# The Value of Habitat Conservation for Bioprospecting

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#### Abstract

Revenue from plant-derived pharmaceutical products has been suggested as a source of funds for tropical habitat conservation. Previous work suggests that the incentives for conservation by private firms for bioprospecting are very small. This paper presents an expanded model that acknowledges that the probability of a species proving commercially useful is spatially dependent on the outcomes for other species. The effect of expected habitat loss on conservation values is also incorporated. Numerical simulations show that the value of protecting land for bioprospecting may be much higher than suggested by other recent studies.

Keywords: biodiversity, habitat conservation, bioprospecting, pharmaceuticals

JEL Codes: Q24, 032

### 1 Introduction

The loss of biological diversity worldwide has attracted considerable attention in recent years. One of the main concerns cited is that the genetic resources threatened by the extinction of species are potential sources of innovations that could directly benefit humanity when exploited via "bioprospecting" for pharmaceutical, agricultural, or other commercial innovations. Indeed, there is no shortage of examples of such discoveries: cortisone and the first oral contraceptives were derived from Central American yam species; the Pacific yew of the western United States yielded the anticancer drug taxol; a drug to prevent blood clotting was developed from snake venom; and the active ingredient in aspirin was synthesized from a substance found in willow trees. By one estimate, one-quarter of all medical drugs used in the developed world were developed from plants (Pearce and Moran, 1994).

Accordingly, economists have turned some attention to the question of what companies may be willing to pay to preserve threatened genetic resources. Much of this work has focused specifically on the potential value of biopharmaceuticals derived from higher plant varieties. Simpson, Sedjo and Reid (1996) argue that the commercial value of the marginal plant species is likely to be extremely small, thus leaving little incentive for companies to invest in habitat conservation. Their result is based on a static model that assumes the probability that any given species contains commercially valuable information is independent and identical across species. Rausser and Small (2000) challenge these findings by noting that firms focus their research efforts on the most promising species, and that promising leads command an information rent because of their role in lowering search costs. For the most promising ecosystems, they find that the value of preservation may be much more promising than suggested by Simpson, *et al.* 

This study presents an expanded model of the commercial value of habitat conservation that accounts for two important factors absent from previous studies. One is that the presence of commercially useful characteristics is not independently distributed geographically, but rather may exhibit spatial correlation. The expected marginal value of a unit of land in species-rich areas is shown to depend on this correlation. The model is then further extended to incorporate the fact that any interest in preserving lands for bioprospecting is driven by ongoing habitat loss and species extinction.

As in the Simpson *et al.* and Rausser and Small papers, this model is applied to eighteen biodiversity "hot spots," as identified by Myers (1988, 2000). The inclusion of spatial correlation and habitat loss dynamics results in land conservation values that differ markedly from previous results.

#### 2 The Basic Model

Simpson, Sedjo and Reid (SSR) developed a model for measuring the marginal value of species preservation for pharmaceutical research that is the starting point for the current inquiry. Previous studies had calculated the average value of species for pharmaceutical research by multiplying an estimate of the probability of discovery of a commercially valuable resource times the value of this discovery. SSR argued that for investment purposes (i.e., pharmaceutical companies' willingness to pay), what is important is the marginal value of a species.

Their main finding was that the marginal value of protecting a single species for pharmaceutical development is very small (at best, just under \$10,000). Under an implicit assumption of perfect substitution, they noted that there is likely to be significant redundancy of useful genetic material across species. There are also only a limited number of desired products being sought. SSR therefore postulated an interesting relationship: "if all species are promising sources of leads, most would be redundant and the marginal species close to valueless. If no species are likely sources of leads, it is unlikely that two or more will prove redundant but also unlikely that *any* species will prove to have value." So the marginal value of a species will be negligible for very low or high values of p, the probability of commercial discovery.

The key elements of the SSR model are as follows. Given revenues R and search costs c, the expected return to a single sample is pR - C. If testing for a particular use ends with the first success, the value of a collection of n species (assuming independent Bernoulli trials) is

$$V(n) = pR - c + (1 - p)(pR - c) + (1 - p)^{2}(pR - c) + \dots + (1 - p)^{n}(pR - c)$$
  
=  $\frac{pR - c}{p}[1 - (1 - p)^{n}].$  (2.1)

The expected value of an additional species, v(n), for any given use is therefore

$$v(n) = V(n+1) - V(n) = (pR - c)(1 - p)^{n}.$$
(2.2)

By taking the partial derivative of v(n) with respect to p and then solving for p, they obtained a statement for the probability of discovery that maximizes the marginal value of a species:

$$p^* = \frac{R + nc}{(n+1)R}.$$
 (2.3)

Inserting this back in to equation (2.2) yields the marginal value of a species at  $p^*$ . SSR argue that this value should be considered an upper bound, as it is quite unlikely that the true p is the one given in equation (2.3). Figure 1 below shows the relationship between v(n) and p calculated by SSR. As the probability of discovery moves away from  $p^*$ , the value of the marginal species drops quickly.

Figure 1: Expected value of the marginal species as a function of the probability of success in any single trial (from Sedjo, Simpson and Reid, 1996)



The values shown above are based on a set of rough empirical estimates for R, c, and the number of new potential products identified,  $\lambda$ . If the discount rate for future returns is r, the expected bioprospecting value of the marginal species according to the SSR model is

$$v(n) = \sum_{t=0}^{\infty} \lambda (1+r)^{-t} (pR-c)(1-p)^n = \frac{\lambda}{r} (pR-c)(1-p)^n.$$
(2.4)

SSR assumed r is 10 percent per year, and developed estimates for the other parameters of  $n = 250,000, R = $450,000,000, c = $3,600, and \lambda = 10.52$ . These estimates are based on data from DiMasi *et al.* (1991), Office of Technology Assessment (1993), Chichilinsky (1993), and elsewhere. Inserting these values into (2.3) yields  $p^* = 0.000012$ .<sup>1</sup> Using this

<sup>&</sup>lt;sup>1</sup>In fact, this optimal value of p is sensitive to both the spatial dependence and dynamic considerations

maximizing value of p, equation (2.4) yields an upper bound estimate for the expected value of a marginal species of \$9,431.

## **3** Spatial Correlation of Beneficial Species

We will now relax the assumption that the probability that a species is beneficial for pharmaceutical purposes is independent across species, while maintaining a static framework. In particular, we wish to consider how spatial correlation of the presence of beneficial species, or "hits," may affect firms' motivation for investing in habitat conservation. If firms perceive such a correlation across uses — i.e., if the previous discovery of a beneficial species makes it more likely that a nearby species will contribute to another pharmaceutical use — they may be more willing to invest in protection of an area once they know that a hit has been found nearby.

Let  $I_j = 1$  if species j = 1, ..., n is beneficial; otherwise  $I_j = 0$ . As in the previous section, the probability of a hit is  $prob(I_j = 1) = p$  for all j, but we will now assume that the correlation between  $I_j$  and  $I_k$  is given by

$$Corr(I_j, I_k) = f(d_{jk}) \tag{3.1}$$

where f is a known positive function and  $d_{jk}$  is a measure of geographic distance between species j and k.<sup>2</sup> Such correlation may arise due to similar ecological conditions or evolutionary pressures faced by species that are located near one another.

For now, let us consider a simple application of this formulation to the eighteen biodiversity "hotspots" identified by Myers (1988, 1990) as "featuring exceptional concentrations of

discussed below. Given that the calculated value of  $p^*$  would change over time in the context presented here, there is no one value of p that maximizes the value of the marginal species. Accordingly, it is not at all clear that SSR's approach actually yields an upper bound estimate. Nonetheless, for comparison purposes we shall continue to use SSR's value for  $p^*$  in later sections.

<sup>&</sup>lt;sup>2</sup>Polasky and Solow (1995) used this expression to describe correlation based on genetic distance measures, such as those described in Nei (1987), but the same formulation is readily applied here.

species with high levels of endemism and [facing] exceptional threats of destruction." These hotspots are listed in Table 1. This approach will also allow us to readily compare the implications of spatial dependence to the findings of Simpson *et al.* Suppose that firms have observed a previous hit  $I_h = 1$  in hotspot  $H_h$ . Equivalently, industry may have otherwise received information suggesting the presence of a hit in  $H_h$ .

One plausible correlation correspondence is  $Corr(I_j, I_h) = \rho$  for all  $I_j \in H_h$ , and  $Corr(I_j, I_h) = 0$  otherwise. This formulation is particularly appropriate when considering those plant species that are endemic to the hotspot of interest. The conditional probability of  $I_k = 1$  given  $I_j = 1$  can then be expressed as

$$prob(I_k = 1 | I_j = 1) = \rho(1 - p) + p.$$
(3.2)

The derivation of this expression is given in the Appendix. Note that  $\rho = 0$  implies that this conditional probability is simply p. If  $\rho = 1$ , the conditional probability is 1, i.e., all other species in the area will be beneficial. It seems reasonable to assume that  $\rho$  is a small positive number.

In order to evaluate the impact of spatial correlation on land conservation values, it is necessary to define a relationship between habitat area and the number of supported species. Let  $A_i$  and  $n_i$  be the area of and number of higher plant species in  $H_i$ , respectively. A common area-species curve used by biogeographers predicts that

$$n_i(A_i) = \alpha_i A_i^Z, \tag{3.3}$$

where  $\alpha_i$  is a parameter that measures the species richness potential of  $H_i$ . Z is a constant that is greater for isolated areas such as islands and mountaintops, and less for non-isolated sample areas within continents (MacArthur and Wilson, 1967). Wilson (1988) suggests a typical value of Z = 0.25, which appears to be appropriate for the semi-isolated areas included in the Myers hotspot lists. This also allows for direct comparison with per-hectare willingness to pay estimates calculated by Simpson *et al.* The predicted extinction of plant species endemic to  $H_i$  resulting from a one-hectare reduction of  $A_i$  is therefore

$$e_i n_i (A_i) - e_i n_i (A_i - 1) = e_i \alpha_i (A_i^Z - (A_i - 1)^Z), \qquad (3.4)$$

where  $e_i$  is the proportion of plant species found in  $H_i$  that are endemic to that region.

By combining the last two expressions with equation (2.4), we can derive an expression for the bioprospecting value of the marginal hectare in  $H_i$ . By the chain rule, the value of the marginal hectare is the product of the value of a marginal species times the change in species quantity resulting from the loss of the marginal hectare:

$$MHV_i = \frac{\lambda}{r} (pR - c)(1 - p)^{n - e_i \alpha_i (A_i^Z - (A_i - 1)^Z)} e_i \alpha_i (A_i^Z - (A_i - 1)^Z).$$
(3.5)

If the firm is aware of the presence of a hit in  $H_i$ , its expectation of the probability of discovery in the region is replaced by  $p_i$ , the conditional probability given in equation (3.2). In this case, the value of the marginal hectare is

$$\widetilde{MHV}_i = \frac{\lambda}{r} (p_i R - c)(1 - p)^{n1} (1 - p_i)^{n2} e_i \alpha_i (A_i^Z - (A_i - 1)^Z),$$
(3.6)

where  $n1 = n - e_i \alpha_i A_i^Z$  is the number of species in the world that are not endemic to  $H_i$ , and  $n2 = e_i \alpha_i (A_i - 1)^Z$  is the number of endemic species remaining in  $H_i$ .

For small values of  $\rho$ , the presence of spatial correlation increases the value of the marginal hectare, i.e.,  $\widetilde{MHV}_i > MHV_i$ . As  $\rho$  gets large this is no longer true, as the contribution of the increased probability of an additional hit in  $H_i$  to the redundancy of the marginal species outweighs the increase in expected revenues. To better illustrate this effect, consider the extreme case when  $\rho = 1$ , i.e., the presence of a hit in  $H_i$  guarantees that all other endemic species in the region are also beneficial. In this case, the marginal contribution of any one species (and by extension, of any one hectare) to the total expected value of the region is zero.

Table 1 shows the willingness to pay for preservation of the marginal hectare conditioned on knowledge of a previous hit in Myers' eighteen biodiversity hotspots if  $\rho = .001$ , evaluated at p = 0.000012. All other parameter values are as given in Section 2. The "upper bound" willingness to pay estimates calculated by Simpson *et al.*, which are identical to what equation (3.6) would yield if  $\rho = 0$ , are also provided. The inclusion of modest spatial correlation with a known prior discovery generally increases the conservation values for the marginal hectare significantly. This effect is most pronounced for the smaller hotspots with a relatively small proportion of the world's plant species. For example, the willingness to pay for the marginal hectare in Southwestern Sri Lanka increases from \$16.84 when  $\rho = 0$  to \$2,562.27 when  $\rho = 0.001$ . Only in the expansive Cape Floristic Province of South Africa, with its large number of endemics, does the redundancy effect described above lower the willingness to pay.

It is also interesting to compare the approach outlined here to the findings of Rausser and Small (2000), who formulated a model of the information rent to promising biopharmaceutical research leads. A full exposition of their model is beyond the scope of this paper, but the main point of their approach is that scientific research is organized around pursuing the most promising leads first. This is in contrast to the SSR model, which Rausser and Small characterize as one of "brute-force testing." In reality, they argue, "no one ever searches for anything by examining large collections of objects in random order." After deriving an expression for the value of a lead, they apply their model to Myers' biodiversity hotspots by defining leads as 1,000 hectare parcels in these areas. The quality of each lead is given by the density of endemic higher plant species in each hotspot. They then compute the incremental "preservation value" for a hectare in any given parcel. Their results are shown in the third column of Table 2.

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	Forest Area	No. of Endemic	Simpson <i>et</i>	WTP given a
Biodiversity Hot Spot	(1,000 ha)	Plant Species	al. WTP	hit, $\rho = .001$
Western Ecuador	250	2,188	\$20.63	\$580.12
Southwestern Sri Lanka	02	500	\$16.84	\$2,562.27
New Caledonia	150	062	\$12.43	\$1,413.56
Madagascar	1,000	2,911	\$6.86	\$93.58
Western Ghats of India	800	1,620	\$4.77	\$236.88
Philippines	800	1,582	\$4.66	\$240.30
Atlantic Coast of Brazil	2,000	3,750	\$4.42	\$26.04
Uplands of Western Amazonia	3,500	3,846	\$2.59	\$13.86
Tanzania	009	528	\$2.07	\$306.95
Cape Floristic Province of South Africa	8,900	6,278	\$1.66	\$0.78
Peninsular Malaysia	2,600	1,624	\$1.47	\$72.78
Southwestern Australia	5,470	2,831	\$1.22	\$18.02
Ivory Coast	400	194	\$1.14	\$236.20
Northern Borneo	6,400	2,674	\$0.99	\$17.03
Eastern Himalayas	5,300	2,205	\$0.98	\$27.10
Colombian Choco	7,200	2,303	\$0.75	\$18.89
Central Chile	4,600	1,450	\$0.74	\$43.71
California Floristic Province	24,600	2,136	\$0.20	\$6.06

P) values are given in dollars per hectare.
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Table 2: Willingness to Pay to Preserve a Hectare of Land in 18 Biodiversity Hot Spots, Assuming Knowledge of a Lead in a
1,000 Hectare Study Site

	Density, Endemic	Rausser and Small	WTP given a
Biodiversity Hot Spot	Species/1,000 ha	"Preservation Value"	hit, $\rho = .001$
Western Ecuador	8.75	\$9,177	\$12,774
Southwestern Sri Lanka	7.14	\$7,463	\$10,444
New Caledonia	5.27	\$5,473	\$7,719
Madagascar	2.91	\$2,961	\$4,275
Western Ghats of India	2.03	\$2,026	\$2,976
Philippines	1.98	\$1,973	\$2,906
Atlantic Coast of Brazil	1.88	\$1,867	\$2,756
Uplands of Western Amazonia	1.10	\$1,043	\$1,616
Tanzania	0.88	\$811	\$1,295
Cape Floristic Province of South Africa	0.71	\$632	\$1,038
Peninsular Malaysia	0.62	\$539	\$919
Southwestern Australia	0.52	\$435	\$762
Ivory Coast	0.48	\$394	\$714
Northern Borneo	0.42	\$332	\$615
Eastern Himalayas	0.42	\$332	\$613
Colombian Choco	0.32	\$231	\$471
Central Chile	0.32	\$231	\$464
California Floristic Province	0.09	20	\$128

Source: Myers (1988, 1990), Rausser and Small (2000), and author's calculations. Willingness to pay (WTP) values are given in dollars per hectare.

The Rausser and Small model is similar in behavioral motivation to the approach described here, in that both allow for firms to have different expectations of the probability of discovery for different areas. In order to more directly compare the implications of the present model to Rausser and Small's findings, each of Myer's hotspots were divided into identical 1,000 hectare areas. To conform with their choice of parameter values, here  $\lambda = 26$ and c = \$485. All other parameter values are as described above. The results for  $\rho = 0.001$ are shown in the last column of Table 2. The two sets of estimates are quite similar. The willingness to pay implied by the correlation model is larger but of the same magnitude for each hotspot except the California Floristic Province, where the relatively low density of endemic species implies no bioprospecting incentive for conservation in the Rausser and Small analysis.

#### 4 Habitat Loss and Extinction

Both the correlation model described above and the SSR model are static, and therefore ignore the change in available habitat area and the number of species that occurs over time. In reality, any interest in conserving land for bioprospecting is driven by ongoing habitat loss and species extinction. If the genetic resources of a region are secure, the commercial value of conservation is zero. Similarly, the value of preserving a unit of land in an area where habitat loss is progressing quickly is higher than in regions where losses are slower.

The importance of this dynamic can be illustrated simply by revisiting equation (2.2). Figure 1 below shows how v(n) changes with n. As the total number of higher plant species declines, the value of the marginal species increases exponentially toward  $\frac{\lambda}{r}(pR - c) =$ \$189,360 (when n = 0). The relationship between n and habitat implied by the areaspecies curve described in (3.3) is similarly illustrated in figure 3, which shows the number of endemic species remaining in the Western Ecuador hotspot as the forest area shrinks. The number of endemic species decreases at an increasing rate as habitat loss progresses.

Figure 2: Value of the marginal species as a function of the number of candidate species, as implied by the SSR model evaluated at  $p^*$ 



The value of conserving land for bioprospecting purposes is therefore a function of expected habitat loss in the current period. If industry expects to observe deforestation of 1,000 hectares of tropical forest in  $H_i$  in period t, the value of the marginal hectare is the difference between the value of the collection of species supported by  $A_i - 1,000$  hectares of habitat and  $A_i - 999$  hectares of habitat. Put another way, the value of the marginal hectare to be preserved is the value of the last, not the first, hectare that would otherwise be lost in a given period.

Another consideration is that the number of candidate species to be tested is presumably decreasing over time. The number of endemic species supported by the Myers hotspots

Figure 3: Number of endemic higher plant species in Western Ecuador as a function of the forest area, as predicted by the area-species curve



decreases as habitat loss occurs. There will also be extinction of higher plant species outside of these hotspots. Finally, species will be eliminated for consideration for pharmaceutical uses through the research process.

The framework developed in the previous sections can be modified to address these concerns. Assume that  $d_{it}$  is the realization of habitat loss in hotspot *i* in period *t*. Let  $U_t$  be the research-based updating (contraction) of the pool of potentially beneficial higher-plant species.  $X_t$  represents the extinction of useful species taking place outside of the forested areas under consideration for conservation, and  $n_{t-1}$  is the number of potentially useful species to have survived the last period. The per-hectare value of preventing deforestation in area i at time t is

$$MHV_{it} = \frac{\lambda}{r}(pR - c)(1 - p)^{\tilde{n}_t}e_i\alpha_i[(A_{it} - E[d_{it}] + 1)^Z - (A_{it} - E[d_{it}])^Z], \qquad (4.1)$$

where  $\tilde{n}_t$  is the expected number of useful species surviving the current period:

$$\tilde{n}_t = n_{t-1} - \sum_{i=1}^q e_i \alpha_i [A_{it}^Z - (A_{it} - E[d_{it}])^Z] - U_t - X_t.$$
(4.2)

For simplicity, the notation necessary to represent the impact of spatial correlation given in equation (3.6) is suppressed here.

The results of two applications of this model to the Myers hotspots are shown in Table 3. The parameter values given in Simpson *et al.* are again used here, and  $U_t + X_t$  is assumed to be 10,000 species. In the second column, the willingness to pay for the marginal hectare if expected habitat loss is two percent of the current hotspot area is given for  $\rho = 0.001$ . This is likely to be a conservative estimate; e.g., Whitmore and Sayer (1992) estimate that 17 million hectares of humid tropical forests are lost each year. The estimates given here are 15–20% larger than those from the correlation model without expectation of habitat loss, extinction, and scientific progress (reported in the final column of Table 1).

The final column reports the conservation value of the last remaining hectare of each biodiversity hotspot, calculated by assuming that the entire habitat area is threatened in the current period. These figures are obviously not representative of the amount of money firms are likely to provide toward habitat conservation. They represent instead an extreme upper bound on the likely bioprospecting returns to any one hectare in each hotspot.

Table 3: Willingness to Pay to Preserve the Marginal Hectare in 18 Biodiversity Hot Spots,Assuming Expected Loss of Habitat in the Current Period

	WTP Given Expected	WTP for the
Biodiversity "Hot Spot"	2% Habitat Loss	Last Hectare
	$(\rho = 0.001)$	$(\rho = 0)$
Western Ecuador	\$673	$$1,\!479,\!947$
Southwestern Sri Lanka	\$2,947	$$465,\!027$
New Caledonia	\$1,628	607,524
Madagascar	\$109	$$1,\!392,\!597$
Western Ghats of India	\$274	$\$819,\!456$
Philippines	\$278	800,133
Atlantic Coast of Brazil	\$30	$$1,\!508,\!540$
Uplands of Western Amazonia	\$16	$$1,\!345,\!077$
Tanzania	\$353	286,998
Cape Floristic Province of South Africa	\$1	\$1,738,829
Peninsular Malaysia	\$84	611,717
Southwestern Australia	21	885,702
Ivory Coast	\$271	$$116,\!640$
Northern Borneo	\$20	$\$804,\!217$
Eastern Himalayas	\$31	$$695,\!363$
Colombian Choco	\$22	$$672,\!580$
Central Chile	\$51	$$473,\!654$
California Floristic Province	\$7	\$458,829

Source: Myers (1988, 1990) and author's calculations. Willingness to pay (WTP) values are given in dollars per hectare. All calculations assume U + X = 10,000 and p = 0.000012.

## 5 Conclusion

The calculations reported above should not be interpreted as definitive estimates. Rather, they are intended to illustrate the potential impact of spatial correlation and the expectation of future habitat loss on the amount of money that pharmaceutical companies may be willing to invest in land conservation. The findings of Simpson *et al.* — that the incentives provided by biopharmaceutical prospecting for habitat conservation are vanishingly small — are shown to be sensitive to these considerations.

The earliest studies of the potential returns to bioprospecting found extremely high values for higher plant species. Farnsworth and Soejarto (1985) estimated \$1.5 million *per year* in lost pharmaceutical revenues for each extinct species (in 1980 dollars). Principe (1989) estimated that each extinction resulted in \$300,000 in foregone drug revenues. These studies evaluated the returns to the average species which, as Simpson *et al.* note, are not appropriate for determining industry's willingness to pay for conservation. When compared to these earlier estimates, the issues raised in this paper may appear to be merely fussing around the edges. The significance, however, is that these considerations can make the difference between viable market-based biodiversity protection programs and a conservationist's failed pipe dream.

It should be noted that certain implicit assumptions of this study may also influence industry's willingness to pay for conservation considerably. For example, the models outlined here assume perfect substitution of compounds that prove beneficial for a given use. In actuality, the extracts of different plants may vary widely in their quality. Competition between firms has also not been considered here. As Rausser and Small note, firms may have "an incentive to acquire options defensively, to keep them from the hands of competitors." The interaction of imperfect substitution and competition may also provide further motivation for conservation, in that if one drug performs the same basic task as another but is clearly superior in some way (e.g., fewer side effects, higher efficacy), the company which develops the superior product may soon capture all of the sales in that field, even if they were not first to market. These considerations would tend to increase firms' willingness to pay. In contrast, the availability of *ex situ* conservation measures, such as genetic libraries, may reduce the incentive to pay for habitat conservation.

The casual reader should be reassured that none of these estimates purport to be a complete accounting of the value of biodiversity. The focus here has been merely on what pharmaceutical companies driven purely by concerns of maximizing profits from drug sales may be willing to invest in conservation. The value of biodiversity to ecological services, research for other industries, ecotourism, ethical considerations, carbon sequestration, etc. are not addressed here. Moreover, this paper considers only the private — not social — returns to biopharmaceuticals. The development of new drugs can provide surplus to consumers that far outweighs industry profits, which in turn warrants a greater commitment to conservation of genetic resources than computed here.

#### Appendix: Derivation of Expression 3.2

Consider two random variables  $I_j, I_k \in \{0, 1\}$ , where  $prob(I_j = 1) = prob(I_k = 1) \equiv p$ and  $corr(I_j, I_k) \equiv \rho$ . By definition,

$$\rho = \frac{cov(I_j, I_k)}{\sqrt{var(I_j)var(I_k)}}$$
(A.1)

Inserting the definitions of variance and covariance yields

$$\rho = \frac{E[I_j I_k] - E[I_j] E[I_k]}{\sqrt{(E[I_j^2] - (E[I_j])^2)(E[I_k^2] - (E[I_k])^2)}}$$
(A.2)

Note that  $E[I_j] = E[I_k] = p$  and  $E[I_j^2] = E[I_k^2] = p$ . The expectation of  $I_jI_k$  is perhaps less obvious. Since  $I_j$  and  $I_k$  can only take on two values — 0 or 1 — their product is non-zero only when  $I_j = I_k = 1$ . The probability of this outcome is

$$prob(I_j = 1 \cap I_k = 1) = prob(I_k = 1|I_j = 1)prob(I_j = 1) = prob(I_k = 1|I_j = 1)p$$
 (A.3)

The expectation of  $I_j I_k$  is therefore

$$E[I_j I_k] = 0 \times prob(I_j I_k = 0) + 1 \times prob(I_k = 1 | I_j = 1)p = prob(I_k = 1 | I_j = 1)p$$
(A.4)

Inserting these expectations into (A.2) yields

$$\rho = \frac{prob(I_k = 1|I_j = 1)p - p^2}{p - p^2}$$
(A.5)

Rearranging terms and solving for  $prob(I_k = 1 | I_j = 1)$  yields the expression given in (3.2):

$$prob(I_k = 1|I_j = 1) = \frac{\rho(p - p^2) + p^2}{p} = \rho(1 - p) + p$$
(A.6)

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