Supporting Text

We provide a basic overview of supply and demand for readers not familiar with this material. In Fig. 1, the upward sloping supply curve indicates the quantity of land of conservation interest that could be provided for development at a given price. Specifically, suppose every landowner in the area who currently owns such land has their own "reservation price," which is the minimum compensation they would need to give up their property. If we arranged the landowners in order of increasing reservation price, the supply curve would show the cumulative distribution.

The demand curve shows the maximum willingness of developers to pay for each acre of land. No developer can afford land that costs more than some "choke price." However, just below this price, a small number of particularly profitable developers are willing to pay a great deal per acre. As the price drops, an increasing number of developers are willing to purchase land, which leads to the downward-sloping demand curve. Many factors will determine the particular shape of the demand curve, such as the availability of substitutes for land for development.

The assumption of perfect competition ensures the market equilibrates at point (q_1, p_1), where the supply and demand curves intersect. In this equilibrium, q_1 acres that were initially of conservation interest are developed, each fetching fixed price p_1. Although many landowners would have been willing to allow development of their land for less (those to the left of q_1), competition between developers drives up the market price. The price equilibrates at p_1, because some developers can no longer afford land and drop out of the market as the price rises. Properties falling to the right of q_1 are worth more as open land than the available market price and remain undeveloped.

To illustrate, we assume linear supply and demand in Fig. 1,

$$p = m_{\mathrm{s}} q + p_{\mathrm{s}} \quad \text{and} \quad p = m_{\mathrm{d}} q + p_{\mathrm{d}}\,, \qquad \textbf{[1]}$$

where p is the price, q is the quantity of initially available land demanded or supplied, slopes

m_{s} and m_{d} are the inverse sensitivities of supply and demand, and intercepts p_{s} and p_{d} are the minimum reservation price of current landowners and the choke price, respectively. In this case, the basic market equilibrium is

$$q_1 = \frac{p_{\mathrm{d}} - p_{\mathrm{s}}}{m_{\mathrm{s}} - m_{\mathrm{d}}} \quad \text{and} \quad p_1 = \frac{m_{\mathrm{s}} p_{\mathrm{d}} - m_{\mathrm{d}} p_{\mathrm{s}}}{m_{\mathrm{s}} - m_{\mathrm{d}}} . \qquad \textbf{[2]}$$

The conservation value of the resulting landscape would be $\alpha(A - q_1)$, where A is the total area initially of conservation interest.

We consider the counterfactual situation in which a conservation group also competes in the land market and has a budget B to spend on reserves. If the conservation group buys land titles outright, its demand curve is $B = pq$. We can construct an aggregate demand curve (Fig. 1) that includes the conservation group and developers by horizontal addition of their respective individual demand curves. For example, with the development demand from Eq. **[1]**, the aggregate demand curve is

$$p = \begin{cases} \frac{1}{2}(m_{\mathrm{d}} q + p_{\mathrm{d}} + ((m_{\mathrm{d}} q + p_{\mathrm{d}})^2 - 4 m_{\mathrm{d}} B)^{1/2}) & \text{if} \quad p < p_{\mathrm{d}} \\ B/q & \text{otherwise} . \end{cases} \qquad \textbf{[3]}$$

Assuming that some development is worthwhile ($p < p_{\mathrm{d}}$) and supply is linear once again (Eq. **[1]**), then the new equilibrium price is given by the intersection of the aggregate demand curve and the supply curve,

$$p_2 = \frac{1}{2}\left(p_1 + \left(p_1^2 - \frac{4 m_{\mathrm{s}} m_{\mathrm{d}} B}{(m_{\mathrm{s}} - m_{\mathrm{d}})}\right)^{1/2}\right) . \qquad \textbf{[4]}$$

From this new price, we can find the total amount of land purchased $q_2 = (p_2 - p_{\mathrm{s}})/m_{\mathrm{s}}$, which can be partitioned into the amount purchased by developers, $q_{\mathrm{d}} = (p_2 - p_{\mathrm{d}})/m_{\mathrm{d}}$, and by the conservation group for reserves, $q_{\mathrm{c}} = B/p_2$. The remaining area of open land will be $A - q_2$. The conservation value of the resulting landscape is thus $q_{\mathrm{c}} + \alpha(A - q_2)$.

The conservation improvement offered by the investment is

$$\begin{aligned} \Delta C &= q_{\rm c} + \alpha(A - q_2) - \alpha(A - q_1) = q_{\rm c} + \alpha(A - (q_{\rm d} + q_{\rm c})) - \alpha(A - q_1) \\ &= (1-\alpha)q_{\rm c} + \alpha(q_1 - q_{\rm d})\,. \end{aligned} \qquad \textbf{[5]}$$

Also, $\Delta C = q_{\rm c} - \alpha(q_2 - q_1)$, and so, provided open land has some value for biodiversity ($\alpha > 0$), the conservation improvement offered by the investment is less than the value of the area set aside as reserves.

Ecological Heterogeneity

To produce Fig. 3, we assumed there were initially 60 undeveloped parcels, each associated with a unique list of species or populations of conservation interest, and that in the absence of conservation investment, 50 of these properties would be developed. We discretized supply and demand and assumed the reservation prices and demand for development were independent of the biodiversity value of particular properties.

Over relatively small scales, interspecific occupancy patterns from a wide range of taxonomic groups are characterized by bimodality, with peaks occurring for both rare and common species (1). For each simulation run, site occupancy lists for each of 400 species were randomly generated in a way that accounted for this pattern. First, the occupancy-extent of each species was assigned from a β-distribution with its mean and variance matched to occupancy data for breeding birds across 391 tetrads (2 km x 2 km) from Berkshire, U.K. (2). Then, for each species a list of occupied sites was drawn at random until this occupancy extent had been exhausted. A fraction, α, of randomly selected species were assumed able to persist on open land. The remaining species were assumed to be only able to persist inside reserves. No species of conservation concern was assumed able to persist in developed areas.

In the main text, Fig. 3 shows the results when $\alpha = 1$ and open lands and reserves are of equal value to biodiversity. The equivalent figures when $\alpha = [0, 1/3, 2/3]$ are shown in Figs. 5-7, respectively. As α is decreased, the change in the number of species that will persist with investment over the baseline that persist with no conservation investment increases. It increases, because the only way in which a growing fraction of species can persist is if the conservation group acquire properties to set aside as reserves. Also, as α tends to zero the distinction between the ecological-economic strategy and the maximal coverage strategy disappears, because there is no longer any additional benefit to considering the impacts of conservation investments on biodiversity in the wider landscape. Finally, as predicted with the deterministic models, the importance of the slopes of supply and demand is diminished when α becomes small.

Optimal Allocation Across Land Markets

To illustrate how variation in supply and demand should determine conservation priorities over larger scales, we examine the optimal allocation of a fixed budget across two distinct land markets. For brevity, we restrict attention to the case where $\alpha = 1$. An additional subscript signifies the relevant location; e.g., the equilibrium in market i with no investment is $(q_{1\mathrm{i}}, p_{1\mathrm{i}})$.

We assume linear dynamics as before, but we now need to account for the possible displacement of development pressure across land markets. We represent development demand and the supply of land as

$$\mathbf{p} = M_{\mathrm{d}}\mathbf{q} + \mathbf{p}_{\mathrm{d}}\,, \qquad \mathbf{p} = M_{\mathrm{s}}\mathbf{q} + \mathbf{p}_{\mathrm{s}}\,, \qquad \textbf{[6]}$$

in vector notation.

Here, the elements of inverse development demand matrix M_{d}^{-1} determine the change in the quantity of land demanded in market i, Δq_{i}, as a consequence of a change to the price in market j, Δp_{j}. For example, although an increase in the price of land in market i would decrease local development demand, it might increase development pressure in market j. We assume that the proximity of the two land markets determines when such spilllovers of development occur and measure proximity with parameter γ. We represent the inverse demand matrix with

$$M_{\mathrm{d}}^{-1} = \begin{bmatrix} \Delta q_1/\Delta p_1 & \Delta q_1/\Delta p_2 \\ \Delta q_2/\Delta p_1 & \Delta q_2/\Delta p_2 \end{bmatrix} = \begin{bmatrix} -1-\gamma & \gamma \\ \gamma & -1-\gamma \end{bmatrix}, \qquad \textbf{[7]}$$

We assume that there are other substitutes for land for development available in the broader economy (accounted for by the -1 term in the diagonal elements). In addition, we assume that the nearer the markets are to one another the more likely a price rise in market i is to displace development pressure on to market j. I.e., the diagonal elements become more negative (local demand undergoes a larger decrease with a local price rise) and the off-diagonal elements more positive (demand elsewhere undergoes a larger increase with a local price rise) the nearer the markets are to one another. With this formulation, the overall change in development demand resulting from a price increase $(\Delta q_1 + \Delta q_2)/\Delta p_{\mathrm{i}}$ remains constant.

We illustrate the case where there are no supply-side spillovers, meaning that M_{s} is diagonal, perhaps because reservation prices for open lands are set primarily by global prices for agricultural commodities. To produce the figures, we set M_{s} equal to the identity matrix.

The amount of land facing development in each market in the absence of conservation investment is given by

$$\mathbf{q}_1 = (M_{\mathrm{d}} - M_{\mathrm{s}})^{-1}(\mathbf{p}_{\mathrm{s}} - \mathbf{p}_{\mathrm{d}})\,. \qquad \textbf{[8]}$$

The amount facing development or set aside as reserves given a particular allocation of conservation funds $\mathbf{B} = [B_1, B_2]^T$ can be found from solving

$$M_{\mathrm{d}}^{-1}(\mathbf{p}_2 - \mathbf{p}_{\mathrm{d}}) + \left[\begin{array}{c} B_1/p_{21} \\ B_2/p_{22} \end{array}\right] = M_{\mathrm{s}}^{-1}(\mathbf{p}_2 - \mathbf{p}_{\mathrm{s}})\,. \qquad \textbf{[9]}$$

The number of species in each land market is assumed to be given by a species-area relationship, $S_{\mathrm{i}} = c_{\mathrm{i}}(A_{\mathrm{i}} - q_{\mathrm{di}})^{z_{\mathrm{i}}}$, where larger c_{i} and z_{i} values indicate greater biodiversity per unit area. Here A_{i} is the total land area initially of conservation interest and we let $T_{\mathrm{i}} = c_{\mathrm{i}} A_{\mathrm{i}}^{z_{\mathrm{i}}}$ denote the size of the original species pool. If the land markets are near one another then we should expect considerable overlap in the species' assemblages. We let Γ signify the number of shared species in the original communities. Then, if we assume no biases in the species "sampled" by conservation investments, the total number of species that will persist in the landscape is

$$S = S_1 + S_2 - \Gamma \frac{S_1}{T_1} \frac{S_2}{T_2} \,. \qquad [\mathbf{10}]$$

The optimal allocation of the conservation budget ($B = B_1 + B_2$) maximizes S.

If we first restrict attention to isolated land markets ($\Gamma = \gamma = 0$), we see that our single market predictions generalize; all else being equal, land markets where the demand curve is flat or the supply curve is steep should be investment priorities (Fig. 8).

However, the level of supply and demand also matter, because these determine the underlying market equilibrium $(\mathbf{p}_1, \mathbf{q}_1)$ and, hence, the overall cost of buying reserves and the distribution of threats to biodiversity. Variations in the underlying market price can arise both from variations in the level of demand and the level of supply (Fig. 9). When it is the level of development demand that varies across land markets, we face an inevitable trade-off between cost and threat in conservation priority setting; in Fig. $9a$, biodiversity is most threatened in region 2 where land is most expensive. The optimal allocation of investments across land markets in this case is equivocal (Fig. $10a$). However, if variations in land prices arise from variations in the levels of supply (Fig. $9b$), perhaps because of variability in land rents derived from biodiversity-friendly production, then biodiversity is most threatened where land can be acquired most cheaply. In this case, the optimal allocation of investment is more clear-cut (Fig. $10b$), because our conservation dollars will go furthest where they are most needed.

The underlying biodiversity value of markets will differ. As one would expect, more speciose areas should be investment priorities. However, the degree of community overlap is also important. When the two areas share few species, a distributed investment ($B_1, B_2 > 0$) is favored for a larger region of parameter space. However, the optimal allocation strategy becomes an either/or one if we relax our assumption that the two land markets are isolated and gradually increase proximity (by increasing γ and Γ).

We used our two land market models to examine the optimal conservation strategy when the distribution of reserves differentiates markets for developers. Specifically, we used inverse demand matrix

$$M_{\mathrm{d}}^{-1} = \begin{bmatrix} -1-\gamma(1-\epsilon|q_{\mathrm{c}}(2)-q_{\mathrm{c}}(1)|) & \gamma(1-\epsilon|q_{\mathrm{c}}(2)-q_{\mathrm{c}}(1)|) \\ \gamma(1-\epsilon|q_{\mathrm{c}}(2)-q_{\mathrm{c}}(1)|) & -1-\gamma(1-\epsilon|q_{\mathrm{c}}(2)-q_{\mathrm{c}}(1)|) \end{bmatrix}. \qquad \textbf{[11]}$$

Suppose the conservation group establishes more reserves in one land market. The difference in reserve creation could result in land elsewhere becoming a poorer substitute for local land in the development process than one would expect based on proximity alone. The parameter ϵ determines the importance of nature reserves and conservation amenities in determining substitutability of land for development across the markets relative to other factors. To focus attention on differentiation of the markets, we first maintained the same overall level of demand, as represented by $(\mathbf{q}_1, \mathbf{p}_1)$.

We also considered the situation where establishing reserves opened up new opportunities to developers and could attract additional development pressure. To represent this scenario, we replaced the underlying market equilibrium $(\mathbf{q}_1, \mathbf{p}_1)$ with $(\mathbf{q}_1 + \nu\mathbf{q}_{\mathrm{c}}, M_{\mathrm{s}}(\mathbf{q}_1 + \nu\mathbf{q}_{\mathrm{c}}) + \mathbf{p}_{\mathrm{s}})$, while also accounting for the change in substitutability of land as before.

To produce Figs. 4, 11, and 12, we assumed the spatial scales over which economic and ecological interactions between the land markets played out were related to each other by $\gamma/4 = \Gamma/\min(T_{\mathrm{i}})$. We also assumed that the strength of changes to substitutability across the land markets and of overall levels of demand when considering new development opportunities were linearly related, $\nu = 4\epsilon$ in Figs. $4b$ and 12.

We illustrate the effects of assuming that conservation investments differentiate the two markets and open new opportunities for developers for a given investment strategy in Figs. 11 and 12, respectively. If conservation investments have no impact on the substitutability of land in each market for development, then the two prices converge with increasing proximity (solid curves in Fig. 11 a and b). However, if variations in the level of conservation investment differentiate the markets, then the effect of proximity in equalizing prices is tempered. Now, the displacement of development pressure across land markets is only partial and two distinct prices can be maintained once more (dashed, dot-dash, and dotted curves in Fig. 11 a and b respectively).

These dynamics determine the amount of land developed, q_{di}, and set aside as reserves, q_{ci}, in each market (Fig. 11 c-f). Consider the case illustrated where conservation investment is concentrated in market 2. When variation in the distribution of reserves is unimportant to developers (solid curves for $\epsilon = 0$), development pressure redistributes itself across the markets in such a way that an increasing amount of land faces development in market 1 and a decreasing amount in market 2, as proximity is increased. This effect is moderated by increasing ϵ values.

The variation in prices with changes to substitutability have consequences for how much land can be bought for conservation with a given level of investment (Fig. 11 e and f). When development demand is unresponsive to conservation investment levels, conservation funds stretch further in market 2 where investments are concentrated, because the conservation group no longer have to work against price increases that result from increased local demand. Instead, some of that price increase is dispersed to market 1, where less land can be purchased as a result. These effects are also tempered when land in market 1 is considered a poor substitute for land in market 2, because of variation in levels of conservation investment.

Finally, Fig. 12 shows the analogous results for the case where establishing reserves create new development opportunities and attracts increased development pressure, as well as serving to differentiate the two markets for developers. As discussed, when developers are unresponsive to conservation investment (solid curves in Fig. 12; $\epsilon, \nu = 0$) prices equalize with increased proximity with knock-on effects for $\mathbf{q}_{\mathrm{d}}$ and $\mathbf{q}_{\mathrm{c}}$. However, as both ϵ and ν increase, price differences are no longer dispersed. Moreover, the additional local development demand attracted by establishing reserves exaggerates price differences (especially in market 2, which enjoys greater conservation investment) with associated consequences for q_d and q_c.

1. Gaston, K. J. & Blackburn, T. M. (2000) *Pattern and Process in Macroecology* (Blackwell Science, Oxford).

2. Standley, P., Bucknell, N. J., Swash, A. & Collins, I. D. (1996) *The Birds of Berkshire* (Berkshire Atlas Group, Reading, U.K.).