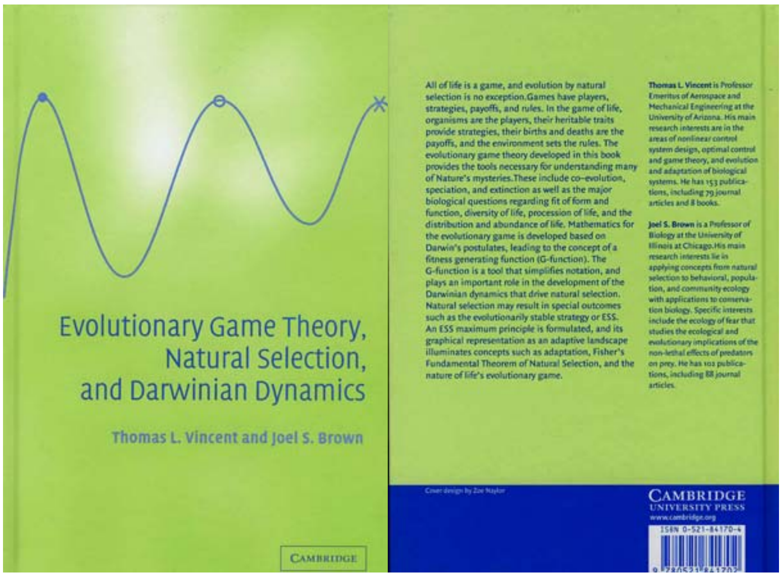
**Vincent, T.L. & J.S. Brown. 2005. Evolutionary game theory, natural selection and Darwinian dynamics. – Cambridge, Cambridge University Press**

Book review by T.J.M. Van Dooren[1]




In evolutionary biology, theoreticians have been in love with the potential effects of frequency–dependent selection for many decades. Bryan Clarke was one of the first who pointed out the capacity of this type of selection to generate biodiversity (1979), and that realization has spurred much theoretical research from the nineties of last century until now (Waxman & Gavrilets, 2005; Rueffler *et al*., 2006). For that reason, there is always much discussion about frequency–dependence and evolutionary games at conferences. At the 2005 conference of the European Society of Evolutionary Biology, a Swedish colleague insisted that I should read the then recently appeared book on Evolutionary Game Theory by Vincent and Brown. Few things kept me away from following his advise, among them a critical paper on their approach (Abrams, 2001). However, Vincent & Browns ideas have had a large impact on my own contribution to evolutionary biology. As a student, I used to work in a library in the evenings, short before the arrival of personal computers there, so that my only means of diversion were trying all sorts of gymnastic jumps in the corridors and reading journals from the shelves. That is where I found papers on evolutionary dynamics by Iwasa *et al*. (1991) and the paper by Brown & Vincent on the evolutionary game (Brown & Vincent, 1987). They introduced me to the concept of an Evolutionarily Stable Coalition, and I still work on it. Such a coalition is a community of species that cannot be invaded by any other species, and where selection is stabilizing on all species (Vincent & Brown call it an ESS coalition).

This concept does not figure prominently in their book, the authors rather try to give an overview of the approach to theoretical modelling they developed themselves. The book is written in an enthusiastic style. In several places you can still perceive the excitement the authors must have felt when they embarked on their work in evolutionary dynamics. For example, on page 159 when they discuss the concept of coevolutionary stable community as used by Rummel & Roughgarden (1985) in models with frequency–dependent selection between species, and their own improved approach which includes frequency–dependent selection within species as well. The book starts with three chapters that introduce the reader to many concepts in evolutionary dynamics, followed by four chapters that review types of G functions (explained below), and their properties in Darwinian dynamics, evolutionary stability and resistance to invasion. In the last four, less technical chapters, speciation models are discussed, matrix games, ecological games and models of evolutionary games in applications.

What becomes apparent quite soon when reading the book is that the authors are very iconoclastic. They have decided to rename ‘adaptive dynamics’ (*e.g*. Hofbauer & Sigmund, 1998; Geritz *et al*., 1998) into strategy dynamics, and consistently refer to papers clearly branded by the authors to be on adaptive dynamics as strategy dynamics. A small issue is that they scale neutral fitness to zero, not to one as is customary in population genetics. Vincent & Brown also work with F – H – and G functions as elements of their standard protocol of model construction, where F and H and no more than rescaled instantaneous growth rates of a strategy in a population and G can be understood as a fitness function based on the instantaneous growth rate of a strategy. The impact of their sketching a clear protocol for handling evolutionary models is now clear: others have chosen

[1] Second version, uploaded 3 July 2006.

to define similar protocols. For example Metz *et al.* (1996) refer to adaptive dynamics as the mathematically more formalized counterpart of Vincent and Browns approach.

Quite often the authors use boldface when they introduce important concepts in the book, and I get the impression they do that to distract readers from the fact that there are very little sharp definitions of those boldface concepts given, or, again, pretty iconoclastic ones. Let's look, for example, at their definition of the "bauplan" (p. 2 and 22), which is "the fixity of certain design rules among definable groups of species" or an "old descriptor for classifying organisms...by common design rules". Defined within their modelling framework, that can work, where *bauplan* just become equivalent to G–function. Consulting Raff (1996: 30), however, yields as usual definition of the *bauplan* or body plan: "a basic pattern of anatomical organization shared by a group of animals". These basic patterns are most often compared between phyla, whereas Vincent & Brown situate it at "a particular group of species or higher taxa" (p. 82). Summarizing, Vincent & Brown have chosen to redefine *bauplan* = G function in a singular way which only has relevance within their protocol. The species concept receives a similar rough treatment, where "species archetypes" are put forward that occur when individual phenotypes show a very clumped distribution around such an archetype. We humans then must have at least two of those: Venus and Mars for women and men. Vincent & Brown decide to call each cluster in phenotype space a 'species', ignoring the existence of many genes of large effect within species, or for example genetic sex determination.

A major lacune in my eyes is that they nowhere make it clear when two G–functions or body plans are really different. One can always construct a new G–function that incorporates all previously defined ones. In a predator prey model, for example, with G1 as *bauplan* for the prey and G2 for the predator, individuals can be given an extra scalar trait (let's call it *z*) from which one can determine whether they are prey or predator. A new function zG1+(1–z)G2, allows individuals to be prey ($z = 0$), predator ($z = 1$), or both ($0 < z < 1$). Strange is that they refer to Geritz *et al.* (1997) to back up their idea of changing body plans, when these authors are very careful to define a single G–function or body plan that applies to all organisms that can occur within a model.

In the historical discussion, one of the first papers on evolutionary games in a genetic context is lacking (Fisher, 1958), but more importantly, the authors ignore discussion on the probability of sympatric speciation, ongoing since 1999 (Dieckmann & Doebeli, 1999). In that discussion, the concept of evolutionarily stable coalitions appears very often, therefore this omission means that the authors missed a lot of the impact of their own ideas. The authors bluntly state that, in general, there will always be some level of assortative mating and strong selection for speciation (p. 252), which is now heavily contested by both models and data (see Waxman & Gavriletz, 2005 and associated commentaries).

Nevertheless, Vincent & Browns F – H – G approach also has some positive aspects. In comparison to its more mathematically solid brother, adaptive dynamics, it does not assume that ecological and evolutionary processes operate on different time scales. The authors also use global arguments, instead of focusing on local shapes of fitness landscapes. What I found nice is the last chapter with applications, showing that there is a future for the application of adaptive dynamics or strategy dynamics in cancer research.

The book structure with several repeats of a theme will make sure readers do not get lost, but I am not sure whether the F – H – G approach will entice young researchers to make use of it. What certainly will keep its value is the enthusiastic tone, but I think that most of Vincent & Brown ideas and protocol are already absorbed into other approaches. Therefore I conclude that this book is a must–read for those interested in the history of evolutionary game theory, but it hardly prepares a student for the future, and it will hardly inspire someone with an interest in palaeontology to model evolution.

Vincent, T.L. & J.S. Brown. 2005. Evolutionary game theory, natural selection and Darwinian dynamics. – Cambridge, Cambridge University Press. 400 pp. ISBN 0521841704. Price £ 60.00/$ 100.00 (hardback).

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