable coexistence situation ($\rho_A > 0$ and $\rho_P > 0$). The γ payoff is associated with the extra benefit that cheaters can have when visiting flowers more efficiently than pollinators. However, γ can also represent the cost associated with the cheating, as making the hole in the flower. In this situation, only the payoffs ρ_A and γ are important to the visitor predominance in the equilibrium (Table 3.4).

Table 3.4: Fixed points of Model (ii) and the γ effect.

(p, a)	Stability
(0, 0)	Unstable Node
(0, 1)	Unstable Node
(1, 0)	Unstable Node
(1, 1)	Unstable Node
(0.5, $0.5 - \gamma/2\rho_A$)	Stable Node
(0.5, 0)	Saddle Node
(0.5, 1)	Saddle Node
(0, $0.5 - \gamma/2\rho_A$)	Saddle Node
(1, $0.5 - \gamma/2\rho_A$)	Saddle Node

The coexistence of visitors is now changed to $\gamma/2\rho_A$. Considering that cheaters are more efficient, then $\gamma > 0$, it results in higher frequencies of cheaters ($a < 0.5$) in the coexistence equilibrium (Figure 3.2A). The coexistence turns into total predominance by cheaters when $\gamma > 0$ and $|\gamma| \geq |\rho_A|$. If the cheater pays a cost to make their visits, then $\gamma < 0$, and pollinators will occur in higher frequencies ($a > 0.5$) (Figure 3.2B). As before, the coexistence turns in total predominance by pollinators when $\gamma < 0$ and $|\gamma| \geq |\rho_A|$. The plants are not affected by this payoff. The stability of the fixed points follows the same qualitative behavior of the coexistence situation of Model (i).

Model (iii): The δ effect

To study the δ effect, we just added this payoff to the Model (i), using the stable coexistence situation ($\rho_A > 0$ and $\rho_P > 0$). The δ expresses an extra harm caused by cheaters in tubular flowers, for instance as an effect of the harm caused by cheaters on

Figure 3.2: Phase portrait of model (ii). For both figures, $\rho_A = 1$. (A) $\gamma = 0.5$, resulting in the coexistence equilibrium point $(p, a) = (0.5, 0.25)$. (B) $\gamma = -0.5$, resulting in the coexistence equilibrium point $(p, a) = (0.5, 0.75)$

the reproductive structures of tubular flowers.

Table 3.5: Fixed points of Model (iii) and the δ effect

(p, a)	Stability
$(0, 0)$	Unstable Node
$(0, 1)$	Unstable Node
$(1, 0)$	Unstable Node
$(1, 1)$	Unstable Node
$(0.5 + \delta/2\rho_P, 0.5)$	Stable Node
$(0.5 + \delta/2\rho_P, 0)$	Saddle Node
$(0.5, 1)$	Saddle Node
$(0, 0.5)$	Saddle Node
$(1, 0.5)$	Saddle Node

We only considered this direct negative effect. Note that we used $-\delta$ in the payoff matrix, thus $\delta > 0$ represents the damage suffered by the tubular flowers. In this situation, only the payoffs ρ_P and δ are important to the plant predominance in the equilibrium (Table 3.5). In this situation, only the shallow flower can have a higher frequency than expected by the Model (i) ($p > 0$) (see Figure 3.3).

Model (iv): The γ and δ effect

To study how γ and δ affect both populations at the same time, we added both payoffs to the Model (i), using the stable coexistence situation ($\rho_A > 0$ and $\rho_P > 0$). The Model (ii) shows that cheaters have higher frequencies when $\gamma > 0$ and pollinators prevail when

Figure 3.3: Phase portrait of model (iii). $\rho_P = 1$, $\delta = 0.5$, resulting in the coexistence equilibrium point $(p, a) = (0.625, 0.5)$.

$\gamma < 0$. The Model (iii) shows that the cost that tubular flowers pay when interacting with cheaters makes the shallow flowers predominate ($p > 0.5$). However, when both effects occur in the system, we studied the different possible scenarios. In this situation, only the payoffs ρ_A , ρ_P , δ , and γ are important to the coexistence in the equilibrium (Table 3.6).

Table 3.6: Fixed points of Model (iv) and δ and γ effects

(p, a)	Stability
(0, 0)	Unstable Node
(0, 1)	Unstable Node
(1, 0)	Unstable Node
(1, 1)	Unstable Node
$(0.5 + (\rho_A + \gamma\delta)/4\rho_A\rho_P, 0.5 - \gamma/2\rho_A)$	Stable Node
$(0.5 + \delta/2\rho_P, 0)$	Saddle Node
(0.5, 1)	Saddle Node
$(0, 0.5 - \gamma/2\rho_A)$	Saddle Node
$(1, 0.5 - \gamma/2\rho_A)$	Saddle Node

The coexistence equilibrium only exists when $-0.5 < (\rho_A + \gamma\delta/\rho_A)\rho_P < 0.5$ for plants and when $-0.5 < \gamma/2\rho_A < 0.5$. We represent on Figure 3.4 the conditions for coexistence and predominance of plants and flowers for $\rho_A = \rho_P = 1$. Because of the opposite effect of γ on plants and visitors coexistence, it is impossible to find a coexistence equilibrium with predominance of cheaters and tubular flowers (*i.e.*, $p < 0.5$ and $a < 0.5$).

Figure 3.4: Representation of the phase transition of model (iv). In this figure, $\rho_P = \rho_P = 1$. In the blue region, only shallow flowers exist, in the yellow region both flowers exist with predominance of shallow flowers. In the green region, the tubular flowers have a higher frequency. The cheaters have higher frequency between the interval $0 < \gamma < 1$, and the pollinators prevail between $-1 < \gamma < 0$. Notice that there is no concomitant prevalence of cheaters and tubular flowers.

Figure 3.5: Phase portrait for model (iv). For both figures, $\rho_A = \rho_P = 1$. (A) $\gamma = 0.5$, $\delta = 1.0$, resulting in the coexistence equilibrium point $(p, a) = (0.875, 0.25)$. (B) $\gamma = -0.5$, $\delta = 1.0$, resulting in the coexistence equilibrium point $(p, a) = (0.625, 0.75)$.

Model (v): The γ , δ and σ effect

To study how the synergetic effect of cheaters and pollinators have over tubular flowers, we added σ to Model (iv), using the stable coexistence situation ($\rho_A > 0$ and $\rho_P > 0$). The synergy can result in an extra benefit ($\sigma > 0$) to the tubular flowers if the presence of cheaters in the environment increases the cross pollination made by the pollinators; or in some detriment ($\sigma < 0$) if the potential pollinators avoid flowers visited by cheaters. We studied both situations and we considered $\gamma > 0$, $\gamma < 0$, and $\delta > 0$.

Table 3.7: Fixed points of Model (v) and δ , γ and σ effects

(p, a)	Stability
(0, 0)	Unstable Node
(0, 1)	Unstable Node
(1, 0)	Unstable Node
(1, 1)	Unstable Node
$(0.5 + (\rho_A + \gamma\delta)/4\rho_A\rho_P + \sigma(\gamma - \rho_A^2)/8\rho_A^2\rho_P, 0.5 - \gamma/2\rho_A)$	Stable Node
$(0.5 + \delta/2\rho_P, 0)$	Saddle Node
(0.5, 1)	Saddle Node
$(0, 0.5 - \gamma/2\rho_A)$	Saddle Node
$(1, 0.5 - \gamma/2\rho_A)$	Saddle Node

The coexistence equilibrium of plants now also depends on the σ value (see Table 3.7). We show on Figure 3.6 and 3.7 the conditions to coexistence and to predominance of each type of plant and animal. We show that, differently from the Model (iv), now tubular and cheaters can coexist in higher frequencies. However, the σ values must be high in absolute value to allow the coexistence and predominance of cheaters and tubular flowers (see Figure 3.8G). The dominance by cheaters occurs when $\gamma > 1$. In these situations, the shallow flowers have higher payoff and the equilibrium goes to $(p, a) = (1, 0)$ (see Figures 3.8A and C). When the pollinators dominate ($\gamma < -1$), the flowers coexist in equal frequencies (see Figures 3.8D and F). The conditions regions shown on Figure 3.8 are identified in the Figure of the conditions 3.7.

Figure 3.6: Representation of the phase transition of model (v). For all figures $\rho_A = \rho_P = 1$. (A) $\delta=0.5$, (B) $\delta=1.0$, and (C) $\delta=2.0$. In the orange region, the shallow flowers prevail in higher frequency, in the blue region the tubular flowers prevails in higher frequency. The yellow area has dominance by the tubular flowers. The cheaters prevail for $\gamma > 0$ and pollinators are in higher frequency when $\gamma < 0$. The coexistence area of both plants and both visitors is in the interval $-1 < \gamma < 1$ inside the orange and blue areas.

Figure 3.7: Identification of the phase portraits of the next figure, Fig 3.8 in the respective phase transition plot.

Figure 3.8: Phase portraits of model (v) varying values of γ and σ . For all the figures, $\rho_A = \rho_P = \delta = 1.0$. (A) $\gamma = 2.0$, $\sigma = 5.0$, (B) $\gamma = 0.5$, $\sigma = 10$, (C) $\gamma = 2.0$, $\sigma = -5.0$, (D) $\gamma = -2.0$, $\sigma = -5.0$, (E) $\gamma = 0.5$, $\sigma = -10$, (F) $\gamma = -2.0$, $\sigma = 5.0$, (G) $\gamma = 0.5$, $\sigma = 5.0$, and (H) $\gamma = 0.5$, $\sigma = 1.0$. See the phase transition of Figure 3.7.

Discussion

In this study we show how the coexistence of tubular and shallow flowers and pollinators and cheaters can change depending on the consequences of cheater behavior. Cheaters in pollination systems are usually considered as generators of harm and promoters of lower reproductive success of pollination events. Here, we considered that cheaters can be more harmful to tubular flower plants (δ effect) and cheaters may have a higher ($\gamma > 0$) or lower ($\gamma < 0$) payoff when interacting with a tubular flower. We analyzed the situation in which the very presence of cheaters increases the reproductive success (pollination) of tubular flowers ($\sigma > 0$) or decreases the tubular pollination success even more ($\sigma < 0$). We considered the σ effect as a synergetic consequence of cheaters and pollinators on tubular flowers.

The positive synergetic effect can be explained as a consequence of the depletion of resource by the cheaters, which results in more movement by the pollinators to reach the necessary amount of resource. To the flowers, it results in more visits by pollinators and potential higher cross pollination levels. One may say that the positive synergetic effect is a kind of contra-defense that tubular flowers can develop to suppress the harm caused by cheaters (δ effect). Because it is not a defense developed by the flowers, we considered it as the tubular flower plants cheating the pollinator. In this situation, we could observe the cheaters and the tubular flowers occurring in higher frequencies than pollinators and shallow flowers ($(p, a) < (0, 5, 0, 5)$). This effect has been described to some tubular flowers and also to some facultative cross-pollination plants (Zimmerman & Cook, 1985; Arizmendi et al., 1996; Maloof & Inouye, 2000; Stout et al., 2000; Zhang et al., 2009; Singh et al., 2014).

The negative synergetic effect can be a consequence of the avoidance by pollinators in plants signalized as cheated. Some species of pollinators can identify flowers already visited by cheaters, and avoid them because of the low expectative of getting resource there. In this situation, the coexistence will be characterized by predominance of shallow flowers. Cheaters will be more frequent if they gain a higher payoff than pollinators when visiting the flowers ($\gamma > 0$) and less frequent if they pay any cost to cheat the flowers ($\gamma < 0$). This effect has been described to some tubular flowers (Irwin & Brody, 1998; Irwin, 2000; Burkle et al., 2007).

We believe this model can be applied to plants with different mating systems in flowers: obligatory and facultative cross-pollination. We predict similar results of the model to the facultative cross pollination flowers. However, the obligatory cross pollination flowers may have a higher harm when interacting with cheaters (δ high), and the possible positive synergetic of cheaters and pollinator should be really high (γ very high) to damp the harm caused by the interaction with cheaters (as observed on Figures 3.8C). We believe the synergetic effect is not so high, resulting in few obligatory cross-pollination plants where cheaters are in high frequency. We also believe the obligatory cross-pollination plants actually can have a strong negative synergetic effect when pollinators avoid the

robbed flowers, resulting in low frequencies or even not existence of this type of mating system in communities with cheaters predominance.

This work relies on the hypothesis of a well mixed population, where everyone is interacting with everyone else. This assumption is clearly unrealistic. For instance, in many cases, evolutionary game theoretic approaches keeping into account for the spatial assortment of individuals over a given complex network is fundamental in determining the dynamics and the success of a given adopted strategy (Nowak & May, 1992; Durrett & Levin, 1994; Hauert & Doebeli, 2004). Thus, we believe that the spatial organization of the flowers and the patterns of interaction of the visitors with the flowers can affect the results here presented. The spatial distribution and organization of the flowers can allow higher frequencies of tubular flowers when cheaters prevail in the community, even when they do not present enough extra payoff through the synergetic effect. The fact that some visitors vary in the number of interactions established with the flowers may result in group formation characterized by individuals with higher fitness with the set individual in these groups than with other groups. This fact may allow higher frequencies of cheaters if the pollinators establish more interactions with the plants than the cheaters inside the groups. In this situation, the tubular flowers can become more frequent even when the positive synergetic effect is not so high if the pollinators establish most of its interaction with tubular flowers. We hope the model we presented in this study helps on the spatial organization and ecological networks structure researches and their consequences to the coexistence equilibrium of pollinators and cheaters and the different types of flowers.

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4 — Batesian mimicry

Mimics without models: the importance of being spatial

Manuscript in collaboration with Paulo R. Guimarães Jr, Francisco C. Santos, and Jorge M. Pacheco

Abstract

Conspicuous colors and behavior are frequently associated to noxious organisms and the warning color avoids the attack by enemies – a pattern called aposematism. However, the warning coloration evolves mimic species resembling a noxious model. The protection mimicry hypothesis, Batesian mimicry, predicts that warning has its effect at low frequency of the mimic species. Although empirical data supported this prediction for some systems, some systems seem to show a paradox: Batesian mimics coexisting with avoider predator in the absence of an unpalatable model. In this study we developed a model based on evolutionary game theory to understand if local interactions and structured populations could explain the mimics predominating in the absence of the model. We first analyzed the equilibrium in the mean field model in which no spatial effect is included (well-mixed scenario). Then, we simulated local interactions in a spatial explicit framework. We show that mimicry can be described as oscillatory frequencies of the different strategies. The population size plays an important role in maintaining mimics and avoiders in higher frequency in a well mixed distribution of individuals on space. We also show that local interactions by preys, which occurs when predators have a larger home range than preys, can result in dominance by mimics and avoiders after some generations. Populations structured with groups of each strategy in space may reinforce this unexpected effect when preys interact locally. We propose the structured population in space and local interactions by preys might be promoters of observed patterns of allopatry of mimics and models. We suggest this model can be useful to study two other types of mimicry: deception mimicry (affecting reproduction) and aggressive mimicry (affecting foraging).

Introduction

Warning coloration has been instigating naturalists since Bates brought evidences of conspicuous butterflies in the Amazon Forest that were not persecuted by predators even when flying in flocks and slowly in front of them. After a long time collecting butterflies, Bates had contact with Darwin and his book (Stecher, 1969) and discussed with Wallace (Wallace, 2010) until he elaborated the basis of the (future Batesian) mimicry theory stating: “Many are enabled to escape extermination, or obtain subsistence, by disguises of various kinds; amongst these must be reckoned the adaptive resemblance of an otherwise defenceless species to one whose flourishing race shows that it enjoys peculiar advantages” (Bates, 1862). Given names to the actors, mimicry occurs when one species, the “mimic”, evolves to resemble a second species, the “model”, because of the selective benefits associated with confusing a third species, the “receiver”, hereafter, the predator (Pfennig, 2012).

There are many evidences of species which present conspicuous colors and behavior, usually reveal some type of toxicity or unpalatability (Ruxton et al., 2004). The toxicity or unpalatability added to the warning colorations – the so called aposematism – increases the frequency of predator which recognizes and avoids these signals (Alatalo & Mappes, 1996). Consequently, adaptive resemblance (Batesian mimicry) can evolve by parasite species of the honest signal sent by the unpalatable model to the receiver. Batesian mimics present warning coloration but save energy and resources that otherwise would be spent on the toxic/unpalatable production or storage. In other words, the Batesian mimic is a cheater of the warning coloration protection, by exploitation of the interaction between the model unpalatable prey and avoider predators (Bronstein, 2001).

Therefore the resemblance parasites are protected only when the model is present and is frequent, eventually teaching the predators the dangerousness of eating them. It means that mimicry, as predicted by the theory, is effective only in high frequencies of models maintaining the avoider’s frequency also high (Ruxton et al., 2004). Evidences point that the conspicuous color and behavior of mimetic species may be deadly where the predators are not in sympatry (coexisting) with the unpalatable model (Benson, 1972; Pfennig et al., 2007).

Batesian mimicry hypothesis therefore predicts that the absence of the model selection will favour the loss of the conspicuous signals by mimic populations. In fact, some Batesian mimic populations revert back to the more cryptical and ancestral forms after unpalatable model dies out (Prudic & Oliver, 2008). Nevertheless, the unpredicted lonely coexistence of mimic preys and avoider predators is not rare and it is persistent over time (Ritland, 1995; Pfennig et al., 2007; Prudic et al., 2002; Pfennig & Mullen, 2010). Most of the mimic butterflies and mimic snakes in the United States and Canada exist in allopatry with the models, *i.e.*, they are theoretically unprotected by the model absence and may attract many predators with its signalization (Pfennig & Mullen, 2010). The kingsnake *Lampropeltis elapsoides* resembles the venomous coral snakes *Micrurus*

fulvius, and they used to co-occur in the southeastern of the United States. However the model species was extinct in some areas, where the mimic species still exists (Akcali & Pfennig, 2014).

Some hypotheses have been developed in order to explain these unexpected evidences the mimicry theory (Pfennig & Mullen, 2010). First, the Batesian model may actually show some degree of protection, being a possible non detected case of Mullerian mimicry (Prudic et al., 2007) or quasi-Batesian mimicry (Rowland et al., 2010)). Second, mimic has converged to model independently and the resemblance phenotype prevents predation as a secondary effect (Brower, 1958). Third, predators possess an innate avoidance behavior against the signals sent by models and mimics, *e.g.*, patterns of colors (Exnerová et al., 2007). Fourth, preys and predators present different home ranges (Grobman, 1978) or recently occurred range contraction of the model or range expansion of the mimics (Mullen et al., 2008). The latter hypotheses illustrate that space distribution and limited space usage by species associated with the ecological dynamics of predators and preys may play an important role in the allopatry of mimics and models. In this work, we developed a model to describe the coevolutionary dynamics of two types (here called strategies) of predators (eater and avoider) and two types of preys (mimic and model) based on evolutionary game theory. We describe the dynamics of the predators and preys in terms of the costs and benefits of interacting with each type of prey and predator. Then, we explored how the results predicted by the model could change with the space usage by predators and preys and with the spatial distribution of species.

Methods

Analytical model

We used the evolutionary game theory approach to understand in which conditions mimicry can be more frequent than the model, when the prevailing predator is an avoider. We use two strategies to define prey types (F) and two strategies to define predator types (P). Preys can be a model (V), which is conspicuous and venomous or distasteful to the predator; or it can be a mimic (M), which resembles the model, but is not dangerous to the predator. In turn, predators can be an eater (E), that feeds on the two types of preys, reaching benefit when eating the mimic, and a cost when eating the model; or it can be an avoider (A), which avoids conspicuous preys.

We set the payoff matrices (Π) for this system, establishing the costs and benefits of the interaction between the different strategies (Table 4.1). The elements of the payoff matrices ($\pi_{i,j}$) represent the amount of cost or the benefit the individual of the strategy in the row i has when interacting with an individual of the strategy in the column j of the matrices. Therefore, Π_{PP} represents the amount of payoff that individuals of predators have when interacting among themselves; Π_{FF} has the payoff that preys have when interacting among themselves; the amount of payoff preys have when interacting with the predators are represented on matrix Π_{FP} ; and finally predators have the payoffs

of Π_{PF} when interacting with preys.

Table 4.1: Payoff matrices of mimicry. Matrix elements represent the payoff an individual of the strategy in the row has when interacting with an individual of the strategy in the column.

Π_{PP}		Π_{FF}	
A	E	M	V
A	$\begin{pmatrix} \kappa & \kappa \end{pmatrix}$	M	$\begin{pmatrix} \kappa & \kappa \end{pmatrix}$
E	$\begin{pmatrix} \kappa & \kappa \end{pmatrix}$	V	$\begin{pmatrix} \kappa - \delta & \kappa - \delta \end{pmatrix}$
Π_{PF}		Π_{FP}	
M	V	A	E
A	$\begin{pmatrix} \kappa & \kappa \end{pmatrix}$	M	$\begin{pmatrix} \kappa & \kappa - \gamma \end{pmatrix}$
E	$\begin{pmatrix} \kappa + \sigma_1 & \kappa - \sigma_2 \end{pmatrix}$	V	$\begin{pmatrix} \kappa & \kappa - \epsilon\gamma \end{pmatrix}$

Predators: E=eater, A=avoider

Preys: M=mimic, V=model

In all the payoff matrices, κ represents the basal payoff the individual has for interacting with other individuals. The two strategies of predators do not directly affect each other, resulting in a neutral payoff matrix Π_{PP} . The preys that are models have the cost of δ related to the defense production and/or its storage (i.e., biochemical pathways to produce and store toxins, venoms or unpalatable substances), a cost that mimetic individuals do not have. The eaters have a benefit of σ_1 when eating the mimic, because it is palatable to them, and a cost of σ_2 when eating the model prey, because of the model hazard. Avoider predators have no extra payoff in the presence of the aposematic models, because they avoid them (innately or learnt). Both preys have a cost γ when interacting with an eater predator, however the cost may be lower to the model, because it can escape with less injury than the mimic ($0 < \epsilon < 1$) when an eater tries to eat it. For instance, the coral snake can attack its predator and escape of death, while the predator can become the prey. All the payoff parameters (the elements of the payoff matrices) are positive.

We calculated the fitness of each individual depending on the payoffs it has when interacting with the other individuals and the respective frequencies of each strategy. Let $\vec{f} = \begin{bmatrix} f \\ 1-f \end{bmatrix}$ and $\vec{p} = \begin{bmatrix} p \\ 1-p \end{bmatrix}$ be the frequencies of mimicry (f) and model ($1-f$), and frequencies of avoiders (p) and eaters ($1-p$). Then we can define the fitness functions of prey and predators as:

$$\vec{w}_F = \Pi_{FF}\vec{p} + \Pi_{FP}\vec{f} \quad (4.1)$$

$$\vec{w}_P = \Pi_{PF}\vec{f} + \Pi_{PP}\vec{p} \quad (4.2)$$

One of the prey strategies coevolve with predators and the other prey as a function of its own fitness compared with the mean fitness of all preys. The same is true to predators, resulting in the replicator equations defined below (Nowak, 2006):

$$\dot{f} = f(1 - f)(w_M - w_V) \quad (4.3)$$

$$\dot{p} = p(1 - p)(w_A - w_E) \quad (4.4)$$

In order to analyze the effects of the prey-predator interaction payoffs of the strategies, we studied the equilibrium states and the respective stabilities of the frequencies in this mean field model. To the stability analysis, we used the trace and determinant of the linearized system given above (Equations 4.3 and 4.4).

Simulations

As we pointed before, space distribution and the local interactions can be important to the mimic existence. In this sense, we tried to understand if the local interactions can explain the predominance of mimics with avoiders in conditions in which the mimicry theory predicts high frequencies of model prey and avoider predator. We designed an individual based model of preys and predators interacting using a deterministic evolutionary dynamics of spatial games (Nowak & May, 1992; Durrett & Levin, 1994; Hauert & Doebeli, 2004). The reproduction or replacement happens after comparison of the fitnesses. If the focal individual is a prey, we compare its fitness with one of its prey neighbors. If the focal individual has a higher fitness, then it reproduces and substitutes the prey neighbor. The same is valid to predators. This dynamics is similar to the Moran process (Wu et al., 2015).

In a first approach, we simulated the mean field model, making all individuals potential neighbors of a focal individual (hereafter well-mixed model). We also simulated other three scenarios to incorporate the spatial effects. In the first one, we set that preys were more limited in using the space (local prey model), for instance because they are slower if compared with predators, or just because the predators have large home ranges. We model this scenario assuming few prey neighbors that a prey can interact with. Because in this case we do not limit the predator usage of the space, a prey may interact with any of all predators. In the other case, we simulated the opposite situation: predators as limited species in using the space (local predator model), for instance as consequence of a sit-and-wait behavior to forage. Finally, we simulated preys and predators both interacting locally (All local model).

To accomplish the local interaction scenarios, we used a regular lattice, applying the von Neumann neighborhood (east, west, north, and south neighbors). The fitness of an individual always depends on its neighbors (preys and predators) and its reproduction depends on its fitness. The limited species were distributed randomly in the space for the initial configurations. To study the importance of stochastic effects, we simulated small (144 predators and 144 preys), medium (576 predators and 576 preys), and large

communities (1024 predators and 1024 preys), over 100 generations each. We used the same time scale to prey and predator reproduction rates.

We studied how the initial frequencies of mimics and avoiders affect the equilibrium of the finite populations. We performed 100 simulations, over 100 generations each, using the initial frequencies from 0.1 to 0.9, every 0.1 steps, with preys and predators interacting in a well mixed population (Wm), preys initially randomly distributed interacting locally (Li -prey), predators initially randomly distributed interacting locally (Li - predator), preys and predators interacting locally randomly distributed (All local). We did a supplementary analysis considering the Li cases starting with structured populations of the species which is interacting locally, grouping them in a given area (LiQ - prey and LiQ - predator).

We used average standard deviation to measure the amplitude of the oscillations. We also characterized the oscillations by the number of oscillations per generation (oscillation frequency) through a smoothed periodogram (spectrum X oscillation frequency) using the data from the simulated time series (Hamilton, 1994). The spectrum P is given by:

$$P(\omega_x) = (\Re[F(\omega_x)])^2 + (\Im[F(\omega_x)])^2 \quad (4.5)$$

where $\Re(z)$ and $\Im(z)$ are the respective real and imaginary parts of z and $\mathcal{F}(f(x)) = F(\omega_x)$ is the Fourier transform of $f(x)$.

Analytical results

The analytical model has five possible equilibria solutions: communities with only one strategy of prey and one strategy of predator ($(f, p) = \{(0, 0), (1, 0), (0, 1), (1, 1)\}$), and a coexistence of the two strategies of prey and predator ($0 < \{f, p\} < 1$). Because we defined all the payoff parameters as positive numbers, only one of the equilibrium solutions is stable: the communities composed of mimics and eaters (see Figure 4.1A). All the other monomorphic prey/predator equilibria are unstable fixed points (see Table 4.2). The coexistence of the two preys and two predators is a center equilibria, which we cannot infer the stability by this kind of analysis (see Figure 4.1B). The stable equilibrium solution occurs when $\delta > \gamma(1 - \epsilon)$, *i.e.*, when the model prey has a higher cost to produce and maintain the venom if compared with the benefit the model has in escaping predators because of its dangerousness. For $\delta < \gamma(1 - \epsilon)$, we observe the coexistence center equilibrium (Figure 4.1A).

Simulations results

We observed a center fixed point as a coexistence solution of the analytical model (Figure 4.1B), leading us to expected oscillation of the strategies frequencies around the fixed point over the time. We simulated the mean field approach and the local interactions situations using payoff values which allow the coexistence center. We present here four

Table 4.2: Equilibria and stability of mimic prey (f) and avoider predator (p) frequencies.

(f, p)	Stability	Determinant	Trace
(0, 0)	Unstable Node	$[\delta - (1 - \epsilon)\gamma]\sigma_2$	$\delta + \sigma_2 - (1 - \epsilon)\gamma$
(0, 1)	Unstable Node	$-\delta\sigma_2$	$\delta - \sigma_2$
(1, 0)	Stable Node	$[\delta - (1 - \epsilon)\gamma]\sigma_1$	$(1 - \epsilon)\gamma - \delta - \sigma_1$
(1, 1)	Unstable Node	$-\delta\sigma_1$	$-\delta + \sigma_1$
$\left(\frac{\sigma_2}{\sigma_1 + \sigma_2}, 1 - \frac{\delta}{(1 - \epsilon)\gamma}\right)$	Center	0	$\frac{\delta[(1 - \epsilon)\gamma - \delta]\sigma_1\sigma_2}{(1 - \epsilon)(\sigma_1 + \sigma_2)\gamma}$

Figure 4.1: Phase portrait of the A) center equilibrium solution and B) and stable equilibrium solution. The parameters used were: $\kappa = 1.0$, $\gamma = 1.0$, $\delta = 0.5$ and $\sigma_1 = 0.5$, $\sigma_2 = 1.0$. For the phase portrait A) $\epsilon = 0.1$ and B) $\epsilon = 0.75$.

of these simulations, represented by four **points of interest**, characterized by the high frequency of: (i) model prey (V) and avoider predator (A) (Figure 4.2), (ii) mimic (M) and avoider (A) (Figure 4.7), (iii) mimic (V) and eater (E) (Figure 4.11), (iv) model (M) and eater (E) (Figure 4.9).

We could observe that all simulation types present the cycling of specific strategy predominance as predicted by the analytical model order: Eater→Model→Avoider→Mimic, agreeing with the clockwise direction of the phase plane portrait of Figures 4.1 A and B. Stochastic effects can exclude one of the strategies of prey and predator, which happened more frequently in the small populations simulations (it happened in 36% of the total simulations for the small populations for the four points of interest analyzed here, and less than 1% for the medium and large populations).

As predicted by the analytical model, oscillations occurred in all the types of simulations (Wm, Li - prey Li - predator, and All local), over the different sizes of populations (144, 576, and 1024), when we started around the coexistence equilibrium

Figure 4.2: Phase portrait (top) from the analytical solution of the payoff parameters simulated (bottom). The parameters used to this simulations were: $\kappa = 1.0$, $\gamma = 1.0$, $\epsilon = 0.0$, $\delta = 0.3$ and $\sigma_1 = 1.0$, $\sigma_2 = 0.5$. The initial conditions were set $f = 0.34$ and $p = 0.71$. The total number of preys and predators is indicated in the columns (144, 576, 1024), and the simulation type is indicated in the rows (Wm: well-mixed, and Li: local interactions, pred: predator).

predicted by the analytical model. We used the standard deviation of the frequencies over the temporal series simulations to estimate the amplitude of the oscillations when the four strategies were coexisting. We observed high amplitude for the Wm simulation type, and in general, the amplitude was greater for the small populations (see Tables 4.3 and 4.4). The simulation types Li - Prey and Li - Pred show lower amplitudes to the preys and predators respectively. The All local simulation type showed the lowest amplitudes in general and also the most different mean of equilibrium frequency.

Table 4.3: Mean frequency and average standard deviation of the point of interest (i).

Size	Simulation type	Predator	Prey
144	Wm	0.67 ± 0.24	0.38 ± 0.25
	Li - Prey	0.69 ± 0.26	0.39 ± 0.22
	Li - Pred	0.68 ± 0.19	0.41 ± 0.28
	All Local	0.64 ± 0.18	0.41 ± 0.19
576	Wm	0.68 ± 0.16	0.35 ± 0.16
	Li - Prey	0.68 ± 0.18	0.34 ± 0.09
	Li - Pred	0.70 ± 0.09	0.37 ± 0.21
	All Local	0.63 ± 0.09	0.41 ± 0.10
1024	Wm	0.69 ± 0.11	0.34 ± 0.12
	Li - Prey	0.68 ± 0.15	0.33 ± 0.06
	Li - Pred	0.70 ± 0.06	0.36 ± 0.16
	All Local	0.63 ± 0.07	0.41 ± 0.07

Figure 4.3: Periodogram of the largest population ($N=1024$ individuals in each population) time series for the point of interest (i). We present the frequency of oscillations of mimic prey and avoider predator. The solid line represents the mean and the shadow represents the standard error based on 100 simulations over 100 generations.

We characterized the oscillation frequency qualitatively, *i.e.* how many peaks and valleys we could observe in one arbitrary unit of time. We analyzed the frequency of oscillations through the power spectrum of the time series. This graph presents the strength (here given by the spectrum) of the frequency band of the time series. We

observed a higher importance of low oscillation frequencies (large period) when both species were interacting locally (All local). Prey and Predator presented a slightly lower oscillation frequency when compared with the well-mixed (Wm) case. The importance of these lower oscillation frequencies increases to preys when predators interact locally (Li - pred), and increases to predators when preys interact locally (Li - prey).

We were interested in understanding how the local interactions may affect the results observed in the mean field and if it could explain the sole existence of mimics in the avoiders predominance in a given community. We made simulations with the same parameters that allow the predominance by the model prey (V) and the avoider predator (A) (point of interest (i)) to accomplish how the initial conditions and the space would affect the final result in strategies frequencies. We chose to analyze this condition because ecological and evolutionary predictions expect that only high frequencies of the model prey allows the mimic existence, and both just have the protection when avoiders are more frequent than eaters.

Figure 4.4 presents one representative simulation made with initial high frequencies of eater predator (E) and mimic prey (M). For well-mixed scenario and assuming medium or large population sizes, we observed the predicted result of large frequencies of model prey and avoider predator. Simulations for the small population sizes were mostly unpredictable in their final result and in different simulations we observed different combinations of predator and prey frequencies, ending up after 100 generations. Eventually, the extinction of one of the strategies occurred at small population sizes specially because the initial conditions of preys and predator frequencies were far from the equilibrium. For the large population size, we could see the oscillations happening through the time in the well-mixed scenario simulations, with average in the frequencies predicted by the analytical solutions and following the expected by the ecological and evolutionary theory of mimicry.

We observed that the local interactions may lead to departures from the well-mixed results. The local interactions of preys (Li - prey) favors the sole coexistence of mimics and avoiders, while the local interactions of predators (Li - pred) favors the sole coexistence of model preys and avoider predators. We analyzed an invasibility plot based on the initial conditions of predators and preys frequencies (Figure 4.5). We noticed that even with the favorable payoffs to the model preys, they can be invaded by mimics with high probability independent of the initial conditions in the small communities when preys interact locally (Li- prey). In larger communities the invasions by mimics in the same conditions are restricted to the initial frequencies far from the center point predicted by the mean field model. We observed an increasing circle of model-avoider prevalence around the region of the equilibrium center ($f=0.33$ and $p=0.70$). The radius of this circle increases with the population size. The larger the populations, the greater the effect of payoffs on the equilibria of frequencies.

The previous result may be a consequence of the order of rotation of species and strategies and also of the largest amplitude oscillations affecting the predators and preys

Figure 4.4: Example of invasibility in the different models and different population sizes. For this simulation, we set $\kappa = 1.0$, $\gamma = 1.0$, $\epsilon = 0.0$, $\delta = 0.3$ and $\sigma_1 = 1.0$, $\sigma_2 = 0.5$. The initial conditions were set $f = 0.90$ and $p = 0.10$. (Wm: well-mixed, and Li: local interactions, pred: predator)

Figure 4.5: The invasibility plot for different initial conditions of frequencies and local interactions. The white regions present a transition of the prevalence given by the top and bottom colors of the legend. We set the parameters: $\kappa = 1.0$, $\gamma = 1.0$, $\epsilon = 0.0$, $\delta = 0.3$ and $\sigma_1 = 1.0$, $\sigma_2 = 0.5$ (Wm: well-mixed, and Li: local interactions, pred: predator).

in the different simulation types. Because the payoffs predict a frequency of 0.67 of model prey (or $f=0.33$ to the mimic prey), the lower initial frequencies of models ($f > 0.3$) will have an initial increment. It can be reinforced by high frequencies of eater ($p>0.70$). In the Li - prey simulations the predators present greater amplitude than the preys. In the clockwise rotation of strategies substitution (Eater→Model→Avoider→Mimic→Eater), we see that avoiders come next to model preys. The high amplitude oscillations contribute to the fast fixation of the avoiders, bringing the mimics after.

When the predators interact locally (Li - Pred), the preys oscillate with higher amplitude. Now, because the payoffs predict a frequency of 0.70 of avoider predator (or $p=0.70$), the lower initial frequencies of avoiders ($f > 0.3$) will cause an initial increment of the model prey frequency. In the Li - pred model the preys oscillate with higher amplitude. Then the initial increment of models can lead them to the dominance ($f=0$) and the substitution sequence brings the avoiders after.

We also simulated a different initial condition, where the species interacting locally had a grouped initial configuration in the space (see Figure 4.13 in the supplementary material). The Li - prey simulations show this condition will result in mimics-avoiders predominance when starting with higher frequency of models ($f < 0.5$), and model-eater when starting with higher frequency of mimics ($f > 0.5$). On the other hand, when predators interact locally (Li - pred), models-avoiders predominate when starting with few avoiders ($p < 0.5$) and mimics-eaters have some predominance in higher initial frequency of avoiders ($p > 0.5$).

Discussion

Mimicry has been intriguing researchers since Bates (1862) brought to public his paper establishing mimicry theory framework. However it took years to understand mimicry as a coevolutionary case, where exists reciprocal evolution change between the interacting predators and preys. The theory predicts the reciprocal evolution changes between predators and preys. and it is reflected in frequency oscillations of the unpalatable model and the parasitic mimic, and of the avoider and eater predators. The success of the mimicry happens when the model is in higher frequency, allowing the mimic to coexist with the avoider predator because of its similarity with the dangerous form. Here, we explored how mimicry could still be successful in the absence or low frequency of the model prey.

Using an evolutionary game theory approach we observed that the protection against predators by the dangerousness warning signal is subjected to the mimics presence. The non-dangerous strategy (here the mimic) is the only stable and single strategy with eater predators. The conditions which allow the model prey and avoider predator coexisting in high frequencies are: (i) the low ratio of venom production or storage costs to the benefit yielded by the dangerousness ($\frac{\delta}{(1-\epsilon)\gamma} < \frac{1}{2}$) and (ii) the benefit of eating a mimic prey is greater than the cost of eating a model prey ($\sigma_1 > \sigma_2$). Even when the payoffs

favor the model prey and avoider predator, the mimics and eaters coexist with them.

The predator and prey population sizes are important parameters to the coexistence equilibrium (the center equilibrium of the mean field model) in finite populations. We observed small populations presenting greater oscillation amplitudes, and diminishing as we increased the number of preys and predators. The local interaction effect is also an important stabilizer of the coexistence equilibrium, promoting small amplitudes of the strategies that interact locally. Small amplitude of oscillations are important to the coexistence equilibrium maintenance because it decreases the chances of losing one of the strategies by stochastic effects (losing diversity), which can turn the community monomorphic in predators and preys. When both prey and predator are interacting locally, both the amplitude of the oscillation and the number of oscillation cycles per generation in the equilibrium decrease in relation to the well mixed simulations.

The simulations show that the unanticipated lonely existence of mimics and avoiders, *i.e.* allopatry of the mimic and its model, is likely to occur when preys interact locally. It may be an effect of large home range of predators or limitation by the preys to move in the environment. The smaller populations are more prone to turn in mimics and avoiders when starting with any initial frequency of mimics and avoiders. The large populations are more prone to turn in mimics-avoiders when initial frequencies are far from the equilibrium center predicted by the payoffs in the mean field approach. It means that these communities can be invaded by mimics even if the predicted advantage is to model preys and avoider predators. When predators interact locally, it is likely the model preys and avoider predators will assume the higher frequencies, as predicted by the payoffs and by the mimicry theory.

Structured communities are affected differently and there is a strong dependency on the initial conditions. For the same parameters studied for the previous cases, we show that mimics and avoiders can dominate a community mostly when the initial frequency of mimics is low and preys are interacting locally (LiQ - prey). Models and avoiders will assume its predicted advantage mostly when the initial frequency of avoiders is low and predators are interacting locally (LiQ - pred). Therefore, structured populations and local interactions of predators are probable promoters of the communities predicted by mimicry theory in the small populations of preys and predators: predominance of model prey and avoider predator. The size of predator and prey populations can contribute to stabilize the equilibrium. Hence, the local interactions and structured populations of predators may strengthen the predicted equilibrium.

Here, we analyzed predators and preys evolving with the same reproduction rate. Most of the mimicry systems are composed of predators larger than preys. Larger animals have lower reproduction rate. Then, we foresee the lower reproduction rate of the predators will damp the predator oscillation, and thereafter the unlikely coexistence of avoiders and mimics will become rarer, even when the preys interact locally, or the community is structured in space. We also believe different reproduction rates can cause longer transients by increasing the period of an oscillation.

We do not consider any mutation or migration rate, which can prevent the community becoming monospecific in prey and predator. However based on the results presented here, once avoiders and models dominate, just mutation/migration rates of preys could bring the system back to the oscillations. In the other way around, once avoiders and mimics dominate, just mutation/migration rates of the predators could bring the system back to the oscillations.

Structured populations and local interactions of preys might be the promoters of model-mimic allopatry in protection mimicry. We believe this result might also be true to two other types of mimicry: deception mimicry (affecting reproduction) and aggressive mimicry (affecting foraging). For instance, it may be the explanation why some deceiving flowering plants exist in some areas without any potential model. These flowering plants deceive pollinators and attract them by resembling rewarding flowers (Gumbert & Kunze, 2001) or even a potential sexual partner to the pollinator. In this case, the plant can be viewed as a prey in our model, and the potential flower visitor as a predator. Because plants have a limited usage of the space (small home range compared to the animal) and because many plants present structured space distribution, we would expect many deceiver flowers being pollinated even in the absence of rewarding flowering plants.

Furthermore, different types of mimicry can act simultaneously. For instance, warning coloration may play important role against predators (protection (Batesian) mimicry) and it can also assist when the mimic is foraging (aggressive mimicry). Snakes of *Lampropeltis* genus resembles coral snakes and its color pattern cause strong reaction and flight by nestling bird parents (Malcolm, 1990). A similar case happens in coral reefs where the mimic blenny *Plagiotremus laudandus* resembles a toxic model blenny *Meiacanthus atrodorsalis*. The mimic also resembles the cleaner fish *Labroides dimidiatus* and it is highly associated with this model in the cleaning stations, where *P. laudandus* feeds on tissues of client fishes (Cheney, 2010). Even the process of mimic predominance might be the same in isolated cases of mimicry (as we suggested before, by structured populations and local interactions), we believe the mixed mimicry cases can result in different equilibrium solutions. We hope future contributions estimating the payoffs, reproduction rates, and population sizes applied to this simple model and a modified model that accomplishes different types of mimicry can shed some light on why Bates never saw the flocks of slow-flying Heliconidae in the woods be persecuted by birds or dragonflies.

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Supplementary material

Below we present how the other three points of interest (point (ii), (iii), (iv)) behave when preys and predators interact in the well mixed model (Wm), when preys interact locally (Li - prey), when predators interact locally (Li - pred), and when both species were interacting locally (All local) models (Figures 4.7, 4.9, and 4.11). We observe similar results as shown to the point of interest (i). The amplitude is the greatest in the Wm model and, in general, the lowest in the All local models, however we also observe low amplitude of prey frequency in the Li - prey model and low amplitude of predators frequency for the Li - pred model (Table 4.4). The period oscillation length of predators and prey frequencies is larger in the All local model (Figures 4.6, 4.8, and 4.10). Preys have a slight increment on period length when predators interact locally, and vice versa to predators. Figures 4.12 and 4.13 are related to the invasibility by the mimic strategy when prey (LiQ - prey) and predator interact locally (LiQ - pred) in a structured population, where the local species is strategy grouped spatially.

Table 4.4: Mean frequency and average standard deviation of the points of interest (ii), (iii) and (iv) for the different simulation types.

	Point of interest	(ii)		(iii)		(iv)	
		Pred	Prey	Pred	Prey	Pred	Prey
144	WM	0.65 ± 0.25	0.64 ± 0.25	0.28 ± 0.23	0.62 ± 0.25	0.31 ± 0.25	0.35 ± 0.25
	Li - Prey	0.62 ± 0.29	0.65 ± 0.20	0.27 ± 0.25	0.61 ± 0.22	0.32 ± 0.27	0.34 ± 0.18
	Li - Pred	0.65 ± 0.21	0.67 ± 0.26	0.28 ± 0.19	0.59 ± 0.29	0.30 ± 0.21	0.32 ± 0.26
	All Local	0.59 ± 0.17	0.61 ± 0.17	0.38 ± 0.18	0.56 ± 0.17	0.47 ± 0.23	0.38 ± 0.21
576	WM	0.68 ± 0.15	0.65 ± 0.16	0.28 ± 0.16	0.65 ± 0.17	0.28 ± 0.15	0.35 ± 0.16
	Li - Prey	0.67 ± 0.19	0.66 ± 0.09	0.28 ± 0.18	0.66 ± 0.10	0.29 ± 0.19	0.33 ± 0.10
	Li - Pred	0.69 ± 0.10	0.65 ± 0.19	0.26 ± 0.09	0.62 ± 0.21	0.26 ± 0.09	0.35 ± 0.20
	All Local	0.59 ± 0.09	0.61 ± 0.09	0.38 ± 0.09	0.56 ± 0.09	0.48 ± 0.12	0.38 ± 0.10
1024	WM	0.69 ± 0.12	0.66 ± 0.12	0.27 ± 0.11	0.65 ± 0.13	0.26 ± 0.10	0.34 ± 0.11
	Li - Prey	0.68 ± 0.15	0.67 ± 0.06	0.27 ± 0.14	0.66 ± 0.07	0.28 ± 0.15	0.34 ± 0.07
	Li - Pred	0.70 ± 0.06	0.65 ± 0.15	0.25 ± 0.05	0.65 ± 0.15	0.25 ± 0.06	0.35 ± 0.16
	All Local	0.59 ± 0.07	0.62 ± 0.07	0.38 ± 0.08	0.56 ± 0.07	0.48 ± 0.10	0.38 ± 0.08

Figure 4.6: Periodogram of the largest population ($N=1024$ individuals in each population) time series for the point of interest (ii). We present the frequency of oscillations of mimic prey and avoider predator. The solid line represents the mean and the shadow represents the standard error based on 100 simulations over 100 generations.

Figure 4.7: Phase portrait (top) from the analytical solution of the payoff parameters simulated (bottom). The parameters used to this simulations were: $\kappa = 1.0$, $\gamma = 1.0$, $\epsilon = 0.0$, $\delta = 0.3$ and $\sigma_1 = 0.5$, $\sigma_2 = 1.0$. The initial conditions were set $f = 0.67$ and $p = 0.71$. The total number of preys and predators is indicated in the columns (144, 576, 1024), and the simulation type is indicated in the rows (Wm: well-mixed, and Li: local interactions). One can notice the fast extinction of avoiders and mimics in the well-mixed simulation, a probable stochastic effect of small populations.

Figure 4.8: Periodogram of the largest population ($N=1024$ individuals in each population) time series for the point of interest (iii). We present the frequency of oscillations of mimic prey and avoider predator. The solid line represents the mean and the shadow represents the standard error based on 100 simulations over 100 generations.

Figure 4.9: Phase portrait (top) from the analytical solution of the payoff parameters simulated (bottom). The parameters used to this simulations were: $\kappa = 1.0$, $\gamma = 1.0$, $\epsilon = 0.6$, $\delta = 0.3$ and $\sigma_1 = 0.5$, $\sigma_2 = 1.0$. The initial conditions were set $f = 0.67$ and $p = 0.26$. The total number of preys and predators is indicated in the columns (144, 576, 1024), and the simulation type is indicated in the rows (Wm: well-mixed, and Li: local interactions).

Figure 4.10: Periodogram of the largest population ($N=1024$ individuals in each population) time series for the point of interest (iv). We present the frequency of oscillations of mimic prey and avoider predator. The solid line represents the mean and the shadow represents the standard error based on 100 simulations over 100 generations.

Figure 4.11: Phase portrait (top) from the analytical solution of the payoff parameters simulated (bottom). The parameters used to this simulations were: $\kappa = 1.0$, $\gamma = 1.0$, $\epsilon = 0.6$, $\delta = 0.3$ and $\sigma_1 = 1.0$, $\sigma_2 = 0.5$. The initial conditions were set $f = 0.67$ and $p = 0.26$. The total number of preys and predators is indicated in the columns (144, 576, 1024), and the simulation type is indicated in the rows (Wm: well-mixed, and Li: local interactions).

Figure 4.12: Example of invasibility in the different models and different population sizes. For this simulation, we set $\kappa = 1.0$, $\gamma = 1.0$, $\epsilon = 0.0$, $\delta = 0.3$ and $\sigma_1 = 1.0$, $\sigma_2 = 0.5$. The initial conditions were set $f = 0.90$ and $p = 0.10$. The total number of preys and predators is indicated in the columns (144, 576, 1024), and the simulation type is indicated in the rows (LiQ: grouped local interactions, pred: predator).

Figure 4.13: The invasibility plot for different initial conditions of frequencies and local interactions. The white regions present a transition of the prevalence given by the above and by the below colors of the legend. We set the parameters: $\kappa = 1.0$, $\gamma = 1.0$, $\epsilon = 0.0$, $\delta = 0.3$ and $\sigma_1 = 1.0$, $\sigma_2 = 0.5$ (LiQ: grouped local interactions, pred: predator).

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5 — Considerações finais

Ao longo deste trabalho, estudei os efeitos de parasitas de interações em redes de interações mutualísticas e também investiguei como organismos que adotam a estratégia de trapaça podem coexistir com mutualismos sem extingui-los. No Capítulo 1, revisei a literatura sobre mutualismos para ilustrar a existência de diversas interações mutualísticas, tais como polinização, dispersão de sementes, estações de limpeza em ambientes recifais, formigas defensoras de plantas, mimetismo e bactérias fixadoras de nitrogênio em raízes de plantas, que persistem na natureza apesar da recorrência de trapaceiros que parasitam essas interações.

No Capítulo 2, mostrei que a existência de trapaceiros aumenta a resiliência de redes mutualísticas. Entretanto, o impacto de trapaceiros sobre a estabilidade depende da estrutura da rede. Sob a presença de trapaceiros, uma maior estabilidade deve ocorrer em redes aninhadas, tais como aquelas formadas por espécies mutualistas de vida livre que formam sistemas de polinização ou dispersão de sementes. O inverso deve ocorrer em redes modulares, típicas de interações íntimas, tais como mutualismos entre mirmecófitas e suas formigas protetoras. Esses resultados enfatizam a importância da incorporação de aspectos da história natural em modelos que buscam gerar entendimento sobre processos dinâmicos em redes ecológicas.

Como trapaceiros ocorrem na maioria dos mutualismos, novos estudos que considerem seus efeitos sobre dinâmicas ecológicas e evolutivas de redes multiespecíficas de interações constituem uma linha de investigação relevante para o entendimento dos processos que geram e mantêm a diversidade biológica. Particularmente, estudos que relacionem a arquitetura de redes de interações às dinâmicas ecológicas subjacentes podem iluminar os mecanismos que determinam como espécies com diferentes papéis estruturais na rede influenciam a estabilidade ao adotarem uma estratégia antagonista. A Ecologia contemporânea experimenta um período muito promissor para o desenvolvimento dessa linha de investigação, graças ao amadurecimento de uma diversidade de ferramentas advindas da teoria de grafos e de redes complexas, tais como a árvore mínima geradora,

a cobertura mínima de vértices e de arestas, e a proliferação de rotas. Cada uma dessas ferramentas nos fornece novas idéias sobre espécies (vértices), como por exemplo, ressaltar aquelas que têm papel central na dinâmica das redes pois seu posicionamento estrutural implica maior ou menor disseminação de efeitos diretos e indiretos.

No Capítulo 3, mostrei que trapaceiros podem coexistir com seus parceiros e com mutualistas se houver algum efeito sinérgico das interações entre mutualistas e trapaceiros. Assim, mesmo que os trapaceiros diminuam a aptidão dos indivíduos com os quais interagem, a aptidão deste parceiro pode ser suficiente para garantir a persistência da estratégia se houver um ganho adicional via efeitos positivos sobre as interações com o parceiro mutualístico. Especificamente, mostramos em que condições as flores tubulares, que sofrem maiores danos ao interagirem com pilhadores de néctar, conseguiriam coexistir com flores planares, polinizadores e pilhadores. Nesse sistema, a coexistência resulta de efeitos indiretos da trapaça sobre o sucesso reprodutivo das flores tubulares: o roubo do néctar pode aumentar o sucesso de uma planta se as interações com pilhadores favorecerem a polinização cruzada, aumentando assim o sucesso reprodutivo das plantas que interagem com ambos os visitantes florais. Apresento, portanto, um novo mecanismo com potencial para explicar a manutenção da cooperação e da diversidade de estratégias, que são os efeitos não lineares (sinérgicos) das interações entre mutualistas e parasitas de interações.

A evolução da cooperação é um tema que já foi intensamente estudados em variadas áreas do conhecimento. Entretanto, o entendimento da ecologia e da evolução de sistemas biológicos cooperativos ainda constituem um desafio, especialmente no que se refere à manutenção das interações cooperativas interespecíficas e aos mecanismos que contrabalançam os efeitos negativos da trapaça. Embora o estudo de efeitos indiretos e em redes de interação pareçam um passo natural para estudar a evolução de interações mutualísticas entre muitas espécies, o desenvolvimento de abordagens quantitativas que permitam o avanço do entendimento mecanístico desses efeitos continua sendo uma área com grandes lacunas. Nesse sentido, pretendo em futuros estudos unir a história natural de mutualismos e seus trapaceiros à teoria de redes complexas (Santos & Pacheco, 2005; Santos et al., 2006) e dinâmicas não lineares para contribuir para o entendimento de mecanismos indiretos de manutenção da cooperação (Nowak & Sigmund, 2005; Santos et al., 2012).

Finalmente, no Capítulo 4, considere cenários de mimetismo Batesiano para investigar como interações locais podem levar os mímicos (trapaceiros) a predominarem no nível de população, subjugando o modelo aposemático. Presas que interagem localmente podem favorecer a predominância de mímicos e de predadores que os evitam após algumas gerações. As interações locais de presas, quando combinadas com uma estruturação de mímicos (trapaceiros) e modelos (cooperadores) no espaço, podem reforçar ainda mais a alopatría entre modelo e mímico.

Em futuros estudos, pretendo entender como mutações, migrações e variações nas interações podem influenciar a evolução do mimetismo e gerar mosaicos geográficos

dinâmicos nos quais coexistem diferentes estratégias. Em outras palavras, pretendo entender a evolução da cooperação e a coexistência entre mutualistas e trapaceiros sob a ótica da teoria do mosaico geográfico de coevolução. Além disso, pretendo entender como variações no estabelecimento de interações entre os indivíduos podem se mapear no problema de mosaicos geográficos de coevolução (Thompson, 2005).

Futuros trabalhos que busquem contribuir para o entendimento da evolução da cooperação podem, ao meu ver, explorar (i) como a evolução de interações entre duas ou mais populações ocorre, (ii) como benefícios e custos variáveis influenciam a estabilidade da cooperação, ainda que na presença de diferentes níveis de trapaça e (iii) como a evolução da cooperação pode resultar em diversificação das estratégias e ainda assim se tornar uma estratégia evolutivamente estável.

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Arte Gráfica

O projeto gráfico da tese foi elaborado por Mathias Legrand e modificado por Ayana de Brito Martins.

Modelo obtido em: <http://www.latextemplates.com/template/the-legrand-orange-book>, sob a licença CC BY-NC-SA 3.0 (<http://creativecommons.org/licenses/by-nc-sa/3.0/>)

A arte das figuras da capa e cabeçalhos dos capítulos foram feitas por Dora Souza Dias, a partir das imagens obtidas de:

- **Capítulo 1:** Fotografia feita por Rafael L. Fonseca.

Formiga do gênero *Ectatomma quadridens* (Ectatommini) em posição para atacar uma lagarta de *Utetheisa ornatrix* (Arctiini) em uma vagem de *Crotalaria pallida* (Fabaceae) em Campinas, SP, Brasil.

- **Capítulo 2:** Figura 1 do manuscrito de Julieta Genini et al. (2010).

Genini, J., Morellato, L. P. C., Guimarães, P. R., & Olesen, J. M. (2010). Cheaters in mutualism networks. *Biology Letters*, 6(4), 494–497.

- **Capítulo 3 e capa:** Fotografia feita por Kathy Keatley Garvey.

Abelha carpinteira *Xylocopa tabaniformis orpifex* (Xylocopinae) roubando néctar de uma flor de *Salvia sp* (Lamiaceae) no jardim botânico da University of Califórnia, Davis, Califórnia, Estados Unidos da América.

Endereço eletrônico: http://ucanr.edu/blogs/bugsquard//blogfiles/16053_original.jpg

- **Capítulo 4:** Prancha de ilustração retirada do manuscrito de Henry W. Bates (1862).

Ilustração de mimetismo batesiano de borboletas do gênero *Dismorphia* (Pieridae) e da tribo Ithomiini (Nymphalidae)

Bates, H. W. (1862). XXXII. Contributions to an insect fauna of the Amazon Valley. Lepidoptera: Heliconiae. *Transactions of the Linnean Society of London*, 23, 495–566.

- **Capítulo 5:** Carta escrita à mão por Charles Darwin a Alfred R. Wallace após sugestão de Henry W. Bates.

Trecho da carta: “his (Bates) first suggestion was “you had better ask *Wallace*”. *My difficulty is, why are caterpillars sometimes so beautifully & artistically coloured?*”

Endereço eletrônico: <http://www.nhm.ac.uk/nature-online/collections-at-the-museum/wallace-collection/item.jsp?itemID=83>