Appendix 1. A sustainability framework for assessing trade-offs in ecosystem services.

Example 1. An efficiency frontier for biodiversity and agricultural productivity

Here, a trade-off is apparent between the biodiversity or species richness (S; a supporting ecosystem service or ecological function) that can be sustained from land area in natural habitat (A_H) on the one hand, and the agricultural production (P; a provisioning service) that can be derived from land area dedicated to crops (A_C) which is the provisioning service, on the other hand. The conceptual basis for this trade-off is well-grounded in empirical relationships between habitat area and species richness, originally harnessed in the development of the theory of island biogeography (MacArthur and Wilson 1967). The mathematical expression takes into account the total land area (A_T) that can be partitioned between habitat (A_H) and crop (A_C) production such that

$$A_T = A_H + A_C. \tag{1.1}$$

Both species richness and agricultural production are a function of area such that

$$S = \alpha A_H^z \text{ and } P = \beta A_C, \tag{1.2}$$

where z is the slope of the log-log relationship between S and A_H, α is a constant (y-intercept) and β is the crop yield per unit area. Note that z, α and β are context dependent and must be empirically determined. The relationship between species richness (S) and agricultural production (P) can thus be written as:

$$S = \alpha(1-P/\beta)^z \tag{1.3}$$

and visualized in Fig. 1A for two contrasting biophysical contexts.

Superimposing human preferences on the efficiency frontier

Utility represents the benefit or contribution to well-being of ecosystem services. We can define a utility function (U) that describes the willingness of consumers to give up a unit of a provisioning ecosystem service, x (e.g., agricultural productivity) for more of another ecosystem service, y (e.g., biodiversity), such that

$$U(x,y) = \Phi \ln x + \boldsymbol{\psi} y \tag{1.4}$$

Where Φ is the loss of biodiversity attributable to provisioning of agricultural productivity and $\boldsymbol{\psi}$ is the marginal utility, or the added benefit of an additional unit of biodiversity. Parameters Φ and $\boldsymbol{\psi}$ can be assigned to allow the curve to approximate empirically determined preference combinations. Increasing levels of utility for a given stakeholder (Fig. 1B) can be superimposed on the efficiency frontier, as in Figure 1C, to show which of the biophysically possible outcomes provides highest utility for a given stakeholder.

Example 2. Water quality and agricultural productivity

We assume that crop production (P; for example, bushels of corn per year) is enhanced by the application of nitrogen fertilizer according to a monod function such that P depends on the maximum production rate (P_{max}), the quantity of nutrients applied (N), and the half saturation constant of P_{max} (h_P), such that

$$P = P_{max}\,(N/N+h_P). \tag{2.1}$$

The function depends in part on the spatial and temporal precision of fertilizer application, which can influence both P_{max} and h_P; enhanced timing of fertilizer addition to coincide with early summer corn growth has been shown in many cases to increase nutrient use efficiency and crop productivity (Tran, Giroux et al. 1997; Ma, Ying et al. 2003; Scharf and Lory 2009). The relationship between agricultural productivity and nutrients applied is shown in Fig. 3A by the black line.

The red line shows the curve that results with greater precision in fertilizer addition aided by technological advances. Nutrients taken up and stored by the terrestrial ecosystem (Fig. 2B) are represented by a monod function in which N_{max} represents the maximum nutrient uptake and h_N is the half saturation constant.

$$N_{storage} = N_{max} (N/N+h_N). \tag{2.2}$$

The extent to which applied nutrients (N) are taken up or leaked into neighboring shallow water bodies (Fig. 3C) depends on the efficacy of plant uptake, soil adsorption and land-use management, which are reflected in the N_{max} and h_N parameters. Shifts in human land-management practices, such as inclusion of riparian buffer strips and cover crops are known to increase ecosystem nutrient storage and reduce nutrient runoff (Gilliam 1994; Lowrance, Altier et al. 1997; Anbumozhia, Radhakrishnanb et al. 2005; Smukler, O'Geen et al. 2012) as we simulate in Fig. 2B. Two different management practices are shown, one in which ecosystem nutrient storage is low (black line) and one in which it is high (blue line).

Nutrient runoff in the water (N_{water}) is a function of the maximum nutrient uptake of the terrestrial system ($N_{storage}$), as above, the half saturation constant (h_N) of N_{max} and the quantity of nutrients applied to crops (N), such that

$$N_{water} = \alpha (N - [N_{max} (N/N+h_N)]. \tag{2.3}$$

We use this function in Fig. 2C to simulate nutrient runoff in relation to applied nutrients for the two cases in which terrestrial ecosystem nutrient storage is high (blue line) and low (black line).

Water quality in shallow lakes depends on the growth of algae that cause turbidity (Keeler, Polasky et al. 2012). Water quality (W), the regulating service of interest, is negatively proportional to algal population size (A). The increased amount of nutrients into waterways causes algal growth, turbidity increase and water quality decline. Water quality was modeled as a function of algal growth, nutrients in the water, and growth of aquatic plants by Scheffer (1990) and Scheffer et al (1993). The model is based on the observations that: 1) algal growth, and hence turbidity, increase with nutrient enrichment, but aquatic plants are less affected; 2) vegetation growth has a negative effect on turbidity by reducing re-suspension of bottom material and providing refuge for zooplankton grazers; and 3) vegetation area declines with turbidity in a sigmoidal way due to light extinction. The complex relationship between water nutrient concentration and algae populations (Fig. 3D) depends on various simple relationships. Algal growth (dA/dt) is basically logistic and depends on the intrinsic growth rate of algae (r) and the population size (A). Growth increases with nutrient concentrations (N) and decreases with vegetation (V) in a monod fashion with the half-saturation constants for nutrients (h_N) and for vegetation (h_V). There is a negative effect of competition on algal growth that increases with algal population size (A) and the strength of the competition coefficient (c).

$$\frac{dA}{dt} = rA\left(\frac{N}{N+h_N}\right)\left(\frac{h_V}{V+h_V}\right) - cA^2 \qquad (2.4)$$

Vegetation abundance is a negative sigmoidal function of algal biomass (A^p)

$$V = \frac{h_A^p}{A^p+h_A^p} \qquad (2.5)$$

where h_A^P is a half saturation constant and p is a power that shapes the relationship. Water quality can then be related directly to agricultural productivity for three scenarios in Fig. 3E: using precision agriculture where agricultural productivity is high for a given amount of nutrients added (red curve), where terrestrial ecosystem storage of nutrients is high, prevent some of the runoff into waterways (blue line) and where agricultural productivity and ecosystem nutrient storage are comparatively low for a given amount of nutrients added (black line).

Variability in ecosystem nutrient storage and leakage as the result of soil, vegetation and landscape features, human management practices and climatic variability results in high variability in the efficiency frontier for the tradeoff between water quality and agricultural productivity (Fig. 3F). It may thus be difficult to manage for optimal outcomes without exceeding sustainability limits with resulting in diminished ecosystem service benefits (low utility).

Example 3. Ecosystem biomass and cattle density

The mathematical expression of the tradeoff includes a primary producer growth function, based on Lotka-Volterra,

$$dB/dt = rB(1-B/K), \tag{3.1}$$

where B is the ecosystem biomass, r is the intrinsic growth rate and K is the carrying capacity. Consumption (dB/dt) is an indicator of the cattle provisioned per unit time. It can be represented by a saturating function that depends on the consumer density (number of cattle), such that

$$dB/dt = \gamma DB^2/(\lambda+B^2), \tag{3.2}$$

where D is density of consumers (cattle), and γ is the efficacy of consumption. Once consumption has reached a threshold (λ), resource needs are met and consumption stays constant, even if resources continue to increase. When a saturating consumption function is coupled with logistic growth of the resource, the steady-state solution can (but does not always) yield the tradeoff surface shown in Figure 4A (black line), with two alternative vegetation states possible for a range of cattle density. Once the steady-state solution for the primary resource growth and consumption functions has been found, the tradeoff surface for ecosystem services can be replotted to represent rates or stocks of the provisioning service. For example, if the rate of provisioning (milk production rate) is desired rather than the stock (the cattle density), the trade-off surface will take a different form, but will represent the same underlying dynamics.

Population growth of cattle is regulated by ecosystem biomass (B), as well as density dependent effects. Cattle population regulation may occur according to various plausible mechanisms. The change in cattle density (dD/dt) can be described as an exponential growth function (r_2D) that is regulated in various possible ways by biomass loss due to consumption, which is a function of cattle density. Two possibilities are shown:

$$\frac{dD}{dt} = r_2 D - \frac{\lambda \tau \mathbf{D}}{\lambda + B^2} \tag{3.3}$$

$$\frac{dD}{dt} = r_2 D \left(1 - \frac{D}{\lambda + B^2}\right) \tag{3.4}$$

The steady state population density of cattle (dD/dt = 0) is constant with increasing ecosystem biomass in the first case (red line, Fig. 4A) and increases with increasing ecosystem biomass in the second (red line, Figure 4C). The dynamics of the system are thus driven by the interacting tendencies of the biomass growth and the cattle population growth, which may result in highly fluctuating ecosystem functions/services (Fig. 4B), or very low services at equilibrium (Fig. 4D).

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