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Evolutionary Game Theory as a Framework for Studying Biological Invasions

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ABSTRACT: Although biological invasions pose serious threats to biodiversity, they also provide the opportunity to better understand interactions between the ecological and evolutionary processes structuring populations and communities. However, ecoevolutionary frameworks for studying species invasions are lacking. We propose using game theory and the concept of an evolutionarily stable strategy (ESS) as a conceptual framework for integrating the ecological and evolutionary dynamics of invasions. We suggest that the pathways by which a recipient community may have no ESS provide mechanistic hypotheses for how such communities may be vulnerable to invasion and how invaders can exploit these vulnerabilities. We distinguish among these pathways by formalizing the evolutionary contexts of the invader relative to the recipient community. We model both the ecological and the adaptive dynamics of the interacting species. We show how the ESS concept provides new mechanistic hypotheses for when invasions result in long- or short-term increases in biodiversity, species replacement, and subsequent evolutionary changes.

Keywords: game theory, invasion biology, evolutionarily stable strategy, G-function, invasive species, adaptive dynamics.

Introduction

Recent studies reveal that evolutionary changes can strongly influence the ecological dynamics of native and nonnative species (Sinervo et al. 2000; Yoshida et al. 2003). Yet most studies have focused on understanding either the ecological or the evolutionary dynamics of biological invasions but not both together (Mooney and Cleland 2001; Lee 2002; Cadotte et al. 2006). Although many have recognized the great potential of invasive species as a model system to study the interplay between the ecological and evolutionary dynamics of species interactions (Bruno et al. 2005; Holt et al. 2005; Vanderhoeven et al. 2010), research efforts may be hindered by a lack of integrated frameworks to generate mechanistic hypotheses about in-

vasions. Recent suggestions of trait-based frameworks have begun to pave the way toward a mechanistic understanding of ecoevolutionary processes affecting the success of an invader (Olden et al. 2004; Facon et al. 2006; Funk et al. 2008; Moles et al. 2008) but generally do not consider the consequences for both the invader and the recipient native community. Thus, invasion ecology could benefit from conceptual approaches that seek to simultaneously understand the ecological and evolutionary processes underlying invasion success and the resulting dynamics for both the invader and recipient species.

Evolutionary game theory should be valuable and well suited for integrating and modeling the strategies (i.e., traits) commonly studied by ecologists and evolutionary biologists interested in biological invasions. In evolutionary game theory, the evolutionarily stable strategy (ESS) is a set of strategies (=species for our purposes) that, by definition, cannot be invaded by rare alternative strategies (Maynard Smith and Price 1973). Successful invasions of nonnative species often occur as a rare event within a recipient community. Thus, the ways in which a recipient community can have no ESS (termed being “non-ESS” hereafter) and be invaded by a rare strategy may provide new insights into the mechanisms that allow nonnative species to invade. Game theory and adaptive dynamics have modeled the phenotypic dynamics of traits in order to generate predictions about speciation (Brown and Pavlovic 1992; Abrams et al. 1993; Doebeli and Dieckmann 2000), niche coevolution (Dieckmann and Law 1996; Ripa et al. 2009), adaptive growth and branching (Geritz et al. 1998), and coevolution between species (Brown and Vincent 1987; Abrams and Matsuda 1997; Mitchell 2000; Apaloo et al. 2005; Krivan and Cressman 2009). We suggest that these same tools of game theory can also model the dynamics of biological invasions.

Here we use evolutionary game theory to explore mechanisms underlying competitive interactions between native and nonnative species and propose a conceptual framework for considering the ecological and evolutionary dynamics of invasions. Under the ESS definition, the vul-

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nerability of a recipient community to invasion can arise via various pathways. In particular, we explore three ways in which a community can be susceptible to invasion by a nonnative competitor: (1) a novel evolutionary technology, where the invader represents a novel competitor with respect to the recipient community and possesses a novel evolutionary technology that is evolutionarily unavailable to the species with which it competes; (2) an empty niche, where the recipient community may have fewer species than would exist at its ESS; an invader with an appropriate strategy to fill the niche may be able to occupy the empty peak of the adaptive landscape; and (3) a non-ESS recipient community, where if a species of a recipient community has a strategy that is away from its ESS (i.e., not occupying the peak of the adaptive landscape), then a species with a strategy closer to or on the opposite side of the peak can successfully invade.

Using evolutionary game theory, we model each of these three pathways to illustrate how an invader can arrive and establish within a recipient community. By modeling the arrival of an invader as a game, this framework draws equal attention to potential changes in trait values and population sizes of the invader and recipient community through each stage of the invasion process: arrival, establishment, and spread/impact (Kohler and Lodge 2001). We use the concept of a fitness-generating function (G-function; Vincent and Brown 2005) to distinguish each of the three invasion pathways and then consider each pathway in detail. The G-function approach is one of several different methods for modeling the evolution of continuous traits above the species level. Here, we use it to illustrate the usefulness of game theory in general. Similar methods built around adaptive dynamics, invasion fitness, and evolutionary branching (Metz et al. 1995; Geritz et al. 1998; Doebeli and Dieckmann 2000; Abrams 2001) are equally applicable. More generally, we hope to demonstrate how competitive interactions between individuals or species, in general, can be thought of as a game and that a game-theoretic approach provides an opportunity to better integrate evolutionary perspectives into the field of community ecology, a timely and key avenue of research (Agrawal et al. 2007).

The Model

The G-function approach has been well described by Vincent and Brown (2005) and is described in the appendix, but in brief, the G-function describes the per capita growth rate and the evolutionary dynamics of a species possessing a particular strategy within a particular environment: $G(v, \mathbf{u}, \mathbf{x})$. The term v is the strategy (heritable trait) of the focal individual, and the vector $\mathbf{u} = (u_1, \dots, u_{n_s})$ describes the different strategies found within the population

or community. For our purposes, we assume that the different strategies of this vector represent different species where u_i is the strategy value of the i th species for $i = 1, \dots, n_s$. The vector $\mathbf{x} = (x_1, \dots, x_{n_s})$ gives the current population sizes of each species within the community, where x_i gives the population size of the i th species, whose strategy is u_i . The strategy of the individual may be scalar or vector valued and composed of several traits (Brown et al. 2007). For ease of presentation, we will consider a scalar-valued strategy where there is just one evolving trait of interest.

Here, we transform a standard Lotka-Volterra population model of competition into a fitness-generating function (G-function), but ideally, the underlying population model for formulating the G-function should be one favored by the researchers and managers and most appropriate to the ecology of the nonnative species and recipient community. To illustrate the general pathways of invasion, we extended a Lotka-Volterra model of competition into a G-function by assuming that carrying capacity (K) is a function of the focal individual's strategy (v ; for more detail, see appendix). We include the strategies of others by letting the competition coefficient (α) describe the competitive effect of species i on the focal individual using strategy v :

$$G(v, \mathbf{u}, \mathbf{x}) = \frac{r}{K(v)} \left(K(v) - \sum_{i=1}^{n_s} \alpha(v, u_i) x_i \right), \quad (1)$$

where

$$K(v) = K_m \exp \left(-\frac{v^2}{2\sigma_k^2} \right) \quad (2)$$

and

$$\alpha(v, u_i) = 1 + \exp \left[-\frac{(v - u_i + \beta)^2}{2\sigma_\alpha^2} \right] - \exp \left[-\frac{\beta^2}{2\sigma_\alpha^2} \right]. \quad (3)$$

The term K_m is the maximum value for the carrying capacity, σ_k is related to the "range of resources," and σ_α is related to a species "niche width." We use Gaussian curves to describe both how strategies influence carrying capacity and competition coefficients. For the carrying capacity function, we standardized the model so that a strategy of $v = 0$ maximizes carrying capacity: $K(0) = K_m$. Carrying capacity declines symmetrically as v deviates from 0. For the competition function, we assume that, in general, competition decreases as individuals have very different strategies. We include the term β to make competition asymmetric in the sense that the species with a higher strategy value has a greater negative impact on the species with the lower strategy value than vice versa. Fi-

nally, we add a term to standardize competition so that individuals using the same strategy will have a competition coefficient equal to 1, and no matter how divergent two strategies are from each other, there will be some minimum level of competition.

Using this G-function, we distinguish among the three invasion pathways. First, we hypothesize whether the fitness consequence of an invader's strategy requires the same G-function or one distinct from that of the recipient community. A single G-function can model any number of ecologically interacting or coevolving species, but these species must be evolutionarily identical in the sense of sharing the same set of evolutionarily feasible strategies and experiencing the same fitness consequences of possessing a given strategy. While species of the same G-function may have distinct strategies, they reside on the same adaptive landscape (G vs. v) and have the potential to evolve interchangeably.

For example, the introduction of the zebra mussel (*Dreissena polymorpha*, family Dreissenidae) from Eurasia into North America has posed a serious threat to the biodiversity of freshwater mussels (family Unionidae; Strayer 1999; Strayer et al. 2006). Although both families share some similarities in morphology (e.g., hinged bivalves) and functional traits (e.g., filter feeders), there are crucial differences between the families (Mackie 1991). Two traits in particular that distinguish these families include the presence of byssel threads, used for attaching to substrates, and having a free-living veliger (i.e., planktonic) larval stage, both of which are present in the dreissenids but generally absent in any native freshwater unionids (Mackie 1991). Therefore, these traits may not be part of the unionids' strategy set. Thus, to model the potential pathways of invasion for the zebra mussel based on these strategy differences, we would hypothesize that species in the unionid family are part of its own "unionid" G-function and the zebra mussel is part of its own "dreissenid" G-function. In the absence of macro-mutations or constraint-breaking adaptations, a unionid species will always be subject to the fitness consequences associated with its "unionid" G-function within a given environment, and the zebra mussel will be subject to fitness consequences of its own G-function. The distinction in G-functions captures the reality that both families possess shared traits such as shell shape and size. These traits may even separate species within each family and can evolve quickly and directionally in response to selection, whereas the traits that phylogenetically distinguish the families (e.g., byssel threads or free-living veliger larvae) are much slower to evolve.

Therefore, to model this pathway of invasion we use two G-functions, expanding on the Lotka-Volterra model. This extension from one to two G-functions poses

some notational challenges; thus we provide the following details. We let G_1 and G_2 represent the G-functions of the resident and donor communities, respectively. For these, v_1 and v_2 represent the strategy of the focal individual for each of these G-functions, respectively. The vectors $\mathbf{u}_j$ and $\mathbf{x}_j$ refer to the species and their population sizes for G-functions $j = 1, 2$. The elements of these vectors, u_{ij} and x_{ij} , refer the i th species of the j th G-function. We now have a resident species (e.g., native unionid mussel),

$$G_1(v_1, \mathbf{u}_1, \mathbf{u}_2, \mathbf{x}_1, \mathbf{x}_2) \quad (4a)$$

$$= \frac{r_1}{K_1(v_1)} \left(K_1(v_1) - \sum_{j=1}^2 \sum_{i=1}^{n_{s_j}} \alpha(v_1, u_{ij}) x_{ij} \right),$$

and an invader (e.g., zebra mussel),

$$G_2(v_2, \mathbf{u}_1, \mathbf{u}_2, \mathbf{x}_1, \mathbf{x}_2) \quad (4b)$$

$$= \frac{r_2}{K_2(v_2)} \left(K_2(v_2) - \sum_{j=1}^2 \sum_{i=1}^{n_{s_j}} \alpha(v_2, u_{ij}) x_{ij} \right),$$

with a symmetric distribution for carrying capacities

$$K_1(v_1) = K_m \exp \left(-\frac{v_1^2}{2\sigma_k^2} \right), \quad (5)$$

$$K_2(v_2) = K_m \exp \left(-\frac{(v_2 + \gamma)^2}{2\sigma_k^2} \right),$$

and the following for the interaction coefficients,

$$\alpha(v_j, u_{ij}) = 1 + \exp \left[-\frac{(v_j - u_{ij} + \beta)^2}{2\sigma_a^2} \right] - \exp \left[-\frac{\beta^2}{2\sigma_a^2} \right],$$

where n_{s_1} is the number of resident species and n_{s_2} is the number of potential invasive species from the donor community with the second G-function. The parameter γ can be thought of as a trait or trait-determined parameter (such as byssel threads or veliger larvae when separating Unionidae from Dreissenidae) that either cannot evolve or would evolve so much slower than u as to occur on a completely different timescale. For carrying capacity, we standardized the model so that a strategy of $v = -\gamma$ maximizes K . Carrying capacity declines symmetrically as v deviates from $-\gamma$.

For this model we have made a number of assumptions that are likely not general and would have to be evaluated system by system. We have assumed that the evolving strategy, u , is the same for both G-functions (or at least can be scaled to appear on the same axis). For illustration purposes this will allow us to plot both adaptive landscapes on the same axis and a separate adaptive landscape for

each G-function. This may hold for traits such as body size and some of the adult shell characteristics found within and between the two families of mussels. Furthermore, we are envisioning that the two G-functions are quite closely related. The two G-functions may describe sister families or families in the same order, when families closely approximate different G-functions.

We have made the competition coefficient between species independent of which G-function they come from. Competition is only a function of an individual's strategy, v , and the strategy of its competitor, u , independent of the competitor's G-function (for many real systems this may be a questionable assumption). What determines the G-function for our example is the value of γ , the parameter that determines the value of v that maximizes carrying capacity. This parameter is assumed to be fixed among the species within a G-function, and it creates a kind of niche-axis shift between the members of the different G-functions. While there are many more sophisticated ways to create different G-functions (e.g., predator-prey coevolution models; Brown and Vincent 1992), this provides a good starting point for showing the consequences of invasion, competition, and coevolution between species from similar, yet distinct, G-functions. In what follows we shall always center the resident species, G_1 , or $\gamma = 0$, and then consider the consequence of different values of $\gamma > 0$ on the invader.

Finally, consider the subsequent invasion of the quagga mussel (*Dreissena rostriformis bugensis*, family Dreissenidae) into the Great Lakes. Like the zebra mussel, the quagga mussel possesses both byssel threads and free-living veliger larvae. We would again use two separate G-functions to model vulnerabilities to invasion of a native Unionid community by the quagga mussel, as outlined immediately above (eqq. [4]). However, we would use the same G-function to identify pathways by which the zebra mussel (the initial invader) might be susceptible to invasion by the quagga mussel (eq. [1]). Evidence for considering the two species as a single G-function and evolving along the same adaptive landscape could be drawn from the known potential of hybridization and phylogenetic relationships (Mills et al. 1996). Determining whether two or more species are a part of the same or different G-functions is an empirical question and, admittedly, a challenging task. As suggested above in the zebra mussel example, a feasible first step is to look to modern taxonomy to provide evidence through which we can hypothesize the evolutionary relationships between native and nonnative species within a given environment. In the absence of genetic knowledge to the contrary, it may be suitable to assume that members of the same genus share the same G-function. For some situations, the taxonomic level of family may approximate G-functions. However, members

of different orders, classes, or phyla will require distinct G-functions. One is more likely to require different G-functions as one moves from more recent to more distant nodes in a phylogeny. Nodes represented by "constraint-breaking adaptations" or "adaptive breakthroughs" make good candidates for new G-functions (Vincent and Brown 2005).

Results

Invader as Novel G-Function: Nonsuperior and Superior G-Function

For this case, we simulate a recipient community with a single species. We let the species be at its ESS, meaning that its strategy value resides on the peak of its adaptive landscape, and it occurs at its equilibrium population size. We refer to this species G-function as G_1 . At its ESS, the following are true: $G_1(v_1, \mathbf{u}_1^*, \mathbf{x}_1^*) = 0$ and $\partial G_1 / \partial v_1 = 0$ when $v_1 = u_{1i}^*$ for all strategies comprising $\mathbf{u}_1^*$. (Note that we are using $\mathbf{u}_1$ and $\mathbf{x}_1$ to denote the resident species and their population sizes; furthermore, we are assuming that the evolutionary and ecological dynamics are convergent stable and will drive the species' strategies and population sizes to $\mathbf{u}_1^*$ and $\mathbf{x}_1^*$; see Geritz et al. 1998 and Apaloo et al. 2009 for further discussion of stability concepts associated with ESS and convergence stability in adaptive dynamics.) Next, we let the invader have a different G-function. Although a different G-function, we imagine that the invader, in its donor community, represents roughly an ecological equivalent of the resident species. We let the invader also reside at its ESS within its donor community, and so it satisfies $G_2(v_2, \mathbf{u}_2^*, \mathbf{x}_2^*) = 0$ and $\partial G_2 / \partial v_2 = 0$ when $v_2 = u_{2i}^*$ for all strategies comprising $\mathbf{u}_2^*$. (Note that we have used $\mathbf{u}_2$ and $\mathbf{x}_2$ to denote the donor species strategies and population sizes.) For illustration, we created two G-functions by using different values for γ in the carrying capacity function, where the resident and invader G-functions have $\gamma = 0$ and $\gamma = 2$, respectively.

At the establishment phase within the newly invaded environment, the invader begins at a very low population size, which is typical of most introduction events, ($x_{i2} \approx 0$, where the subscript $i2$ denotes the i th species of the donor community's G-function), and the resident species at its equilibrium size of $\mathbf{x}_1^*$. Hence the resident landscape remains unchanged even though its G-function is now influenced by the invader: $G_1(v_1, \mathbf{u}_1, \mathbf{u}_2, \mathbf{x}_1, \mathbf{x}_2)$, where all elements of $\mathbf{x}_2 = 0$ at the onset of the invasion. However, the invader experiences a different adaptive landscape from the one in its native/donor range. Its G-function is now amended as $G_2(v_2, \mathbf{u}_1, \mathbf{u}_2, \mathbf{x}_1, \mathbf{x}_2)$, where all elements of

$\mathbf{x}_2 = 0$, and $\mathbf{x}_1 = \mathbf{x}_1^*$ for the community of resident species in the absence of the invader.

The landscape of the invader within the recipient community determines the ecological (invasion potential) and evolutionary (invasion window) prospects of the invasion. If the invader has a positive per capita growth rate when $v_2 = u_{12}^*$ (the single invader species possesses a strategy value that would have been an ESS within its donor community), then the invasive species has positive invasion potential and $G_2(v_2, \mathbf{u}_1^*, u_{12}^*, \mathbf{x}_1^*, 0) > 0$ when $v_2 = u_{12}^*$, $x_{12} = 0$, and the resident population is at its conditional ESS (conditional in the sense that the invader is not yet present and influencing the ecological and/or evolutionary dynamics of the resident's community). Furthermore, the range of values for the invader's v_2 for which $G_2 > 0$ defines the invasion window. The invasion window is represented by the region of the invader's adaptive landscape that lies above 0. If the invader has positive invasion potential, then there must exist an invasion window and u_{12}^* must be part of the nonnative species' invasion window. However, the reverse is not necessarily true. The presence of an invasion window does not mean that the nonnative species has positive invasion potential (i.e., a strategy that confers positive population growth).

Under this scenario, three general outcomes are possible. First, the invader can arrive in the recipient community with no invasion window and negative invasion potential (fig. 1a). In other words, all the strategy values of the invader's adaptive landscape have negative population growth rate ($G_2(v_2, \mathbf{u}_1^*, u_{12}^*, \mathbf{x}_1^*, 0) < 0$ for all values of v_2). Regardless of the invasive species' strategy value, it can never have positive invasion potential. Second, the invader can arrive with a range of strategies that confer positive per capita growth; thus, an invasion window exists in its adaptive landscape, but it does not arrive with positive invasion potential. When this occurs, the invader is under strong selection to evolve toward the peak of its adaptive landscape, which will in time move the invasive species into a range of positive fitness and hence positive invasion potential. Thus, the possibility exists for the invader to successfully invade, but it requires evolution to rescue the population from extinction (Gomulkiewicz and Holt 1995; Holt et al. 2005). Ecologically, the arrival of the invader should have little to no effect on the resident species. However, if the nonnative species persists long enough to evolve toward a strategy within its invasion window, it will begin to impact both the population size of the resident species and the shape of its adaptive landscape.

Depending on the circumstances and the nature of the two G-functions, the nonnative species may evolve to out-compete the resident species. Or, as shown in figure 1b,

1c, a new ESS may result where the resident and nonnative species coexist and they evolve to the peaks of their respective landscapes. Each will have influenced the population size and evolution of the other. Figure 1b shows the establishment phase where the invasive species has negative invasion potential but a positive invasion window. Figure 1c shows the new ESS resulting from the evolution and changes in population sizes of both the nonnative and resident species.

Third, the invader can arrive with both an invasion window and positive invasion potential. Here the invader arrives with a strategy that falls within the invasion window, the range of values with positive per capita growth. This results in an immediately successful invasion by the novel invader (fig. 2a). Although the invader and resident species continue to coevolve, the nonnative species can immediately establish and grow to some positive equilibrium population size (fig. 2b). This new ecological equilibrium will result in changes to the population size of the resident species, and it will alter the adaptive landscapes of both species. If both the nonnative species and resident species coexist following this establishment, then both may coevolve to a new ESS where both occupy new peaks on their respective landscapes (fig. 2c).

An extreme case of this third outcome occurs when the nonnative species' G-function represents a different and superior evolutionary technology. In the recipient community, the invader's superior G-function appears with a peak that is higher than the peak on the recipient community's landscape. Not surprisingly, this gives the invader an invasion window within the new environment. If the invader arrives with positive invasion potential, the recipient species will eventually be replaced by the invader. This demonstrates the process of incumbent replacement (Rosenzweig and McCord 1991), whereby a key adaptation within a group of organisms with similar ecological niches, that is, large overlap of each G-function's adaptive landscape, will eventually lead to the extinction of the group that does not contain this adaptation, which is modeled by increasing the peaks of the invader's adaptive landscape relative to those of the resident's landscape. Figure 3 shows the sequence whereby the invader with a superior G-function invades and replaces the resident species (both G-functions for our illustration possessed $\gamma = 0$, but we gave the superior invader G-function a $K_{\max} = 110$ while the resident G-function had $K_{\max} = 100$). At the establishment phase, the invader's G-function lies above that of the resident species (fig. 3a). Once the invader establishes, it will achieve an equilibrium population size that leaves no region of the resident species' landscape with positive fitness (fig. 3b). The resident species will become extinct, and the invader may evolve to the peak of its landscape (fig. 3c).

Figure 1: An example where the recipient community (solid line) is at threat of invasion from a donor community (dashed line) with a different G-function (distinct evolutionary technology). Each adaptive landscape plots potential fitness versus the strategy of an individual from the particular G-function. For this illustration and all subsequent figures: $r = 0.25$, $K_m = 100$, $\sigma_\alpha^2 = 4$, and $\beta = 2$. *a*, The species of the recipient community is at its evolutionarily stable strategy (ESS), the adaptive landscape of the nonnative species offers no invasion window, and the nonnative species (dashed line, open dot) has negative invasion potential. In this example, for illustrative purposes we have given both G-functions the same evolutionary strategy. However, this strategy has different consequences for fitness, depending on the G-function. For this specific example, $\sigma_K^2 = 4$, $\gamma = 1$, $u_{i1} = 1.213$, $x_{i1}^* = 83.2$ (strategy and population size of species of recipient community), $u_{i2} = 0.213$, $x_{i2} = 0$ (species of donor community). *b*, The adaptive landscape of the nonnative species offers an invasion window (gray box), but the nonnative species (dashed line, black dot) starts with negative invasion potential ($u_{i1} = 1.213$, $x_{i1}^* = 83.2$, $u_{i2} = -0.78$, $x_{i2} = 0$). *c*, If the nonnative species were able to evolve a strategy within its invasion window, then it would successfully invade and establish a new ESS with both

Invader within the Same G-Function as a Recipient Community: Empty Niche

A recipient community can be non-ESS if there is an unoccupied peak in its adaptive landscape. This can arise if the recipient community's G-function currently has fewer species than are required for the ESS. Here the invader represents a species that exploits the unoccupied peak in an existing adaptive landscape within the recipient community. In this scenario, we imagine a community of one or more resident species that have evolved to occupy local peaks of the adaptive landscape (Cohen et al. 1999). They are both ecologically and locally evolutionarily stable. But, the ESS contains more species, with a valley separating the occupied peaks of the landscape from the region of the landscape that offers a positive invasion window (fig. 4). Under this scenario two outcomes are possible.

First, the recipient community has an invasion window; however, the invader does not arrive with positive invasion potential. The invader may become extinct, or in response to strong selection pressure, it evolves into the invasion window. Alternatively, the invader may arrive with a strategy that falls within the invasion window (fig. 4a). It can be successful immediately, even in the absence of evolution. The invader can establish and grow to a positive equilibrium population size. The ecologically successful invader is under selection to evolve toward the unoccupied peak. In so doing, it will likely have small impacts on the population sizes and strategies of the recipient species. By way of this invasion, the ESS diversity of species can be filled, with all species occupying their respective peaks. This community is no longer invadable by alternative strategies from within the same G-function. For instance, if the ESS requires three species and the community starts with two, the invader can establish the three-species community (fig. 4b).

Invader within the Same G-Function as a Recipient Community: Non-ESS Recipient Community

For this case, we imagine a recipient community with a single species that is non-ESS. Thus, it is not at its peak on the adaptive landscape. This leaves open an invasion window for a strategy that is closer to the peak. The invader

species coexisting ($u_{i1} = 1.15$, $x_{i1}^* = 79.9$, $u_{i2} = -2.916$, $x_{i2}^* = 11.81$). The small effect of the invasive species on the population size and strategy of the resident species is due to the asymmetric competition coefficient, where bigger strategies have a larger effect on smaller ones than vice versa. This illustration has the same parameter values as *a* except that the invasive G-function now has $\gamma = 4$. (The subscripts ij refer to the i th species of the j th G-function.)

is part of the same G-function; therefore, both reside on the same adaptive landscape, giving the invader an opportunity to exploit the open invasion window. In this scenario, if the invader arrives, then one of three outcomes is possible. First, the invader arrives with a strategy that has a negative population growth rate and, thus, negative invasion potential. The invader is under strong selection pressure to evolve toward the peak of its adaptive landscape. Because the landscape contains an invasion window, the recipient community does face the possibility of invasion by the invader. If the invader can persist long enough to evolve toward a strategy with positive fitness, then it may impact the resident species. But more likely, the invader will become extinct as the resident species has a “head start” on evolving toward the peak.

The next two possibilities result from the invader arriving with a strategy that falls within the invasion window. First, the invader can arrive with a strategy that lies between the resident species’ strategy and the peak or, in some cases, just on the other side of the peak (fig. 5a). The invader’s population will increase to its equilibrium. As its population grows, it depresses the adaptive landscape in a manner that leaves the resident species with negative fitness (fig. 5b). It is not possible for the two species, with their respective strategies, to coexist, and the invasive species can be expected to drive the resident species extinct in “ecological” time. Rapid evolution toward the single peak provides the only means for the resident species to persist in the face of the invasive species. While it would require many more assumptions and much more knowledge of the system to know, the nonnative species, by being closer to the peak, may also have an evolutionary advantage over the resident species. When the nonnative species arrives between the native species’ strategy and the current peak of the landscape, the native species likely loses twice (ecologically and evolutionarily), and replacement likely ensues.

Alternatively, the invader can arrive within the invasion window and on the opposite side of the peak from the recipient species (fig. 5c). Ecologically, the invader and recipient species can coexist as the landscape shifts in such a way that both species have zero growth rates ($\partial x_1/\partial t = \partial x_2/\partial t = 0$) and positive population sizes (see Cohen et al. 1999). While coexistence of the two species is ecologically stable, this new community is not evolutionarily stable as both species are under selection to evolve toward the same peak. Over time, whichever species reaches the peak first will outcompete the other (fig. 5d). In the meantime, both species coexist and the invasion will seem to have added to the species diversity of the community while causing little harm.

Finally, we include a caveat to all of the preceding examples. First there are issues of notation that can become

Figure 2: An example where the recipient community (solid line) is susceptible to invasion from the current nonnative species. The nonnative species from the donor community (dashed line, black dot) has a different G-function (distinct evolutionary technology) than the species of the recipient community (solid line, black dot). a, When the species of the recipient community (solid line, black dot) is at its evolutionarily stable strategy (ESS), the adaptive landscape of the nonnative species offers an invasion window (gray box), and the nonnative species (dashed line, black dot) starts with positive invasion potential ($u_{11} = 1.213$, $x_{11}^* = 83.2$, $u_{12} = -4.79$, $x_{12} = 0$). b, After a successful invasion both species coexist and equilibrate on new population sizes (the original species declines in abundance somewhat), but the community no longer has an ESS ($u_{11} = 1.213$, $x_{11}^* = 63.7$, $u_{12} = -4.79$, $x_{12}^* = 49.5$). c, If evolution occurs, a new ESS can be established with both species coexisting; the nonnative species experiences more evolutionary change than the recipient species ($u_{11} = 0.875$, $x_{11}^* = 65.5$, $u_{12} = -5.46$, $x_{12}^* = 64.6$). This illustration has the same parameter values as figure 1, except that the invasive G-function now has $\gamma = 6$.

Figure 3: An example where the recipient community (solid line) is invaded and replaced by a species with a generally superior G-function (dashed line). The nonnative species from the donor community (dashed line, black dot) has a different G-function and an adaptive landscape that lies above that of the recipient community (solid line). *a*, Even when the species of the recipient community (solid line, black dot) is at its evolutionarily stable strategy (ESS), the adaptive landscape of the nonnative species offers an invasion window (gray box), and the nonnative species (dashed line, open dot) may have a positive invasion potential ($u_{11} = 1.213$, $x_{11}^* = 63.7$, $u_{12} = 0.5$, $x_{12} = 0$). *b*, When established the nonnative species will equilibrate at a population size that drives the resident species extinct, even though the nonnative species may not be at its ESS ($u_{11} = 1.213$, $x_{11}^* = 0$, $u_{12} = 0.5$, $x_{12}^* = 106.6$). *c*, The nonnative species may evolve to its ESS, making conditions even less favorable for the extirpated native species ($u_{11} = 1.213$, $x_{11}^* = 0$, $u_{12} = 1.213$, $x_{12}^* = 91.52$). This illustration has the same parameter values as figure 1, except that the invasive G-function has $K_m = 110$.

cumbersome. When there is more than one G-function, we require a subscript for each G-function and a subscript for the strategies (= species) currently within a G-function. For all of the examples with two G-functions, we maintained the possibility of multiple species within a G-function, although all of our examples had just one species present. This does not need to be the case, and it will be of interest to explore the outcomes when several G-functions concurrently have several extant species within each. The “empty niche” example provides just such a G-function with multiple species at the ESS. Second, there is the issue of what is the actual ESS when there are several G-functions. When only one of the G-functions is present, there is an ESS for each that is conditional on the absence of the other (by virtue of geographical isolation, the two G-functions may never “meet”). Once the two G-functions are introduced together, there is a possibly new ESS for the complete system (witness, e.g., the Great American Interchange, when the Isthmus of Panama allowed hitherto separated orders and families of mammals to invade and mingle). Third, we have not dealt directly with the important issue of convergence stability (Cohen et al. 1999). The ESSs of this article’s examples are indeed convergent stable, but this should be verified whenever working with a new model.

Applying a Game-Theoretic Framework

Applying this game-theoretic framework begins with hypotheses about whether the invader of interest represents a strategy that is part of a novel strategy or an existing strategy set relative to the recipient community (fig. 6). Although other approaches offer suggestions of how to distinguish the invader from the recipient community (i.e., phylogenetic history, identifying overlapping functional traits; Shea and Chesson 2002; Funk et al. 2008), game theory and the G-function approach can formalize these differences and explicitly model invasion mechanisms.

When the invader represents a novel G-function, the recipient community is vulnerable regardless of whether the residents are at an ESS. To succeed, the invader needs only an invasion window and positive invasion potential in its own adaptive landscape. Thus, we can eliminate hypotheses related to an “empty niche” or resident species being off their peaks. Instead, for a novel invader, the G-function approach draws equal attention to the traits directly influencing competitive interactions and those traits that distinguish the invader and recipient species as separate “evolutionary technologies.” Additionally, we suggest a new insight. The mechanisms vital to invasion success may not be ecologically relevant to the interaction between the invader and recipient community. For example, throughout much of the world, freshwater crayfish are key

Figure 4: An example of an empty niche where the recipient community (*solid line*) has just two species when the evolutionarily stable strategy (ESS) community would permit three species. This example has a single G-function and adaptive landscape. *a*, The two species have evolved to local peaks of the adaptive landscape; but there is a large invasion window (*gray box*) and the opportunity for a nonnative species (*black box*) with a positive invasion potential ($u_1 = 4.46$, $x_1^* = 39.0$, $u_2 = 1.014$, $x_2^* = 52.1$). *b*, Following such an invasion a new ecological equilibrium exists with all three species coexisting, but the community is still not at an ESS. Subsequent evolution by all three species could result in the ESS of three species ($u_1 = 4.125$, $x_1^* = 39.3$, $u_2 = 0.77$, $x_2^* = 47.8$, $u_3 = -3.10$, $x_3^* = 12.4$). The single G-function of this illustration uses all of the same parameter values as figure 1 for the resident species, except that $\sigma_K^2 = 20$ (the niche axis has been broadened, which enhances the number of species at the ESS). Note that the subscripts in this figure legend refer to different coexisting species within a G-function (because there is just one G-function, we have not used the double subscript for $\mathbf{u}$ and $\mathbf{x}$).

invaders that often have a large impact on aquatic ecosystems (Lodge et al. 2000; Taylor 2002). Some of the most well-known crayfish invaders are from two families (Cambaridae and Astacidae; Taylor 2002) that are largely differentiated by the male reproductive structure called a gonopod. In the Cambaridae, the gonopod annually changes shape as the males can alternate between reproductively active and inactive forms (Reynolds 2001; Scholtz 2001). This trait likely allows species in the Cambaridae family to minimize trade-offs associated with energy allocation to key processes, such as foraging, avoiding predators, and reproduction. This is not possible for species in the Astacidae. Through this trait, species in the Cambaridae family may have a higher per capita growth rate than species in the Astacidae family. Surely this influences competitive interactions, yet the contribution of this trait to competitive displacement is indirect. Furthermore, it provides an a priori hypothesis of traits related to invasion success, as opposed to many hypotheses regarding invasion success that are arguably post hoc.

In addition, a game-theoretic framework also formalizes hypotheses by which an invader may be not only novel but superior to the G-function of the recipient community. We suggest that, in general, this pathway generates hypotheses similar to the novel weapons hypothesis, whereby the invader possesses a new strategy or is on a different and, potentially, competitively superior coevolutionary trajectory in its ability to compete (Thompson 1999; Callaway and Ridenour 2004). The new insight that game theory and the G-function approach provide is that a re-

cipient community can still be invaded and eventually displaced, even though it is well adapted to its environment. Rather, displacement may be a consequence of the recipient species lacking the evolutionary potential to evolve the key adaptation of the superior G-function.

If the invader and recipient species are part of the same G-function, game theory points to just two hypotheses. The recipient community either (1) contains an empty niche or (2) was off its peak and non-ESS to begin with. Various mechanisms may generate either an empty niche or non-ESS communities. For example, disturbance, either natural or anthropogenic, may have increased invasion vulnerability by changing the environment in a manner that likely knocks recipient species from their peaks. Disturbance has frequently been implicated as a cause of invasion (Davis et al. 2000; MacDougall and Turkington 2005), but the novel insight here is that game theory links to and draws equal attention to not only this ecological factor but also an evolutionary mechanism (i.e., native species off its peak) that could lead to species replacement.

Yet species replacement occurs only when the invader arrives closer than the recipient species to the peak on their adaptive landscape. The chance that an invader would arrive closer to the peak relative to a locally adapted recipient species seems small. In fact, most introductions fail, and even fewer result in large impacts (e.g., the “tens rule”; Williamson and Fitter 1996). Here we suggest that a game-theoretic framework adds a new evolutionary mechanism for how and why failed invasions occur. Specifically, following the tens rule, we can hypothesize that

Figure 5: Examples of species replacement or species coexistence when the species of a resident community is not at its evolutionarily stable strategy (ESS) value (perhaps as a consequence of anthropogenic changes). This example uses just a single G-function with a single-species ESS with the same parameterization as the resident G-function of figure 1. *a*, When the resident species (*black dot*) has a strategy value that is not at the ESS value, then there is a positive invasion window (*gray box*) with two parts ($u_1 = -2$, $x_1^* = 60.65$). A nonnative species (*black box*) that comes in with a strategy between the solid and dashed vertical lines will result in species replacement (shown in *b*: $u_1 = -2$, $x_1^* = 0$, $u_2 = -1$, $x_2^* = 88.25$). A nonnative species with a strategy value between the dashed and solid lines will result in species addition and new ecological equilibrium for the two-species system (shown in *c*, $u_1 = -2$, $x_1^* = 39.23$, $u_2 = 2.5$, $x_2^* = 32.61$). *d*, The species replacement or the species addition is not an ESS, and evolution should result in convergence on the single-species ESS ($u_1 = 1.213$, $x_1^* = 83.2$).

the 90% of failed introductions may occur because the invader either has arrived farther from the peak than the recipient species or has arrived with negative invasion potential. Of that 10% that succeed, the 10% that become pest species then represent the invaders with traits that have positive invasion potential and/or are closer to the peak on the adaptive landscape.

Reconciling Recurring Themes and Offering New Insights in Invasion Biology

We suggest that a game-theoretic framework converges on themes that often arise in similar approaches that aim to draw equal attention to both the ecological and evolutionary mechanisms of biological invasions (Facon et al. 2006; Funk et al. 2008; Moles et al. 2008). First, many frameworks aim to distinguish invaders based on their degree of similarity to the native species, yet there remains

ambiguity on how to identify and define what constitutes “different” or “novel.” Second, many frameworks recognize a pathway of invasion that involves an empty niche, yet the definition of an empty niche often encompasses multiple scenarios that generally lack an evolutionary context. Below we expand on these recurring themes and aim to demonstrate that game theory and the G-function provide an opportunity to clarify these ambiguities and offer new insights about the mechanisms underlying invasion success.

Formalizing a Definition of Trait Similarity between the Invader and Native Species

The idea of limiting similarity has been suggested as a way to predict invasion success based on similarities in the invader’s and the native species’ traits (Facon et al. 2006; Funk et al. 2008; Moles et al. 2008). But how might we

Figure 6: Flowchart illustrating the three pathways of invasion explored and possible outcomes of each. Boxes with dashed lines represent hypothesized invasion pathways. Gray boxes represent the possible outcome of invasion pathways. ESS = evolutionarily stable strategy.

define “similar”? Some frameworks suggest identifying relevant and overlapping functional traits in order to relate trait similarity to invasion success, which can be challenging, or considering the influence of phylogenetic history (Shea and Chesson 2002; Funk et al. 2008). We agree that phylogenetic history is useful but offer the additional distinction that if differences in functional traits represent constraint-breaking adaptations, then the invader represents an evolutionarily novel technology to the recipient community. Therefore, we would suggest that for an invader to represent a “novel weapon,” as defined by Callaway and Ridenour (2004), it must possess a strategy that is not readily evolvable by the recipient species (i.e., a novel G-function pathway). In contrast, we suggest that for the invader and recipient species to be “similar,” they must be capable of evolving the strategies and experiencing the same fitness consequences of possessing those strategies (i.e., the same G-function). As such, the pathway and probability of invasion are directly related to the size of the invasion window left open by the non-ESS native community.

Interestingly, it is not only the size of the invasion window that matters but whether the invader arrives within that window that provides an additional insight into the mechanisms behind competitive displacement. When a recipient community is non-ESS, species from the same G-function can invade and coexist ecologically with the recipient communities by being on opposite sides of

unoccupied peaks, but these are not evolutionarily stable. Subsequent evolution toward the single peak may eliminate one of the two species. We see this as a distinct invasion pathway that provides new insights into how seemingly benign invaders can ecologically coexist with native species for long periods of time but evolutionarily result in displacement. Hypothesizing whether a seemingly benign invader is similar or novel relative to the recipient community draws attention to invasions that should be watched carefully.

Defining an Empty Niche

The concept of empty or vacant niches has been widely cited as contributing to the invasion success of nonnative species (Simberloff 1981, 1995). However, an empty niche has been used to describe multiple invasion scenarios that we suggest are distinct from one another and generate different predictions about the impact of the invader on the recipient community. The scarcity of extinctions and the small effects of nonnative species on native fauna was initially suggested as evidence for empty niches (Simberloff 1981; Walker and Valentine 1984). While many saw this as weak support (Herbold and Moyle 1986), the concept of an empty niche incorporated the idea that a species can invade and add to the diversity of the recipient community with little to no impact on native species. However, since then, the term “empty niche” has been applied to invasions

that result in major ecological impacts on native species. For example, the brown tree snake on Guam has been frequently cited as an example of an invasion of an empty niche (Simberloff 1995; Moles et al. 2008), but it is equally cited as an invasion that has led to severe impacts on native fauna (Fritts and Rodda 1998). In cases of predator invasion, the lack of a shared evolutionary history between native prey and nonnative predators has provided some evolutionary context behind the notion of an empty niche (Cox and Lima 2006; Sih et al. 2010). However, in general, we suggest that there has been little formal integration of an evolutionary context related to an empty niche. Without such, it remains an ambiguous concept with little predictive power.

Evolutionary game theory and the G-function approach provide an evolutionary context for formalizing the empty-niche concept and for distinguishing among invasion mechanisms that have invoked “empty niches.” Following game theory, we define an empty niche as an unoccupied peak in an existing adaptive landscape. Therefore, invasion of an empty niche can occur only when the invader is part of an existing G-function in the recipient community. With the evolutionary context of an empty niche defined, the ecological outcome of a successful invasion can only be coexistence with the recipient community. Invasion by a species with a novel evolutionary technology (e.g., the brown tree snake) represents the arrival of a novel G-function and, as our models illustrate, can result in either coexistence or species replacement. Because replacement can occur, we suggest that invasion via a novel G-function does not represent invasion via an empty niche.

Conclusion

We suggest that evolutionary game theory and the G-function approach contribute new insights to invasion biology by drawing equal attention to both the ecological and evolutionary contexts of invasions, as well as the consequences of invasion for both the invader and recipient species. This provides more focused hypotheses about the pathways through which a recipient community is vulnerable to invasion by a nonnative species. However, there are limitations to the G-function approach. First, the models presented here address only competitive interactions between native and nonnative species and not invasions that result in a novel predator impacting resident prey species or novel prey for native predators. In general, predators and prey will be represented by different G-functions in an evolutionary game. Our own preliminary work and that of others (Křivan and Cressman 2009) suggests a myriad of potential outcomes from the arrival of a novel predator within a community of prey, including extinction of

prey, large disruptions of the ESS and the prey’s adaptive landscape, and possibilities for enhanced prey diversity in the future. Second, this approach to modeling evolutionary game theory focuses on the heritable phenotypes that influence ecological interactions and that are subject to natural selection. Genes are not explicitly considered but could be by using trait dynamic models derived from population genetic or quantitative genetic frameworks (Abrams et al. 1993, 2001; Case and Taper 2000).

Finally, we have used deterministic models where the dynamics of the invasion occur with certainty. Yet obviously there are many uncertainties associated with invasion dynamics. Adding stochasticity into the models will alter the likelihood of particular outcomes and produce probability distributions around outcomes rather than deterministic outcomes. However, in light of the few truly integrated ecoevolutionary frameworks that exist for studying invasions, evolutionary game theory holds much promise for formulating *a priori* predictions about the ecological and evolutionary outcomes of invasions.

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APPENDIX

Detailed Description of the G-Function

We used a fitness-generating (G-function) approach to distinguish among the three pathways: novel evolutionary technology, empty niche, and recipient community non-evolutionarily stable strategy (ESS). The G-function describes the per capita growth rate and the evolutionary dynamics of a species possessing a particular strategy within a particular environment: $G(v, \mathbf{u}, \mathbf{x})$. The term v is the strategy (i.e., trait) of the focal individual and may

be scalar or vector valued. However, it should represent the heritable traits of the species that are hypothesized to be relevant for their population ecology and species interactions. The vector $\mathbf{u} = (u_1, \dots, u_{n_s})$ describes the different strategies found within the population or community. For our purposes, we will assume that the different strategies of this vector represent different species, where u_i is the strategy value of the i th species for $i = 1, \dots, n_s$. The vector $\mathbf{x} = (x_1, \dots, x_{n_s})$ gives the current population sizes of each species within the community, where x_i gives the population size of the i th species whose strategy is u_i .

Ecologically, the G-function describes the change in population size over time of the i th species when the strategy of the focal individual is set to that of the i th species: $G(v, \mathbf{u}, \mathbf{x}) = (1/x_i)(\partial x_i / \partial t)$ when $v = u_i$. We will express this as $G(v, \mathbf{u}, \mathbf{x})|_{v=u_i}$. Thus, in modeling the ecological dynamics,

$$\frac{\partial x_i}{\partial t} = x_i G(v, \mathbf{u}, \mathbf{x}) \Big|_{v=u_i},$$

for $i = 1, \dots, n_s$.

Evolutionarily, the G-function describes the change in the i th species' mean strategy value as an adaptive dynamic (i.e., change in the frequency of strategies within the community). Thus, for modeling evolutionary change,

$$\frac{\partial u_i}{\partial t} = k \left(\frac{\partial G(v, \mathbf{u}, \mathbf{x})}{\partial v} \right) \Big|_{v=u_i},$$

for $i = 1, \dots, n_s$, where the rate of change in the i th species' strategy is in the direction of and proportional to the fitness gradient. The plot of G versus v is the adaptive landscape and the gradient of this landscape is given by $\partial G(v, \mathbf{u}, \mathbf{x}) / \partial v$. By evaluating the gradient with respect to the strategy of the focal individual, we are considering the fitness consequence of an individual unilaterally changing its strategy. The term k represents aspects of heritability, population size, and the additive genetic variance within the population. For evolution by natural selection to occur, there must be a fitness benefit to an individual of possessing a change in strategy (nonzero fitness gradient), and there must be heritable variation within the population with respect to the strategy (nonzero k).

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