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# Land Conversion, Interspecific Competition, and Bioinvasion in a Tropical Ecosystem

Edward B. Barbier

This paper investigates the relationships among land-use change, biological invasion, and interspecific competition in a tropical ecosystem by linking a behavioral model of land conversion by agriculture and an ecological model of interspecific competition between a native species and an exotic invader. The model is used to examine how relative farm prices and access to forest areas influence land clearing and thus the ability of the invasive species to eliminate the native species. Simulations show that only a 20% rise in relative prices and a 2.75% increase in forest access are necessary for this outcome to occur.

*Key Words:* biological invasion, interspecific competition, land clearing, tropical ecosystem, tropical forest

**JEL Classifications:** O13, Q20, Q24

One of the “cardinal rules” of biogeography for native species is that, while their number is inversely related to latitude, a species range is positively correlated with latitude (Brown and Lomolino; Rhode; Sax). This implies that, compared to temperate systems, tropical ecosystems are more abundant in native species, and that these species are packed into smaller habitat ranges. At the same time, there is now substantial evidence showing that human-induced land-use conversion and change, which is widespread in tropical regions, is not only a direct cause of habitat range loss for native species, but it also contributes indirectly to their loss by aiding interspecific competition by successful invaders (Lozon and MacIsaac; Mack et al.; Peterson; Tilman and Lehman; Vitousek et

al.). This is particularly true for terrestrial plant species, where it has been shown that the change in environmental conditions brought on by land-use change and disturbance both aids the initial establishment of exotic plant invaders in the host habitat and allows them to outcompete and displace native species within the same range (Lozon and MacIsaac; Tilman and Lehman). It is well known that, in the tropics, few exotic species become successfully established as invaders, but those that do tend to have very large geographical ranges (Sax). Examples include the bracken fern (*Pteridium aquilinum*), which has invaded many tropical areas where shifting cultivation is practiced, and the Miconia woody shrub (*Miconia calvascens*), which is rampant in South Pacific islands from Tahiti to Hawaii due to land conversion for development (Burnett et al.; Schneider). Thus, if land-use changes in the tropics assist the establishment of invading exotic species through aiding their interspecific competition with native species, then many tropical ecosystems that consist of abundant species packed into small ranges are highly vulnerable.

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In tropical areas, land conversion occurs as a deliberate economic activity. In most developing countries, which contain the vast majority of tropical forest ecosystems, the decline in forest and woodlands is mainly the result of land conversion, in particular agricultural expansion for crop production (Chomitz et al.; FAO 1997, 2003). For example, stratified random sampling of 10% of the world's tropical forests reveals that direct conversion by large-scale agriculture may be the main source of deforestation, accounting for around 32% of total forest-cover change, followed by conversion to small-scale agriculture, which accounts for 26% (FAO 2001). In many tropical regions, a key factor influencing such agricultural land conversion is thought to be the lack of effective property rights and other institutional structures controlling the clearing of pristine forests (Barbier 2005, ch. 5 and 6; Barbier and Burgess; Chomitz et al.; FAO 1997; Kaimowitz and Angelsen; van Kooten, Sedjo, and Bulte). Large- and small-scale farmers are often motivated by profits, but the lack of institutional controls on converting new land means that forest areas are treated as "open-access" sources of additional agricultural land. As a World Bank report concludes, economic incentives that boost the profitability of farming translate into greater open-access land clearing: "Low wages, good soils, favorable climate, and higher prices for agricultural goods all motivate deforestation . . . This suggests that road improvements or agricultural policies that boost farm profitability will tend to accelerate deforestation" (Chomitz et al. pp. 11–12).

In spite of the relationships among land-use change, biological invasion, and interspecific competition in tropical ecosystems, no integrated economic–ecological model of this process has been constructed. This paper attempts to address this gap in the literature by linking a behavioral model of land conversion by an economic activity (e.g., agriculture) and an ecological model of interspecific competition between a native species and an exotic invader in a given habitat area.

The economic model of land conversion is adapted from Barbier (2005, ch. 6), and it uses a representative agent model of a profit-

maximizing farm owner in the agricultural sector of a developing country to determine the equilibrium level of cleared land. The purpose of this model is to capture the influence of two key determinants of the profitability of farming and, thus, the motivation for increased open-access land clearing. As the previous quote from the World Bank report suggests, one of the determinants is the "accessibility" of forest and other "undisturbed" tropical ecosystems that may serve as a potential source of cleared land for smallholders. In tropical regions, accessibility will be inversely related to the distance of ecosystem land from the "center" of agricultural development activity as well as the presence of roads and other infrastructure that "open up" natural forest areas. The second determinant is prices, specifically, the price of farming output to a key input.

The model of interspecific competition is adopted from standard ecological models of biological invasions (Barbier 2001; Rose; Shigesada and Kawasaki). The basic assumption is that the existing tropical ecosystem contains a representative native (i.e., endemic) species that has a range restricted to that ecosystem. The ecosystem, however, is on the periphery of a larger range of a potential exotic species invader. The peripheral population of the exotic species in the tropical ecosystem is therefore augmented by a constant rate of immigration from the much larger population of its species of stable density inhabiting a nearby ecosystem. Within the natural ecosystem, the native species and the exotic invader engage in interspecific competition, where both species exhibit carrying-capacity constraints. However, land conversion in the ecosystem affects this competition in two ways: (1) it reduces the effective carrying capacity of the native species and its ability to compete with exotic species; and (2) it increases the rate of immigration into the ecosystem by the exotic species.

By integrating the two models, the analysis here shows how the important economic determinants of land clearing, changes in relative agricultural prices, and accessibility of ecosystem land to local markets affect the interspecific competition between the exotic and



native species. The analysis also demonstrates the conditions under which changes in these two economic incentives affect the tendency of the exotic species to "eliminate" the native species. These various effects are analyzed both qualitatively (i.e., via phase-diagram analysis of the dynamic paths of the system and its feasible equilibria) as well as through numerical simulations of the effects of changes in relative prices and market access on land clearing. A comparison is made between simulations of the effects of changes in prices with those of changes in market accessibility. As discussed later, the results have direct relevance on the policy debate as to what has the more pernicious effect on land clearing, road building or rising agricultural prices. This model contributes to the debate by including the effects of land clearing on biological invasion and the possible extinction of native species.

### The Ecological Model of Invasion and Interspecific Competition

Let  $x_1$  be the population density of a native (endemic) plant species that has a habitat range that is restricted by a natural tropical forest ecosystem. The ecosystem, however, is on the periphery of the much larger range of a potential exotic plant invader. The invasive species is already established in a nearby ecosystem, and it has achieved a large population size of stable density there. The peripheral population density of the exotic species in the natural tropical ecosystem,  $x_2$ , is therefore augmented by a constant rate of immigration,  $c$ , from the larger population inhabiting the nearby invaded ecosystem.

Thus, following Barbier (2001); Rose; and Shigesada and Kawasaki, competition between the native and invasive species in the tropical ecosystem can be modeled as

$$(1) \quad \begin{aligned} dx_1/dt = \dot{x}_1 &= x_1[g(x_1) - h(x_2)], & g' < 0, \\ h' > 0, & g(K_1) = 0, \quad K_1 > 0, \quad h(0) = 0 \end{aligned}$$

and

$$(2) \quad \begin{aligned} dx_2/dt = \dot{x}_2 &= x_2[j(x_2) - k(x_1)] + c, \\ j' < 0, & k' > 0, \quad j(K_2) + c/K_2 = 0, \quad K_2 > 0, \\ k(0) &= 0. \end{aligned}$$

Equation (1) indicates that the existing native species population in the ecosystem is increased through biological growth,  $g(x_1)$ , but declines in response to competition from the exotic species invader,  $h(x_2)$ . The carrying capacity of the tropical ecosystem habitat limits the maximum population density of the native species to  $K_1$ . The established invasive plant population also grows biologically,  $j(x_2)$ , and is diminished by interspecific competition,  $k(x_1)$ . But the population of invasive plant species also increases through a flow of migrants,  $c$ , from the larger population already established in a nearby ecosystem. There is also a maximum carrying capacity,  $K_2$ , that limits the population density of the invasive species in the tropical ecosystem. Finally, the condition  $j(K_2) + c/K_2 = 0$  ensures that when the plant invader is at its maximum population density in the tropical ecosystem, either migration stops, or there must be a decline in the invasive species population such that  $c/K_2 > 0$ .

Note as well that in this model, there is no boundary equilibrium corresponding to a zero population density for the exotic plant invader in the tropical ecosystem. From dynamic Equation (2), when  $x_2 = 0$ , then  $\dot{x}_2 = c$ . That is, the population of the plant invasive never falls to zero because of constant migration of new invaders from the adjacent ecosystem. If an equilibrium where  $x_2 = 0$  is unattainable, then the conditions on Equations (1) and (2) also rule out the possibility that  $x_1 = K_1$ . That is, because the invasive plant species is already established in the tropical ecosystem, the native species can never reach its maximum population density. On the other hand, the boundary equilibrium ( $x_1 = 0$ ,  $x_2 = K_2$ ) is feasible under these conditions for Equations (1) and (2). The invasive plant can completely wipe out the native species and expand to full carrying capacity. These features of the model invoke some of the realistic aspects of interspecific competition between an endemic and established invader species in an ecosystem.

Interspecific competition in the tropical ecosystem is in equilibrium when  $\dot{x}_1 = \dot{x}_2 = 0$ . From Equations (1) and (2), this equilibrium



is represented by

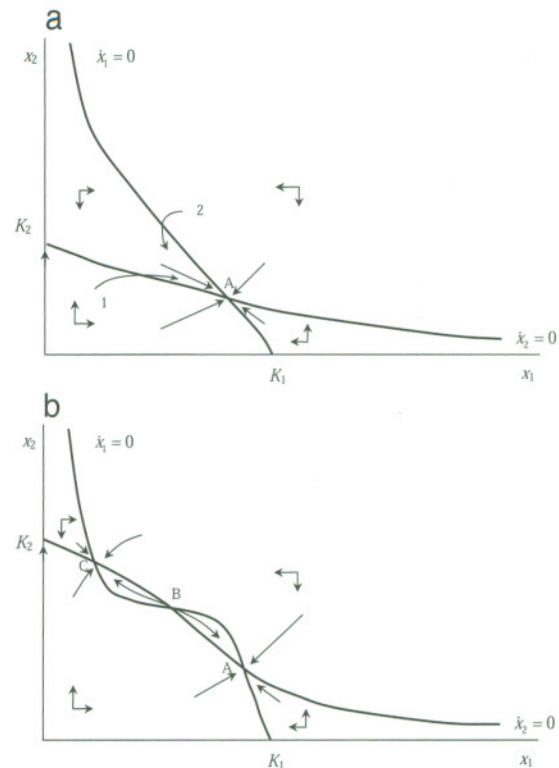
$$(3) \quad g(x_1^*) = h(x_2^*) \text{ and}$$

$$(4) \quad j(x_2^*) + c/x_2^* = k(x_1^*),$$

where an asterisk is used to denote the equilibrium, or steady-state, population density levels of the native and invasive species. Equation (3) indicates that the steady-state native species,  $x_1^*$ , will occur when its biological growth is just offset by competition from the invasive plant,  $x_2^*$ . Equation (4) states that the equilibrium for the plant invader will occur when interspecific competition from the native species offsets both growth in the existing population of invasive species in the ecosystem as well as additional migration into the system.

As already discussed, the corner solution  $(0, K_2)$  is a possible equilibrium that satisfies Equations (3) and (4). In the appendix to this paper, it is demonstrated that the two stationary loci representing Equations (3) and (4) are downward sloping in  $(x_1, x_2)$  space. Provided that the  $\dot{x}_1 = 0$  isocline crosses the  $\dot{x}_2 = 0$  locus from above, then there is at least one stable interior equilibrium  $(x_1^*, x_2^*)$ . However, since both curves are nonlinear, the possibility of more than one interior equilibrium point cannot be ruled out. Figure 1 depicts two possible phase diagrams for the ecological model of invasion and interspecific competition. Figure 1a shows the case with one stable interior equilibrium, and Figure 1b is the diagram with multiple possible equilibria.

In Figure 1a, point A is an interior equilibrium that satisfies necessary and sufficient stability conditions (see Appendix). The stationary loci and optimal trajectory of this figure suggest that, despite the invasion of an exotic species in the ecosystem, interspecific competition tends to favor the native species. Even if, initially, the population density of the endemic species is well below its carrying capacity level,  $K_1$ , while the population density of the invasive species is relatively high, the former will eventually dominate the competition between the two species. Initially, the populations of both species might rise (trajectory 1) or fall (trajectory 2), but in the long

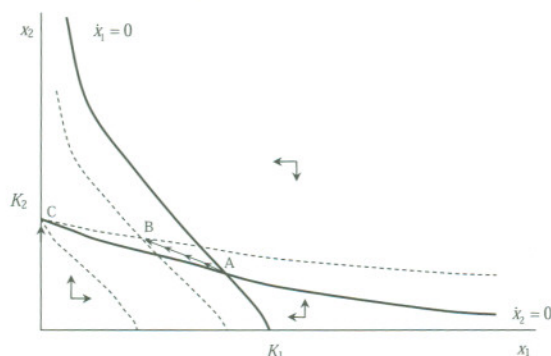


**Figure 1.** Phase Diagrams for the Ecological Model of Invasion and Interspecific Competition (a) Single Interior Equilibrium (b) Multiple Interior Equilibria

run, the population of invasive species will decline, whereas the population of natives will increase until equilibrium A is reached.

Figure 1b depicts three possible multiple interior equilibria. However, only points A and C are stable, whereas point B is not. Any trajectory leading to point B will only stay there for an instant before moving either in the direction of point A or C. Equilibrium point A has a similar interpretation as in Figure 1a. Note, however, that if the population density of the native species is very low, and the population density of the invasive is high, then the optimal trajectory may lead to equilibrium C rather than A. In the latter long-term steady state of the ecological system, the invasive species outcompetes the native species.

The phase diagrams of Figure 1 assume that the habitat area of the natural tropical ecosystem remains undisturbed. We now want to investigate what happens if land conversion



**Figure 2.** The Effects of Land Conversion on Invasion and Interspecific Competition

occurs. Before further investigating the economics underlying this land conversion, let us first examine the effects of land conversion in the context of the ecological model only.

Let  $A$  represent some measure of the area of natural habitat of the tropical ecosystem that is altered through land conversion. In the ecological model, an increase in  $A$  is likely to have three effects: (1) it lowers the carrying capacity, or maximum population density, of native species,  $dK_1/dA < 0$ ; (2) it inhibits the ability of native species to compete with exotics,  $dh(x_2)/dA > 0$ ,  $dk(x_1)/dA < 0$ ; and (3) it increases the migration rate of exotic species into the ecosystem,  $dc/dA > 0$ .<sup>1</sup>

It is easy to see from the equilibrium conditions in Equations (3) and (4) that the result of these effects of an increase in  $A$  is a downward shift of the  $\dot{x}_1 = 0$  stationary locus, but the  $\dot{x}_2 = 0$  isocline swivels out.<sup>2</sup> The resulting outcome is illustrated in the case of the single-equilibrium phase diagram (see Figure 2).

As the figure shows, if the ecosystem is initially at the original equilibrium represented by point  $A$ , the effect of land conversion is to

cause the population density of invaders to rise and the population of endemic species to fall. Eventually, the ecosystem will reach a new long-term equilibrium with a higher population density of invasive species and lower density of natives (point  $B$ ). However, if the decline in the  $\dot{x}_1 = 0$  locus is large, then the long-term outcome may even be complete extinction of the endemic species by the invader  $(0, K_2)$ , which is equilibrium point  $C$ . Thus, as this example demonstrates, the effect of land conversion of natural habitat could be to completely alter the outcome of interspecific competition between a native and invasive species.<sup>3</sup>

### The Economic Model of Land Conversion

As discussed in the introduction, the economic incentives to clear additional forest land are often driven by farm profitability. To explore the key determinants underlying this relationship, this section adapts the economic model of land conversion from Barbier (2005, ch. 6) that motivates the land clearing of a tropical forest ecosystem. The resulting model depicts the economic decision of an owner of agricultural land who is intent on expanding operations into a nearby open-access tropical forest area. The model is sufficiently general to represent the land-clearing behavior of both the landowner of a large-scale agricultural activity (e.g., palm oil, soybean or coffee plantation) and a smallholder who produces food and possibly some cash crops. We therefore assume that all landowners adjacent to the tropical forest ecosystem can be

<sup>1</sup> As noted in the introduction, examples of these three effects of land conversion on biological invasion in the ecological literature can be found in Lozon and MacIsaac; Mack et al., Peterson; Tilman and Lehman; Vitousek et al.

<sup>2</sup> The conditions  $j(K_2) + c/K_2 = 0$  and  $k(0) = 0$  ensure that an increase in  $A$  has little effect on the  $\dot{x}_2 = 0$  isocline for coordinates along that locus close to the corner equilibrium  $(0, K_2)$ .

<sup>3</sup> The comparative static effects of an increase in  $A$  can also be calculated explicitly. Employing Cramer's rule on the steady-state conditions in Equations (3) and (4) yields  $dx_1^*/dA = \{\phi[j'(x_2^*) - c/(x_2^*)^2] + \sigma h'(x_2^*)\}/D < 0$  and  $dx_2^*/dA = [g'(x_1^*)\sigma + \phi k'(x_1^*)]/D > 0$ , since  $\phi = \{\partial h(x_2^*)/\partial A\} - [\partial g(x_1^*)/\partial K_1] (\partial K_1/\partial A) > 0$ ,  $\sigma = \partial k(x_1^*)/\partial A - (1/x_2^*)(\partial c/\partial A) < 0$ , and  $D = g'(x_1^*)[x_2^*j'(x_2^*) - c/(x_2^*)^2] - h'(x_2^*)k'(x_1^*) > 0$  as a result of the necessary and sufficient stability conditions for an interior equilibrium (see Appendix). Thus, the effect of land conversion is to cause the equilibrium population density of invaders to rise and the population of endemic species to fall.



represented by the single agent of the following model.

Assume that the representative owner and operator of an agricultural holding near the tropical forest ecosystem plans to expand his or her farming activity by converting new land from the forest. The farm owner is a price taker in both input and output markets. Farm and off-farm labor are assumed to be perfect substitutes, such that the opportunity cost of the farm owner's time (i.e., his or her own wage rate) is determined exogenously. In any time period,  $t$ , let the profit function of the farm owner's production decisions be defined as

$$(5) \quad \max \pi(p, w, w_N) = \max_{N, x} pf(x, N) - wx - w_N N,$$

where the variable inputs include newly cleared tropical forest land by the farm,  $N$ , and a vector,  $x$ , of other inputs (e.g., labor, fertilizer, seeds) used in production of a single agricultural output.<sup>4</sup> The corresponding vector of input prices is  $w$ , and  $p$  is the price of the farm output. Finally,  $w_N$  is the rental "price" of land. If the farmer owner purchased or rented additional cleared land from a market, then  $w_N$  would be the market rental price of land. However, here, we are assuming that the farm operator clears land from a freely accessible forest area, in which case  $w_N$  is an implicit price, or opportunity cost.

Utilizing Hotelling's lemma, the derived demand for cleared forest land by the farm,  $N$ , is therefore

$$(6) \quad N = N(p, w, w_N) = -\partial \pi / \partial w_N, \\ \partial N / \partial w_N < 0, \quad \partial N / \partial p > 0.$$

As expected, the farm owner's demand for clearing new forest land will decline with its implicit price but rise with the price of agricultural output.

As the farm is providing its own supply of newly cleared land, one can view this type of supply as a form of "production" of converted

land governed by the following conditions. The source of the cleared land (i.e., the nearby tropical forest ecosystem) is an open-access resource, so that land is cleared up to the point where any producer surpluses (rents) generated by clearing additional land are zero. The principal input into clearing land is labor,  $L$ , which is paid some exogenously determined wage rate,  $w_L$ , and the production function is assumed to be homogeneous. This production of cleared land may also be affected by a range of exogenous factors,  $\alpha$ , that may influence the accessibility of forest land available for conversion, including roads, infrastructure, and closeness of the forest ecosystem to the "center" of agricultural activity in the area (where farm output is presumably marketed). Thus, one can specify a cost function, based on the minimum cost to the farm of producing a given level of cleared land,  $N$ , for some fixed levels of  $w_L$  and  $\alpha$ , as

$$(7) \quad C = C(w_L, N; \alpha).$$

Under open-access conditions, the farm owner will convert forest area up to the point where the total revenues gained from converting  $N$  units of land,  $w_N N$ , is equal to the total costs represented by Equation (7). As the farmer is essentially supplying his or her own newly cleared land, then in equilibrium, the implicit price,  $w_N$ , ensures that the costs of supplying the land will be equated with the farm owner's derived demand for converted land. Thus, the following cost conditions for the farm supplying its own cleared land must hold

$$(8) \quad w_N = c(w_L, N; \alpha), \quad \partial c / \partial w_L > 0, \\ \partial c / \partial N > 0, \quad \partial c / \partial \alpha < 0.$$

The right-hand side of Equation (8) is the average cost curve for clearing land, which may be increasing with the amount of land cleared, as, among other reasons, one must venture further into the forest to clear more land. Equation (8) is therefore the equilibrium "own" supply condition for farmer exploiting a pure open-access resource. That is, in equilibrium, the farm owner's implicit price

<sup>4</sup>The existing farm land of the owner is assumed to be fixed and can thus be ignored in the subsequent analysis.

for cleared land will be equated with the per unit costs of forest conversion, thus ensuring that any rents from clearing are dissipated. Together with the farmer's derived demand for converted land (Equation [6]), Equation (8) determines the equilibrium level of land clearing by the farm owner as well as its implicit price. Although the latter variable is not observed, it is possible to solve for the reduced-form equation for the equilibrium level of cleared land by substituting Equation (8) for  $w_N$  in Equation (6) and then rearranging to arrive at

$$(9) \quad N = N(p, w, w_N(w_L, \alpha)) = N(p, w_I, w_L; \alpha), \\ dN/dp > 0, \quad dN/d\alpha > 0,$$

where the wage rate,  $w_L$ , is now distinguished from the vector of prices for inputs other than labor,  $w_I$ . The amount of land converted should increase with the price of output and the accessibility of forest land. However, the impact of a change in the wage rate or other input prices is ambiguous.<sup>5</sup>

Note that Equation (6) is homogeneous of degree zero, and as a result, can be rewritten as a function of relative prices using one of the input prices other than wages,  $w_I$ , as a numeraire. This supply and demand analysis for cleared land can be conducted in relative prices, and thus an alternative version of Equation (9) is

$$(10) \quad N = N(p/w_I, w_L/w_I; \alpha), \\ dN/d(p/w_I) > 0, \quad dN/d\alpha > 0.$$

<sup>5</sup> In the case of the impacts of a change in the wage rate on land clearing, the ambiguity of the impacts arises because of two possible counteracting effects. First, a higher wage rate should make it more costly for the farmer to convert more land area, thus reducing the equilibrium amount of land converted. However, labor is also used in agricultural production, and if land and labor are substitutes, then a higher wage rate may also increase the use of converted land in production. Whether the equilibrium level of cleared land will increase or decrease in response to a rise in the wage rate will depend on the relative magnitude of these two effects. See Barbier (2005, ch. 6) for further details.

## Simulations of the Integrated Ecological-Economic Model

By integrating the ecological model of biological invasion and interspecific competition with the economic model of land conversion, it is possible to determine how two of the predicted incentive effects on land clearing—a change in output prices and an improvement in forest access—will affect competition between the exotic and native species in the tropical forest ecosystem. To conduct this simulation, several assumptions need to be invoked.

First, the continuous time ecological model from Equations (1) and (2) is transformed into discrete time, and specific functional forms are adopted.<sup>6</sup> The new equations are

$$(11) \quad x_{1t+1} - x_{1t} = x_{1t}[g(x_{1t}) - h(x_{2t})], \\ g(x_{1t}) = r_1 \ln[K_1/x_{1t}], \quad h(x_{2t}) = b_1 x_{2t}$$

and

$$(12) \quad x_{2t+1} - x_{2t} = x_{2t}[j(x_{2t}) - k(x_{1t})] + c, \\ j(x_{2t}) = r_2 \ln[K_2/x_{2t}], \quad k(x_{1t}) = b_2 x_{1t}.$$

Second, it is assumed that the equilibrium equation for cleared land (Equation [10]) at any time  $t$  takes a Cobb–Douglas specification

$$(13) \quad N = N(p/w_I, w_L/w_I; \alpha) \\ = N_0 \alpha^{\beta_1} \left(\frac{p}{w_I}\right)^{\beta_2} \left(\frac{w_L}{w_I}\right)^{\beta_3}.$$

It follows that the parameter  $\beta_1$  is the elasticity of forest clearing with respect to improved access,  $\alpha$ , and  $\beta_2$  is the elasticity with respect to a change in relative prices,  $p/w_I$ .<sup>7</sup>  $\beta_3$  is the elasticity with respect to a change in relative input prices  $w_L/w_I$ .

Third, the measure of the altered area of tropical ecosystem,  $A$ , is assumed to be related

<sup>6</sup> The types of functional forms for the discrete versions of Equations (1) and (2) that are used in Equations (11) and (12) are common in the ecological literature; e.g., see Rose.

<sup>7</sup> As explained below, the Cobb–Douglas specification of Equation (13) was used in a panel analysis of land-use change in Mexico by Barbier (2002), who found this specification to be robust relative to other possible specifications.



to the equilibrium area converted to agricultural land by the farm owner; specifically, let  $A = \ln N$ . It follows that an increase in land clearing,  $N$ , will now have a direct effect on reducing the maximum population density of native species, inhibiting the ability of native species to compete with exotics and increasing the migration of new members of the exotic species into the tropical ecosystem. These effects are made explicit by assuming the following functional relationships:  $\ln K_1 = -\gamma_1 \ln N$ ,  $b_1 = \gamma_2 \ln N$ ,  $b_2 = -\gamma_3 \ln N$ , and  $c = \gamma_4 \ln N$ .

Finally, values need to be assigned to the various parameters of the ecological-economic model. The first step is providing parameter values to run a base-case simulation of the model under the assumption that land clearing,  $N$ , does not change. In the case of the two carrying-capacity variables, if units of the two species  $x_1$  and  $x_2$  are chosen in terms of percentage of their respective maximum population densities, then it follows that  $K_1 = K_2 = 1$ . Values of the remaining ecological parameters (i.e.,  $r_1$ ,  $r_2$ ,  $b_1$ ,  $b_2$ , and  $c$ ) are then chosen to satisfy two conditions: (1) that, starting from an initial situation where the population density of the native species is half of its maximum, whereas the population density of the invasive species is well below its maximum, the ecological model would converge to a stable steady-state equilibrium in a finite period of time, e.g.,  $t = [0, 30]$ ; and (2) this single interior equilibrium would represent closely the one depicted in Figure 1a, i.e., a high native species population relative to the exotic species. The results of the base-case simulation are depicted in Figure 3.

The base case assumes that the initial population density of the native species is 50% of its maximum, and the population density of the exotic species is only 15% of its maximum. As shown in Figure 3, from this starting point, the base-case simulation easily reaches convergence to an equilibrium steady state within 30 time periods.<sup>8</sup> The steady-state

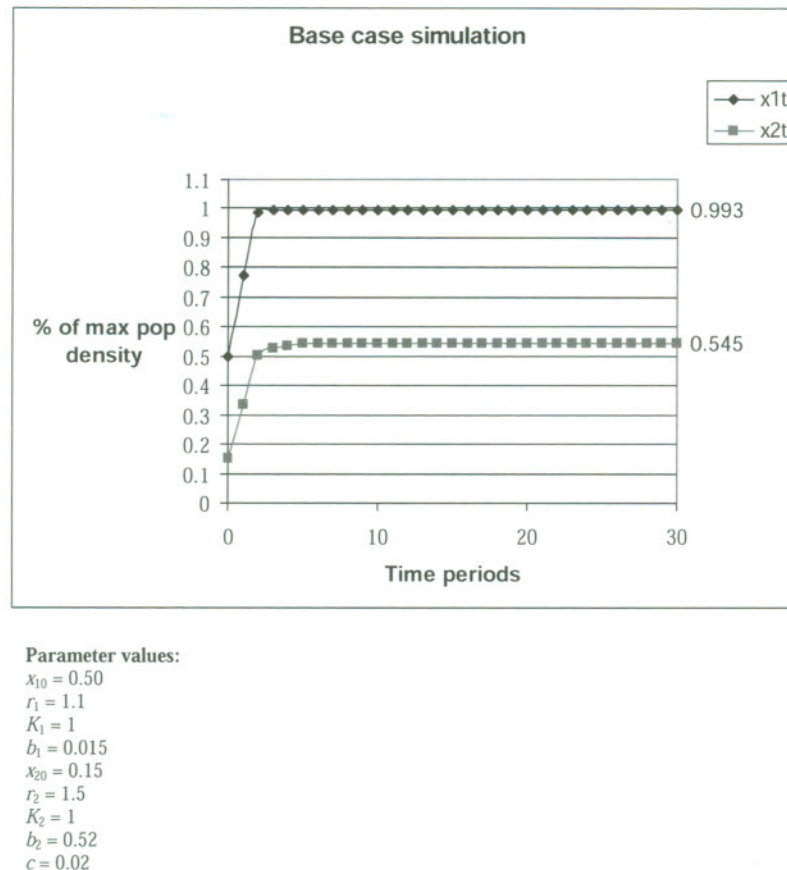
population density of native species is almost at its maximum carrying capacity (99.3%), whereas the steady-state population of the invasive species is just over half of its carrying capacity (54.5%).

However, the base-case simulation of the ecological model assumes that the land area of the tropical ecosystem is not altered by agricultural conversion. As we have seen from the economic model of land conversion, an increase in the relative price of agricultural output or in the accessibility of potentially converted forest areas to local markets will lead to more land clearing. The next step in simulating the ecological-economic model is to examine the effects of a change in either relative agricultural prices or market access on forest clearing and thus the competition between the invasive and native species in the tropical forest ecosystem.

The procedure for conducting this simulation was, first, to choose appropriate values for the elasticities  $\beta_1$  and  $\beta_2$  of forest clearing with respect to improved access and relative prices, respectively, from the empirical literature on tropical deforestation, as well as appropriate parameter values for  $\gamma_1$ ,  $\gamma_2$ ,  $\gamma_3$ , and  $\gamma_4$ . Second, given the initial starting point of the base-case equilibrium (e.g.,  $x_1 = 0.993$  and  $x_2 = 0.545$ ), the simulation determines the effects of changes in prices and access via land clearing in "moving" the ecological model to a new equilibrium. This part of the simulation is not straightforward, since the impacts of a change in  $N$  are composed of two effects. The initial impact is to cause a movement in  $x_1$  and  $x_2$  away from their initial equilibrium values, placing them on a different trajectory to a new equilibrium (see Figure 2). However, because a change in  $N$  simultaneously affects four ecological parameters,  $K_1$ ,  $b_1$ ,  $b_2$ ,  $c$ , the new trajectory must also reflect changes in these parameters.

Figure 4 shows the simulation for a change in relative prices. The elasticity estimate for  $\beta_2$  used in the simulation is from Barbier (2002), who conducted a panel analysis of various economic factors that influence agricultural land expansion across 31 states in Mexico. In this regression, the elasticity of agricultural

<sup>8</sup>Although difficult to see from the graph, the native species,  $x_1$ , converges to its equilibrium population density in 14 periods, whereas the exotic species,  $x_2$ , converges in 19 periods.



**Figure 3.** Base-Case Simulation of Ecological–Economic Model

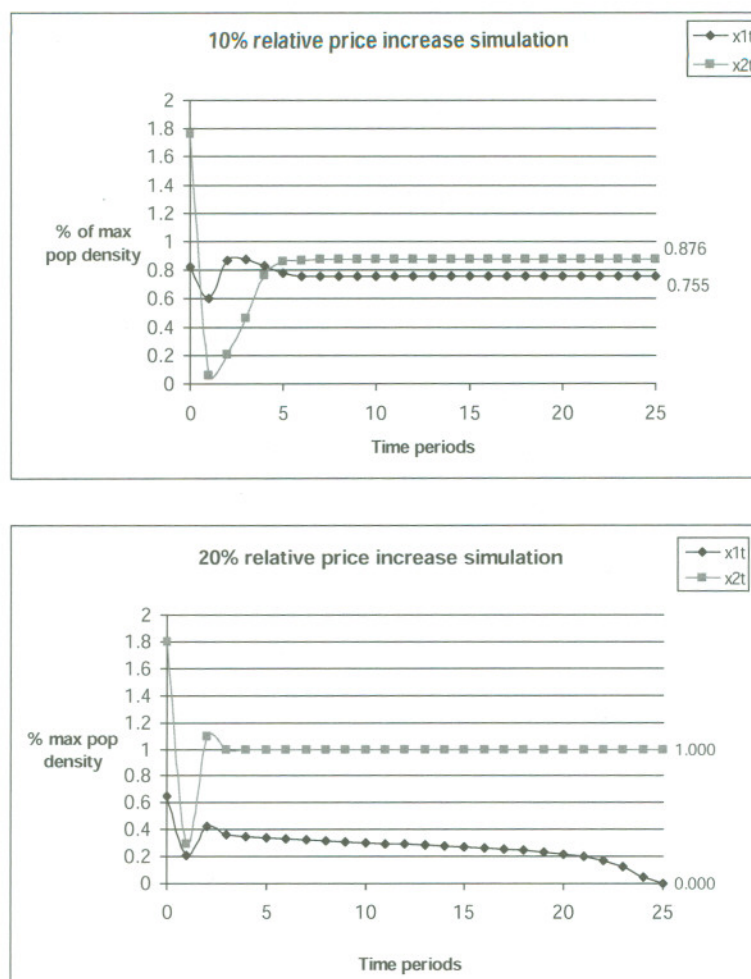
land expansion with respect to a 1% increase in the maize–fertilizer price ratio is calculated to be 1.147%. Assuming that agricultural land expansion results in land clearing of forest, this elasticity serves as the estimate for  $\beta_2$ .

The top diagram in Figure 4 depicts what happens in the ecological–economic model as the result of a 10% change in relative prices, which corresponds to the value  $\beta_2 = 0.1147$ , i.e., a 11.5% increase in land clearing. As shown in the diagram, the immediate effect of increased land clearing from the price increase is to cause the population density of native species to fall from the base-case equilibrium of 99.3% to 82.0% and the population density of exotic species to rise from 54.5% to 176.3% of its carrying capacity. As expected, the parameters  $K_1$ ,  $b_1$ ,  $b_2$ , and  $c$  also change, and the two species interact along a different trajectory to converge to a new equilibrium

within 25 time periods. At this new equilibrium, the population density of native species has fallen to 75.5% of its carrying capacity, whereas the population density of the invasive species has now risen to 87.6%.<sup>9</sup> Consequently, the additional land clearing caused by the 10% increase in relative agricultural output to input prices substantially boosts the ability of the invasive species to dominate the remaining tropical forest ecosystem at the expense of the native species.

<sup>9</sup> Although it is not clear from the diagram, both  $x_1$  and  $x_2$  converge to their respective new steady states by period 20. Note that, for comparison purposes with the base case, the population density values of  $x_1$  are expressed in terms of the original maximum population density of  $K_1 = 1$ . For example, under this simulation of a 10% relative price increase the carrying capacity of  $x_1$  has fallen to 90.8% of its original base-case carrying capacity, and the steady-state value of  $x_1$  is 75.5% of the base-case carrying capacity of  $K_1 = 1$ .





Parameter values: New parameters for 10% price change:

$\gamma_1 = 0.8$   
 $\gamma_2 = 1.4$   
 $\gamma_3 = 0.3$   
 $\gamma_4 = 1.5$   
 $\beta_2 = 0.1147$   
 $K_1 = 0.9082$   
 $b_1 = 0.1757$   
 $b_2 = 0.4856$   
 $c = 0.1922$

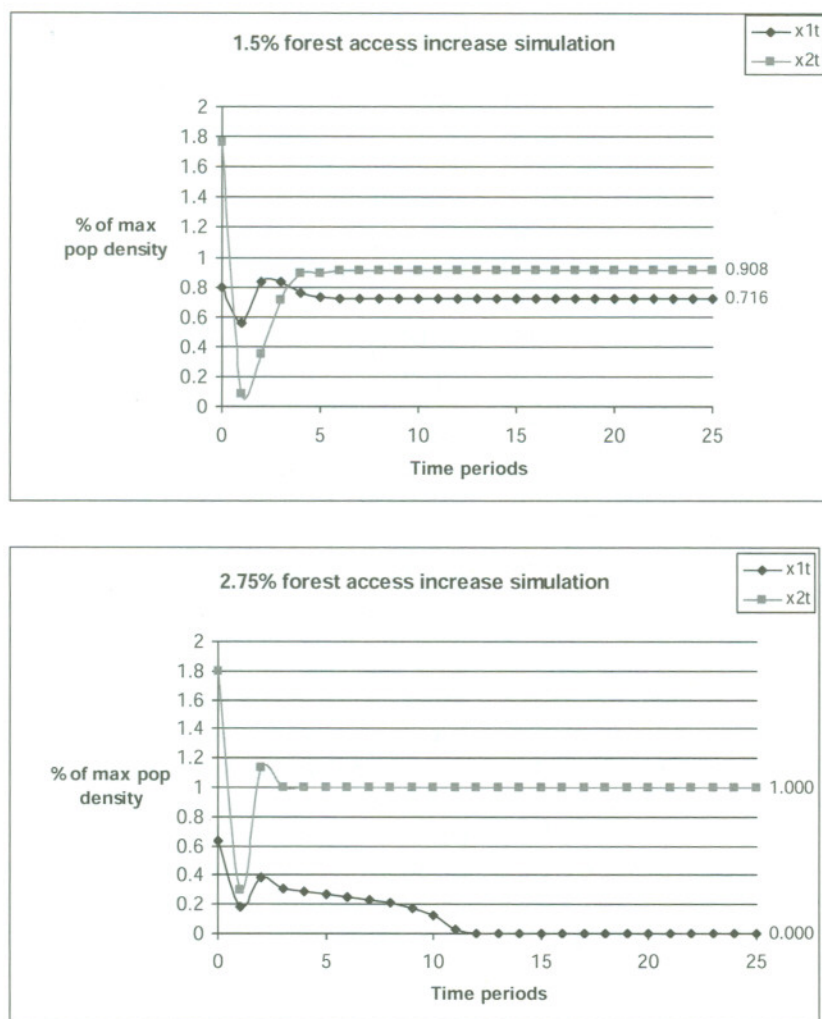
New parameters for 20% price change:

$\beta_2 = 0.2295$   
 $K_1 = 0.8164$   
 $b_1 = 0.3364$   
 $b_2 = 0.4511$   
 $c = 0.3643$

**Figure 4.** Relative Price Change Simulation of Ecological-Economic Model

An important question is: how much do relative agricultural prices have to rise in order to induce the invasive species to completely eliminate the native species from the tropical ecosystem? As the simulation in the bottom diagram indicates, this scenario occurs if the relative price increase is 20% rather than 10%. The doubling of the price increase causes a 23% rise in land clearing. Compared to the base-case simulation, the result is an immediate fall in native species to

64.8% of its carrying capacity and an explosion in the invasive population to 179.6% of its carrying capacity. However, this time, the respective populations adjust along a trajectory that sustains the invasive species at its maximum carrying capacity of 100%, whereas the native population is wiped out by period 25. The striking outcome of this simulation is that it does not take much of an increase in relative prices and subsequent land clearing to cause this scenario of



Parameter  
values:

$\gamma_1 = 0.8$   
 $\gamma_2 = 1.4$   
 $\gamma_3 = 0.3$   
 $\gamma_4 = 1.5$

New parameters for 1.5% access  
change:

$\beta_1 = 0.1287$   
 $K_1 = 0.8971$   
 $b_1 = 0.1952$   
 $b_2 = 0.4814$   
 $c = 0.2131$

New parameters for 2.75% access  
change:

$\beta_1 = 0.2360$   
 $K_1 = 0.8112$   
 $b_1 = 0.3453$   
 $b_2 = 0.4492$   
 $c = 0.3739$

**Figure 5.** Forest Access Change Simulation of Ecological-Economic Model

complete elimination of the native species by the invader to occur.

Figure 5 shows the corresponding simulation for a change in market access to the forest. The elasticity estimate for  $\beta_1$  is taken from Cropper, Puri, and Griffiths analysis of the role of roads in contributing to deforestation in North Thailand. It is based on what the authors term an "impedance-weighted distance from each plot to the nearest market

town" (Cropper, Puri, and Griffiths, p. 176), which is an algorithm adjusted for paved versus unpaved road and slope of the agricultural plot that computes the shortest distance from each farm to the closest market town. The authors' estimates suggest that a reduction of impedance-weighted distance by 150 increases the probability of clearing additional forest by 5%. Based on this estimate, the elasticity of land clearing with respect to a 1%



increase in forest access is calculated to be 0.0858, which is used for  $\beta_1$ .

The top diagram in Figure 5 depicts what happens in the ecological-economic model as the result of a 1.5% improvement in forest access, which corresponds to the value  $\beta_1 = 0.1287$ , i.e., a 12.9% increase in land clearing. As shown in the diagram, increased land clearing from the change in access causes the population density of native species to fall instantly from the base-case equilibrium of 99.3% to 79.9% and the population density of exotic species to jump from 54.5% to 176.7% of its carrying capacity. As once again the parameters  $K_1$ ,  $b_1$ ,  $b_2$ , and  $c$  change, the two species interact along a different trajectory to converge to a new equilibrium within 25 time periods. At this new equilibrium, the population density of native species has fallen to 71.6% of its carrying capacity, whereas the population density of the invasive species has now risen to 90.7%.<sup>10</sup> This outcome is very similar to the simulation of the 10% rise in relative agricultural output to input prices; thus, it appears that the additional land clearing caused by both improvement in forest access and a relative price increase will induce the invasive species to expand its range in the remaining tropical forest ecosystem at the expense of the native species. Note, however, that compared to the price rise, only a very small increase in forest access (1.5%) is required to have a dramatic change in the balance of species in the tropical forest ecosystem.

This result suggests that the native species in the ecological-economic system is vulnerable to collapse from small changes in forest access. This case is confirmed in the simulation shown in the bottom diagram of Figure 5. A 2.75% improvement in forest access causes land clearing to rise by 23.6%, but this induces complete takeover by the invasive species, which occurs relatively quickly, i.e., by period 3. With  $x_2$  at 100% of carrying capacity, the native species cannot compete, and it declines

rapidly until it disappears completely by period 12. The fact that only a relatively small increase in forest access causes such a dramatic, and very rapid, change in the competition between the native and exotic species is a salient outcome of these simulations.

### Final Remarks

As noted in the introduction, a distinguishing feature of tropical terrestrial ecosystems is that these systems contain an abundance of native species that are "packed" into smaller habitat ranges, which make these species highly vulnerable to competition from invasive species that are added by habitat conversion, notably through extensive land clearing. Throughout tropical regions, forest ecosystems are in particular vulnerable to clearing, especially for agricultural land expansion. Much of the forest land prone to conversion is virtually open access, and numerous studies of the deforestation process suggest that economic incentives, particularly the profitability of agricultural systems and the access of forest areas to markets, are important determinants of land clearing for farming (e.g., for reviews, see Barbier 2005, ch. 5 and 6; Barbier and Burgess; Chomitz et al.; FAO 1997, 2003; Kaimowitz and Angelsen; and van Kooten, Sedjo, and Bulte).

Field studies indicate that such human-induced disturbances are important factors in both the successful establishment of exotic invaders and their range expansion. For example, in their survey of ecological field literature, Lozon and MacIsaac (their Table 1) identified 94 cases where exotic plants have successfully invaded tropical terrestrial environments. Disturbance of the natural habitat was required for successful establishment of the exotic species in all but one case and for range expansion of the invader in all but five cases. Economic studies have also begun to link land-use change to successful establishment of exotic species and their range expansion in tropical areas. For example, Burnett et al. described the spread of *Miconia* woody shrub in disturbed environments of the South Pacific, noting that in Tahiti, vast tracts

<sup>10</sup>The native species,  $x_1$ , converges to its equilibrium population density in 17 periods, whereas the exotic species,  $x_2$ , converges in 19 periods.



of *Miconia* have wiped out native forest and reduced forest cover and, thus, increased the potential for soil erosion, landslides, and other economic damages. Similarly, over the past 20 years in southern Mexico, there has been a fourfold increase in the area covered by bracken fern, which has spread due to the fires and forest clearing from shifting cultivation (Schneider). While acknowledging this important link between land clearing and successful establishment and spread of an exotic invasive, economic studies have generally focused on controlling the damages associated with the invasion. In the case of bracken fern, Burnett et al. explored control policies to obtain the minimum present-value costs of population reduction and expansion of the invader in Hawaii. Schneider and Geoghegan examined the factors that determine the land-abandonment decision of shifting cultivators who are faced with diminished returns from continuing to use an invaded plot. What is lacking in the current literature, however, is an analysis of the integrated ecological-economic effects that arise from the relationships among land-use change, biological invasion, and interspecific competition in a tropical ecosystem.

This paper represents the first attempt to capture these effects by linking an economic model of open-access land clearing for agricultural activity to an ecological model of invasion and interspecific competition between the invader and native species in a tropical forest ecosystem. The results of the model and subsequent simulations are striking in several respects.

First, only small changes in economic incentives appear to cause dramatic changes in the ability of the invasive species to outcompete the native species. Starting from a base-case equilibrium in which the native species is dominant, i.e., it attains 99.3% of its carrying capacity, whereas the invasive species reaches only about half of its maximum population density, only relatively small changes in prices or in forest access cause dramatic reversals in this outcome. For example, the additional land clearing caused by a 10% increase in relative farm output to input prices or by only a 1.5% improvement in

forest access is sufficient to cause native species to decline to around 72–76% of their carrying capacity and invasive species to increase to 88–91% of carrying capacity.

Second, the native species in the ecological-economic system is highly vulnerable to collapse through land clearing induced by either an increase in relative prices or in forest access. If relative prices rise by only 20% or if road improvements or other factors increase the accessibility of the forest area to nearby market towns by 2.75%, then this will induce enough additional land clearing to “tip the balance” in favor of the exotic invading species. Note the important distinction here: complete land clearing does not have to occur to cause this outcome. In fact, a 20% increase in relative prices causes land clearing to rise by around 23%, whereas a 2.75% increase in forest access induces land clearing to rise by 24%—yet in both cases, complete takeover of the forest ecosystem by the invader occurs. In other words, this model predicts that the forest ecosystem is highly vulnerable to the *ecological disturbance* caused by land clearing. Long before complete conversion of the forest system occurs, land clearing will sufficiently disrupt the interspecific competition between an invasive and native species so that the latter is eliminated. This result has important policy considerations. If the aim of policy is to control deforestation—i.e., keep agricultural conversion of forest areas low—then a modest increase in land clearing by 23–24% may seem tolerable. However, if the aim of the policy is to reduce ecological disruption and complete takeover of forest habitat by an invasive species—i.e., to control damaging biological invasions—then as this model shows, even a modest increase in land clearing is not acceptable.

Third, forest access is a particularly key influence in our model. This is mainly from the higher elasticity estimate for land clearing due to increased access of forest areas to nearby market towns. However, many studies of tropical deforestation illustrate that land clearing is accelerated by such improvements in forest access (Barbier and Burgess; Chomitz et al.; Cropper, Puri, and Griffiths; Kaimowitz and Angelsen). Thus, the model used in this



paper shows that, if road improvements and other factors dramatically increase the profitability of frontier farming, and thus land clearing, the resulting ecological disturbance of the remaining forest ecosystem and the propensity for invasive species to eliminate native species in these ecosystems may be catastrophic.

Of course the major caveat of the ecological-economic model developed here is that it is only illustrative. The results, although intriguing, are simulated and purely representational. The next, and perhaps urgent, step is to combine actual field ecological experiments with empirical economic analysis of land clearing in specific tropical forest locations to determine the extent to which the model predictions simulated here are an accurate reflection of the relationship between the economic incentives driving agricultural conversion and interspecific competition between invasive and native species. In addition, it would be useful to extend the approach to a fully comprehensive analysis of the relative welfare effects of loss of native species compared to the introduced invader. Evidence from both ecological and economic studies suggests that the damages associated with plant invasions in tropical environments disturbed through human land-use changes are significant (Burnett et al.; Mack et al.; Schneider and Geoghegan; Tilman and Lehman; Vitousek et al.). Extension of the dynamic economic-ecological model developed here of the economic incentives behind land-use change, biological invasion, and interspecific competition between invasive and native species in tropical ecosystems should shed light on the relative benefits of control versus prevention strategies to reduce the damages arising from such disturbance-induced invasions.

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### Appendix: Stability Conditions for Equilibrium in the Ecological Model

As discussed in the text, for the ecological model with invasion and interspecific competition defined by the dynamic Equations (1) and (2), there is no corner equilibrium in  $(x_1, x_2)$  space defined at point  $(K, 0)$  since at that point,  $\dot{x}_2 = c$ . There is a corner equilibrium defined at  $(0, K_2)$ , however. Also note from Equation (3) that as  $x_2 \rightarrow \infty$ , the stationary locus of points satisfying  $\dot{x}_1 = 0$  also tends toward infinity; similarly, in Equation (4), as  $x_1 \rightarrow \infty$ , then so does the  $\dot{x}_2 = 0$  stationary locus.

The slopes corresponding to the stationary loci, or isoclines, in  $(x_1, x_2)$  space defined by the equilibrium conditions in Equations (3) and (4) are, respectively

$$(A1) \quad \left. \frac{dx_2}{dx_1} \right|_{\dot{x}_1=0} = \frac{g'(x_1^*)}{h'(x_2^*)} < 0, \\ \left. \frac{dx_2}{dx_1} \right|_{\dot{x}_2=0} = \frac{k'(x_1^*)}{j'(x_2^*) - c/(x_2^*)^2} < 0.$$

Thus, the two isoclines are downward sloping in  $(x_1, x_2)$  space, and both loci are nonlinear. It follows that, as the two isoclines may intersect more than once, there is the possibility of multiple interior equilibria. In addition, whether the  $\dot{x}_1 = 0$  stationary locus crosses the  $\dot{x}_2 = 0$  isocline from above or below is determined by the stability conditions governing these equilibria.

Assume that at least one interior equilibrium  $(x_1^*, x_2^*)$  is feasible at  $\dot{x}_1 = \dot{x}_2 = 0$ . Linearizing the dynamic equations for interspecific competition (Equations [1] and [2]) around this equilib-

rium yields the following system

$$(A2) \quad \begin{bmatrix} \dot{x}_1 \\ \dot{x}_2 \end{bmatrix} = \begin{bmatrix} x_1^* g'(x_1^*) & -x_1^* h'(x_2^*) \\ -x_2^* k'(x_1^*) & x_2^* j'(x_2^*) - c/x_2^* \end{bmatrix} \\ \times \begin{bmatrix} x_1 - x_1^* \\ x_2 - x_2^* \end{bmatrix},$$

once Equation (3) is used to substitute for  $h(x_2^*)$  in the first element in the Jacobian matrix of coefficients,  $J$ , and Equation (4) is employed to substitute for  $k(x_1^*)$  in the last element of  $J$ . Following the Routh–Hurwitz theorem, the necessary and sufficient conditions for stability in a system of equations with such a  $2 \times 2$  Jacobian matrix are  $\text{tr}(J) < 0$ ,  $|J| > 0$ , which for the above matrix require  $x_1^* g'(x_1^*) + x_2^* j'(x_2^*) - c/x_2^* < 0$  and  $g'(x_1^*) [j'(x_2^*) - c/(x_2^*)^2] > h'(x_2^*) k'(x_1^*)$ . The first condition is satisfied, but the second condition holds according to Equation (A1) only if the slope of the  $\dot{x}_1 = 0$  isocline is steeper than the slope of the  $\dot{x}_2 = 0$  stationary locus in the neighborhood of the interior equilibrium  $(x_1^*, x_2^*)$ . That is, for an interior equilibrium to be locally asymptotically stable, the  $\dot{x}_1 = 0$  isocline must cross the  $\dot{x}_2 = 0$  locus from above.

Finally, note that since  $-x_1^* h'(x_2^*) < 0$  in  $J$ , then any point above (below) the  $\dot{x}_1 = 0$  isocline is associated with a decreasing (increasing) value of  $x_1$ . Similarly, as  $-x_2^* k'(x_1^*) < 0$ , then any point to the right (left) of the  $\dot{x}_2 = 0$  locus is associated with a decreasing (increasing) value of  $x_2$ . These conditions determine the direction of the trajectories in the phase diagrams corresponding to the equilibria for Equations (3) and (4) in  $(x_1, x_2)$  space, as depicted in Figure 1.



