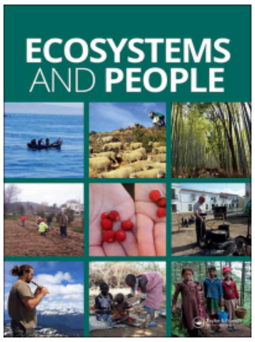

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Substitutability of natural and human capitals: lessons from a simple exploratory model

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ABSTRACT

Most ecosystem services (ES) are co-produced, to varying degrees, by interactions between people and ecosystems. Although ES research has tended to emphasize the role of ecosystems, or natural capital, in ES provision, the need for a deeper understanding of the role of human-derived capitals, like technology, labour, and management, is increasingly being recognized. Understanding the capacity for, and limitations of, human-derived capitals to enhance or substitute for natural capital is important for environmental decision-making, especially for decisions about when to promote conservation of natural capital to provide ecosystem services and when to employ technological alternatives. From the perspective of long-term sustainable ecosystem management, such decisions are further complicated by dynamics and interactions between different types of capital. We created a simple simulation model to compare how different assumptions around the temporal dynamics and interactions between natural and human-derived capitals affect long-term outcomes of different management choices on ES provision. We found that the extent to which different capitals are substitutable in the long-term depends on how individual capitals change over time and how different capitals interact with each other, and that replicating the near-term function of natural capital does not necessarily mean human-derived capitals are a viable long-term substitute. With an understanding of the dynamics and interactions of natural and human-derived capitals, it is possible to determine general long-term ES management strategies that are more likely to produce the desired benefits.

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Ecosystem service; co-production; management; technology; natural capital; sustainability

1. Introduction

Although the concept of ecosystem services (ES) is inherently linked to nature and ecosystems, functionally nearly all ecosystem services are the outcome of interactions between people and nature (Spangenberg et al. 2014; Díaz et al. 2015; Palomo et al. 2016). On one hand, the provision of ES is fundamentally tied to ecosystem components, structures, and functions, or 'natural capital', such as specific species, biodiversity, or biogeochemical cycles. On the other hand, the provision of many ES is influenced by or mediated through a wide variety of non-natural capitals, which we refer to collectively as 'human-derived capitals', including machinery, infrastructure, labour, or specific management practices. The interaction of natural and human-derived capitals to provide ES is known as co-production (Palomo et al. 2016).

In part due to its origins as an instrument for promoting environmental conservation (Gómez-Baggethun et al. 2010), ecosystem service research has tended to emphasize the role of natural capital while obscuring the role of anthropogenic factors that influence ES provision (MA 2005; IPBES 2019). However, as the concept of ES has become more prominent in sustainable development, the need for a more complete understanding of both the natural and human sides of ES co-production has become clearer. A past focus on the natural drivers of ES provision has risked over-promising or under-delivering benefits to people in contexts where natural and human-derived capitals depend on or influence each other (Palomo et al. 2016; Rieb et al. 2017; Mastrángelo et al. 2019).

Understanding when, where, how, and to what extent human-derived capitals can be used in place of, or alongside, natural capital to enhance ES provision is important for ES management, as many ES management decisions involve choices between preserving or restoring natural capital versus purchasing, constructing, or implementing human-derived alternatives (Morandin et al. 2016; Davies and Lafortezza 2019). For instance, water system managers can choose between constructing treatment plants (HC) or investing in watershed conservation (NC) for purifying drinking water (Chichilnisky and Heal 1998; Blanchard et al. 2015), farmers can use both man-made fertilizers (HC) and ecologically-based practices like green manures and crop rotations (NC) for

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nutrient management (Wu and Ma 2015), and coastal communities can reduce flood risk with seawall construction (HC) or mangrove restoration (NC; Barbier 2016). In other cases, people can benefit from the simultaneous use of multiple complementary forms of capital, such as by combining crop varieties developed to be resistant to climate change (HC) with conservation agriculture practices (NC) to achieve greater productivity than either in isolation (Makate et al. 2019). The range of choices managers have is likely to vary by ecosystem service, with some, like agriculture, offering a wide range of management strategies and others, like spiritual practices tied to particular places or species, depending heavily on specific types of natural capital.

Both natural and human-derived capitals have their own advantages and trade-offs for ES management. Human-derived capitals often have the advantage of providing specific benefits in a more rapid, portable, controllable, and predictable way (Guerry et al. 2015). On the other hand, there is growing interest in natural capital-based management (e.g. Faivre et al. 2017; TNC 2019), which tends to provide multiple benefits that simultaneously support different aspects of wellbeing for diverse groups of people (Moberg and Rönnbäck 2003; Raudsepp-Hearne et al. 2010). If well managed, natural capital also tends to be self-sustaining and resilient to a reasonable range of disturbances (Ekins et al. 2003). Both natural and human-derived capitals carry different practical and logistical considerations, such as cost and availability, and both may require technical expertise to deploy them for the provision of ES. In order to weigh all these criteria and choose the best management strategy for a particular context, it is essential that decision makers are able to accurately estimate how much ES provision they can expect to receive from a variety of combinations of natural and human-derived capitals.

Various efforts have been made to develop conceptual frameworks of ES that explicitly integrate human-derived capitals (Reyers et al. 2013; Jones et al. 2016). For example, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) conceptual framework that includes both natural capital and 'anthropogenic assets' (Díaz et al. 2015), and the framework by Fedele et al. (2017) that casts human assets as 'mediating factors' of ES provision. Place-based empirical studies have revealed varying levels of co-production, with some using more human-derived capital and others using more natural capital, across a range of services, locations, and production systems (Outeiro et al. 2017; Robinson et al. 2019; Bruley et al. 2021).

The role of natural capital in supporting economic growth and people's wellbeing is also a longstanding question for natural resource, environmental, and ecological economists (Dasgupta 2021). This has often been framed as a debate around the ideas of weak and strong sustainability. Proponents of weak sustainability argue that economic growth can be maintained despite declines in natural capital through the use of human-derived substitutes (e.g. Solow 1974), while those promoting strong sustainability maintained that, without nature, economic growth could not be sustained indefinitely, both due to humans' inability to replicate some aspects of nature (Chiesura and de Groot 2003) and the physical constraint that, ultimately, most human production is derived from materials and energy from the earth and its ecosystems (Daly 1997; Ayres 2007). Empirical and modelling work on the question of weak or strong sustainability has led to mixed conclusions, with both evidence for a relatively high degree of substitutability between natural and human-derived capitals (Markandya and Pedroso-Galinato 2007; Malaczewski 2019) and a need to treat this substitutability with caution due to the amount of uncertainty involved (Baumgärtner et al. 2017; Gollier 2019). Additionally, much of existing empirical work has been critiqued for insufficient consideration of non-market goods, including many ES (Cohen et al. 2019), suggesting that the body of work likely paints an incomplete picture of natural capital substitutability with respect to people's wellbeing especially for cultural and regulating ES (Baumgärtner et al. 2017; Drupp 2018; Oh and Muneepeerakul 2019).

Despite the growing recognition, conceptualization, and evidence of ES co-production by both nature and people, potential mediation of ES provision by human-derived capitals is only considered in about one in 10 ES assessments (Mandle et al. 2021). There remains a need for a more practical and generalizable understanding of the role of both natural and human-derived capitals to inform sustainable ES management in diverse real-world contexts (Mastrángelo et al. 2019). While there may be discipline-specific knowledge about the role of human-derived capitals, this knowledge is rarely integrated into more generalized ES assessments and tools. For instance, even though there is evidence that negative interactions between managed honeybees (HC) and wild bees (NC) influence the provision of pollination in some landscapes (e.g. Greenleaf and Kremen 2006; Eaton and Nams 2012; Ropars et al. 2019), many studies and ES models continue to quantify the marginal effects of each in isolation. The pollination model from the InVEST platform, which is commonly used in ES assessments, focuses solely on pollination by wild pollinators, but does not account for potential provision by, or interactions with, managed bees (Lonsdorf et al. 2009). Likewise, Cavigliasso et al. (2021) found that precision honeybee management resulted in 70% more pollinator visits and 13% more fruit than conventional management but did not consider pollination by wild pollinators. In each of these cases, the marginal effect of the capital studied (wild pollinators for InVEST and honeybees for Cavigaliasso et al. 2021) may be dependent on the amount of the capital that was not studied, meaning that the findings may not be consistent across contexts where the unexamined capital varies.

Simply knowing the degree to which capitals are complements or substitutes for each other in a given moment may not be enough to ensure sustainable management of co-produced ES. Dynamic change and interactions among capitals are likely to have important impacts on long-term ES provision that can only be understood through temporally-explicit models. Since natural capital typically consists of, or is related to, populations of organisms, the quantity or quality of natural capital is likely to change over time according to dynamics that are well understood by population ecologists (Krebs 2019). For example, pollination benefits from restored habitat tend to increase over time as pollinator populations become established (Blaauw et al. 2014).

Here, we propose a simple simulation model to investigate the potential roles of capital interactions over time on the provision of ES. This model is not intended to represent any particular system in its entirety (although we do connect each model specification to a real-world example for concreteness), nor is it intended to make quantitative predictions for ES management. Rather, we explore possible behaviours of a simplified system across a range of scenarios (Gelfert 2019). Although there is ongoing debate around how simple models can contribute to scientific understanding (e.g. Reiss 2012; Evans et al. 2013; Fumagalli 2016), they have successfully been used to explore a wide range of questions, such as the dynamics of freshwater ecosystems (Scheffer 1990), effects of climate change on food webs (O'Gorman et al. 2019), the adaptive capacity of social-ecological systems (Carpenter and Brock 2008), the resilience of agricultural systems (Anderies et al. 2006), and the size of groups needed for successful collective action (Casari and Tagliapietra 2018). The benefits of these models are not necessarily their quantitative outputs, but rather the way they allow environmental managers and decision-makers to test assumptions and build a deeper understanding of the systems in which they are involved. Given that many ES are non-market goods that are difficult to measure empirically (Cohen et al. 2019), simulation modelling offers an opportunity to experiment with different assumptions about these systems, learn about the range of behaviours that may be expected, and develop hypotheses that can later be tested in the real world.

2. Methods

To explore how the dynamic behaviour of capitals might affect the long-term provision of ecosystem services, we built a simulation model that calculated ES provision at discrete time steps as a function of natural and human-derived capitals, for all possible initial combinations of the two capitals (Figure 1). We assumed that the provision of a hypothetical ecosystem service (*ES*) is positively related to human well-being or utility (*U*) as described by the general utility function $U = f(ES)$. With a very flexible model specification and a set of simple scenarios, we explore the behaviour of our model over time with three types of capital dynamics: growth or decline in a single capital, a one-way interaction where one capital affects the other, and a two-way interaction where both capitals interact with each other. For each scenario, we examined how the dynamic nature of the capitals affected ES provision over time across a gradient of different capital-ES production functions, from the capitals being perfect substitutes to perfect complements. Each scenario was linked to a real-world example of an ecosystem service management challenge for context (Table 1). From this, we derive a set of implications for better management of ecosystem services when provision is influenced by different general types of co-production relationships. We then present an example illustrating how our generalized model could be applied in a more realistic ES decision-making context to provide useful insights for ES management.

We use a general social welfare function to describe the cumulative benefits provided by on ES over a period of time:

$$W = \Sigma_{t=0}\, e^{-\delta t} u(ES_t)$$

where u is the utility function describing the relationship between provision of an ES and the benefits realized by beneficiaries. The discount factor $e^{-\delta t}$ includes δ, the discount rate, representing time-based preference for ES provision. Because here we focus on the provision of the ES itself as a proxy for well-being, we standardize $u(ES_t) = ES_t$. For simplicity we also assume a discount rate of zero ($\delta = 0$), though a non-zero discount rate does not qualitatively affect the patterns observed (see Appendix A). Together, these assumptions mean that a one unit increase in ES provision translates into a one-unit increase in well-being. For specific contexts where beneficiaries and their relationship with ES are well specified, a different utility function or discounting rate could be used instead.

We assume a general production function by which the provision of ecosystem services at time t is a function of both natural capital (N) and human-derived (manufactured or human) capital (H):

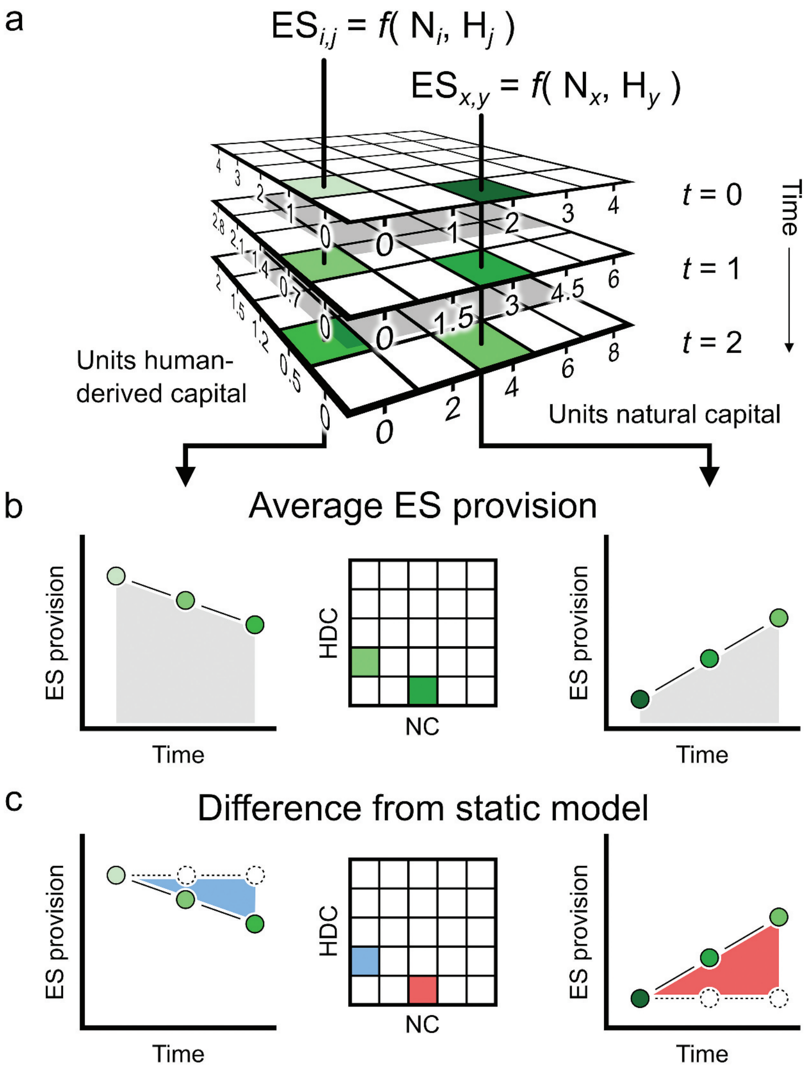

Figure 1. Illustration of modelling approach for two scenarios, each representing a management decision to use certain amounts of natural and human-derived capital to produce an ES. Layers in the figure represent a theoretical 'decision space', defined by the amounts of natural (*x*-axis) and human-derived capitals (*y*-axis) used to provide an ES. (a) Point (*i,j*) has an initial value of 0 units of natural capital (*N*) and 1 unit of human-derived capital (*H*), and point (*x,y*) has an initial value of 2 units of *N* and 0 units of *H*. ES provision is calculated for each point at each time step (light green = high ES provision, dark green = low ES provision). (b) The amount of each type of capital changes over time for each pixel, as determined by the dynamics included in the model. For each pixel, the amount of ES provision is added across all time steps to calculate cumulative ES provision. (c) this cumulative provision is subtracted from what would be expected if the amounts of capitals were not changing to determine the difference from the static model (red = more ES provision than expected in a static scenario, blue = less ES provision). For our evaluation, this process was repeated for all combinations of values of natural and human-derived capital from 0 to 100 units (10201 total pixels) and run for 100 time-steps.

$$ES_t = f(N_t, H_t)$$

Although production of human-derived capital requires, and is limited by, natural capital at a global scale (Ayres 2007), we assume that these variables are decoupled at local scales, and we treat them as independent in the model. For example, even though fertilizer production has important environmental impacts globally, a farmer's decision whether or not to purchase synthetic fertilizer from the global market has a negligible direct, short-term impact on the natural capital on their specific piece of land. This assumption allows us to keep the model reasonably simple and tangible, while still representing local ES management systems, like a farm or a forest plot, in a useful way. Exploration of larger-scale management actions, like national-level agricultural policies, would obviously require a more complex model that accounts for these connections.

We assume that f is a constant elasticity of substitution (CES) production function (Arrow et al. 1961), a function form that has been widely used to describe the production of an economic good as the function of two substitutable production factors (McFadden 1963; Gollier 2019), and allows us to

Table 1. Examples of modelled dynamics and interactions that may be found in ES-providing systems. The examples are intended to illustrate specific dynamics and interactions of natural and human-derived capitals, and therefore may not be inclusive of all the dynamics and interactions affecting provision of a given ES.

	Production function	
Dynamic or interaction	Substitutes	Complements
Static model (no dynamic or interaction between capitals)	**Water provision (short time frame)**: Forested watersheds (natural capital, NC) or water filtration plants (human-derived capital, HC) both have the ability to purify water to meet drinking water quality standards (Chichilnisky and Heal 1998; Blanchard et al. 2015). In the short term at a local scale, if the watershed ecosystem is stable and the filtration plant is well maintained, this could be represented by a static model where the two capitals are substitutes.	**Agriculture (short time frame)**: At minimum, most agricultural systems need soil in which to plant crops and the seeds or plants themselves (NC), and the human labour needed to plant, care for, and harvest the crops (HC). While the relative importance of these components may vary across different types of agricultural systems (Bengtsson 2015), at the most fundamental level an agricultural system could be represented by a static model where the two capitals are complements.
Growth (the amount of one capital increases over time, while the amount of the other remains constant)	**Pollination**: Insect-pollinated crops can benefit from both managed honeybees (HC) and habitat (NC) that supports populations of wild pollinators. When wild pollinator habitat is restored, wild pollinator populations tend to increase over time as they become established in the habitat (Blaauw et al. 2014).	**Maple syrup production**: Maple syrup production requires both maple trees (NC) and a sap collection system (HC; Farrell 2013). Larger trees can support more taps and produce more sap (assuming they're mature and healthy), so syrup production would be expected to increase over time as trees grow (Heiligmann et al. 2006). In contrast, the maximum capacity of a tapping system is fixed and will not increase.
Decline (the amount of one capital decreases over time, while the amount of the other remains constant)	**Coastal flood protection**: Restoration of oyster beds (NC) and grey infrastructure such as seawalls (HC) both have potential to mitigate coastal flooding (Reguero et al. 2018). However, grey infrastructure degrades over time unless maintained (CPRA (Coastal Protection and Restoration Authority of Louisiana) 2017), while oyster beds maintain themselves once established, assuming favourable ecological conditions (Kroeger 2012).	**Mechanized agriculture**: Modern conventional agricultural systems rely both on soil quality (NC) and various types of farm equipment (HC), among other inputs. Over time the equipment inherently becomes less reliable and effective (Cross and Perry 1995), whereas soil quality, if well-managed, can be maintained over time.
Positive one-way interaction (one capital has a positive effect on the amount of the other)	**Water treatment & riparian vegetation**: Riparian vegetation (NC) and water treatment technology (HC) can both serve to purify water. In one case, riparian vegetation was shown to also lower water temperature, increasing the effectiveness of water treatment technology and avoiding the need for additional expensive treatment steps to filter out byproducts produced by treating warmer water (Honey-Rosés et al. 2013).	*No clear example identified*.
Negative one-way interaction (one capital has a negative effect on the amount of the other)	**Agricultural pest control**: Pest control on farms can be provided either by populations of wild predators (NC) or through the use of synthetic pesticides (HC). As most pesticides are not species-specific, use of these pesticides often has negative effects on the species providing natural pest control in addition to those they are intended to control (Desneux et al. 2007).	**Outdoor recreation**: Provision of outdoor recreation requires both attractive natural environments in which people want to recreate (NC) and the necessary infrastructure for people to be able to access and enjoy these areas (HC; Paracchini et al. 2014). However, the presence of these same man-made features detracts from the inherent 'naturalness' of a place, at least in some contexts (Sæþórsdóttir 2010).
Positive two-way interaction (both capitals have a positive effect on the other)	**Coastal protection**: Coastal protection can be provided by both natural (NC) and artificial coral reefs (HC; Pickering et al. 1999). As dispersal of some coral larvae is limited by distance (Carlon and Olson 1993), recruitment may be higher near to existing reefs, investments in either type of reef may help increase the health and growth rate of both natural and artificial reefs nearby. While over time the line between NC and HC may become blurred, this synergy between the two represents an important initial interaction.	*No clear example identified*.
Negative two-way interaction (both capitals have a negative effect on the other)	*No clear example identified*.	**Wildlife tourism**: Wildlife tourism depends on both wildlife (NC) to attract tourists (Tisdell and Wilson 2003) and other facilities to support tourists' visits such as lodging, food service establishments, and roads of other infrastructure to access and view wildlife (HC; Reynolds and Braithwaite 2001). However, there are inherent trade-offs between these two realms. Tourist infrastructure can have numerous negative effects on wildlife populations, including changes in or loss of habitat, behavioural effects such as habituation or stress avoidance behaviours, or increased mortality such as through vehicle collisions or easier access by poachers (Reynolds and Braithwaite 2001). When the focal species has negative impacts on local communities, such as crop damage by elephants (Hoare 1999) or livestock predation by lions (Hemson et al. 2009), this may reduce communities' ability to invest in or maintain tourist facilities, though this feedback is likely to be weaker when investments in tourism come from outside local communities, or where there are systems in place to compensate local people for damage from wildlife (Nyhus et al. 2005).

make various assumptions about the degree of substitutability between natural and human-derived capital. The CES specification for our case is:

$$ES_t = \left(\gamma N_t{}^{1-\rho} + (1-\gamma)H_t{}^{1-\rho}\right)^{1/(1-\rho)}$$

where γ represents the contribution of natural capital to ES provision relative to human-derived capital and ρ is the inverse of the elasticity of substitution. Because we model natural and human-derived capitals as standardized quantities and do not specify units, we assume that $\rho = 0.5$, and that any relative difference in the contribution of each capital can be accounted for in the way N and H are quantified.

The choice of functional form for ES flow has long been debated in the literature (e.g. see early debates among Daly 1997; Solow 1997; Stiglitz 1997). Here we follow Solow-Stiglitz reasoning using the CES production function, which flexibly captures the important dynamics between natural and human capitals. This functional form allows us to model the continuum of situations in which natural and human-derived capitals are substitutes (e.g. protected forested watershed to 'produce' high-quality drinking water versus a water treatment plant) to cases where they are compliments (e.g. trees and tapping systems are both needed to produce maple syrup). With this we are able to explore the full breadth of potential substitutability of natural and human-derived capitals in ES provision.

We looked at three implementations of the CES production function: when ρ approaches 0, 1, and ∞, which correspond to linear, Cobb-Douglas, and Leontief production functions, respectively. In a perfect substitutability case, ρ approaches 0 (the elasticity of substitution approaches ∞), and the production function simplifies to a simple proportional linear function:

$$ES_t = \gamma N_t + (1-\gamma)H_t$$

In the perfect complementarity (zero-substitutability) case, ρ approaches ∞ (the elasticity of substitution approaches 0), and the production function becomes a Leontief function:

$$ES_t = \mathrm{Min}\left(\gamma^{-1}N_t, (1-\gamma)^{-1}H_t\right)$$

An intermediate case exists when ρ approaches 1 (the elasticity of substitution also approaches 1). Here an n% increase in natural capital relative to human-derived capital corresponds with an n% decrease in the marginal effect of natural capital on ES provision relative to human-derived capital. The production function is the Cobb-Douglas production function, which serves as an intermediate case between complete substitutability and complete complementarity (Richmond et al. 2007):

$$ES_t = N_t{}^{\gamma} H_t{}^{(1-\gamma)}$$

Arrow et al. (1961) and McFadden (1963) provide detailed mathematical explorations of the relationships between these production functions in environmental contexts.

We model the dynamics of the capitals over a sequence of discrete time steps in which the quantity of each capital in the next period $t+1$ is a function f or g of the amount present in period t:

$$N_{t+1} = f(N_t, H_t)$$
$$H_{t+1} = g(N_t, H_t).$$

Here N_t and H_t represent the amount of natural and human-derived capital, respectively, at time t. The specific equation forms we used for f and g are based on the classic Lotka-Volterra model of interspecific competition (Lotka 1978). The dynamics captured in these equations have an advantage of being conceptually simple, carrying few restrictive assumptions, and also accurately capturing first-order dynamics between systems as diverse as predator-prey relationships to the wild population responses to resource scarcity. These functions are simply:

$$N_{t+1} = N_t + rN_t + \alpha N_t H_t$$
$$H_{t+1} = H_t + sH_t + \beta N_t H_t$$

where r and s are the intrinsic growth rates for natural and human-derived capital, and α and β are parameters indicating the effect of human-derived capital on natural capital and the effect of natural capital on human-derived capital. We restrained the model from letting the value of either capital fall below zero (i.e. $N_{t+1} = 0$ where $N_t + rN_t + \alpha N_t H_t < 0$).

For the growth and decline scenarios, we set α and β to zero so that the amount of each capital at each time step is determined solely by its own amount at the previous time step and its inherent rate of change. For the interaction scenarios, we set r and s to zero, so that the amount of each capital at each time step is determined solely by the amount of the other capital at the previous time step and the strength of the interaction between the two capitals.

We ran the model over a series of t time steps. At each time step, we calculated the amount of ES provision from the production function equation. Then we calculated the amount of each capital for the subsequent time step, using the equation describing the dynamics of the capitals. We then used these new amounts of capitals to calculate the ES provision at the next time step. We ran the model using all possible combinations of starting capitals to explore the full decision space.

Although longer timeframes resulted in greater quantitative changes in ES provision, the model outcomes were qualitatively stable over a range of reasonable timeframes (Appendix B). Therefore, we present all results for an arbitrary timespan of 100 steps, and we focus our analysis on the effects of the remaining parameters.

Mathematically, this setup also carries several assumptions that should be considered when interpreting results. Since our focus is on the co-production of ecosystem services, we assume N and H are not inherently scarce and thus do not get 'used up' in the process of producing ES (although this type of change could be modelled with our growth and decline scenarios). For example, we might model synthetic herbicides as 'static', even though they may need to be applied to crops one or more times each time step. This simplification allows us to focus our exploration on longer-term trends across multiple time steps, such as the development of herbicide resistance in weeds, which we account for in the model using a negative growth rate for human-derived capital. Second, we do not consider natural capital an input in the production of human capital, since, for example, a farmer buying fertilizer does not have a measurable or immediate impact on the natural capital of the farm where the fertilizer is used. Thus, our model is particularly suitable for thinking through local- or landscape-scale management efforts, where resources can be imported into the system from elsewhere. Obviously, for global systems, there is no 'elsewhere' and thus no ability to rely on resources from outside the system. Finally, our representation of dynamics assumes smooth transitions between one period and then next, and therefore does not represent threshold effects very well. Thus, our simple system of equations does not capture all elements of complexity related to ES co-production, nor do we suggest these quantitatively predict ES provision in any specific context. We also discuss some practical limitations of the model in Section 4.2 below. However, given our goal of providing evidence of system behaviours that are not commonly considered in ES management, we think these assumptions are reasonable.

The model was run in R 4.0.4 (R Core Team 2021) and used package 'gridBase' (Murrell 2014) for visualizing model output. Complete code for the model is included in Appendix C.

3. Results

We begin by describing the quantitative behaviour of the model across a set of different model structures and parameters (Sections 3.1–3.3). For each scenario, we describe how managers may need to adjust their strategy to achieve ES provision objectives in each type of system (Table 2). We then apply our approach to a hypothetical but realistic ecosystem service management case study to illustrate how this approach might help inform decision-making (Section 3.4). Figure 2 below describes a base-case where both capitals do not change over time against which later model outcomes can be compared.

3.1. Growth or decline of a single capital

In the 'growth/decline' scenario, we modelled a system where the amount of one capital increased or decreased exponentially (the 'dynamic capital') and the amount of the other remained constant (the 'static capital'; Figure 3). Real-world examples of each scenario can be found in Table 1. This type of functional form is typified in the exponential growth of populations (e.g. Bowen et al. 2003) or, say, the exponential loss of nutrients from decaying organic matter (e.g. Havis and Alberts 1993). This scenario may be relevant for understanding a system such as maple syrup production, where the ES provision depends on natural capital (maple trees) that grows over time, or one where human-derived capital depreciates over time such as mechanized agriculture or man-made coastal flood control.

When capitals were perfect substitutes, less (more) of the growing (declining) dynamic capital is needed to provide the same level of ES compared to the static model (Figure 3a,d). Similarly, when capitals were perfect complements, less (more) of the dynamic capital is needed when growth is positive (negative) for a given level of ES provision relative to the standard case (Figure 3c,f). In the intermediate scenario where capitals can behave like complements or like substitutes, ES provision was either greater or less for all combinations of capitals, depending on whether the dynamic capital was growing (Figure 3b) or declining (Figure 3e), respectively. In general, even our modest declining growth rate shows that much greater levels of the other capital are needed to provide similar levels of ES to people.

3.1.1. Management implications – growth/decline

In a static scenario where capitals are substitutes, there is no difference between the capitals in terms of ES provision – a manager can freely substitute one for the other based on factors such as cost or convenience (Table 2). Having positive or negative growth of a capital does not change this fundamental substitutability, but it changes the ratio at which units of one capital can be substituted for the other. The amount of investment needed in a dynamic capital to achieve a certain change in overall ES provision will be large or small depending on how the capital changes over time.

In a static scenario where capitals are complements, the most efficient management strategy is to maintain an equal ratio of the two capitals because any increase in one without a corresponding increase

Table 2. Summary of management implications for each type of modelled dynamic and production function. For scenarios characterized by a particular production function (columns) and type of dynamic or interaction involving capitals (rows), this table describes strategies for choosing the appropriate amount of natural and human-derived capitals to enhance ES provision (assuming all other factors are equal).

	Production function	
Dynamic or interaction	Substitutes	Complements
Static model (no dynamic or interaction between capitals)	Investments in both capitals increase ES provision. Managers can choose between capitals based on cost, accessibility, convenience, or previous management practices.	ES are provided most efficiently with a 1:1 ratio of the two capitals. Investments in a single capital will not increase provision.
Growth (the amount of the 'dynamic capital' increases over time, while the amount of the 'static capital' remains constant)	Investments in the dynamic capital let managers take advantage of its intrinsic growth.	Investments in the static capital are needed to ensure that it does not limit provision as the dynamic capital grows.
Decline (the amount of the 'dynamic capital' decreases over time, while the amount of the 'static capital' remains constant)	Investments in the static capital reduce the impact on ES from declines in the dynamic capital.	Sufficient investments should be made in the dynamic capital so that it can decline without reaching the level where it limits ES provision.
Positive one-way interaction (the 'driving capital' has a positive effect on the amount of the 'responding capital')	Investments in the driving capital let managers benefit from its positive effect on the responding capital.	Sufficient investments should be made in the driving capital to ensure it does not limit provision as the responding capital grows due to the interaction.
Negative one-way interaction (the 'driving capital' has a negative effect on the amount of the 'responding capital')	Highest ES provision can be achieved by maximizing one capital and minimizing the other. The choice may be based on cost, accessibility, convenience, or previous management practices.	Reducing the driving capital to the minimum for the desired level of ES provision minimizes the effect of the interaction. Increasing the amount of the responding capital helps compensate for declines due to the interaction.
Positive two-way interaction (both capitals have a positive effect on the other)	Investments in either capital let managers benefit from its positive effect on the other capital.	ES are provided most efficiently with a 1:1 ratio of capitals. Investing in a single capital will provide a smaller increase in provision than an equivalent investment in both.
Negative two-way interaction (both capitals have a negative effect on the other)	Highest ES provision can be achieved by maximizing one capital and minimizing the other.	Reductions in ES provision can be minimized by maintaining a 1:1 ratio of capitals. Provision will always be less than the static model. Investments in a single capital will cause a decline in provision.

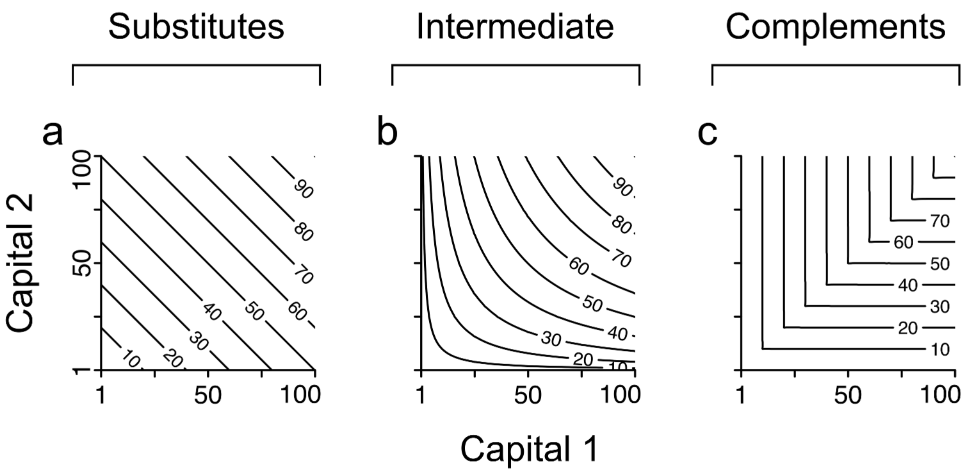

Figure 2. Expected ES provision from a static model where capitals do not interact with each other or change over time. Two capitals, where one represents natural capital and the other human-derived capital, are shown in the *x* and *y* axes (arbitrary units). The amount of ES co-produced by each combination of the two capitals (arbitrary units) is indicated by the contour lines. The three panels illustrate three possible forms of the relationship between capitals and ES provision: perfect substitutes (panel a), perfect complements (panel c), and an intermediate scenario where capitals behave more like substitutes when both are present in similar amounts, but behave more like complements as the difference between them increases.

in the other will not produce an increase in ES provision. Growth in one capital over time offers on opportunity to benefit from increased provision in the long term, but only when the dynamic capital is the limiting factor for ES provision. Once this capital grows past the point where it is no longer limiting, investment in the static capital is needed. Conversely, when one of the capitals declines over time, a higher relative investment in the dynamic capital would be needed to compensate for its decline. To minimize the negative effects of a decline, a manager should aim to maintain

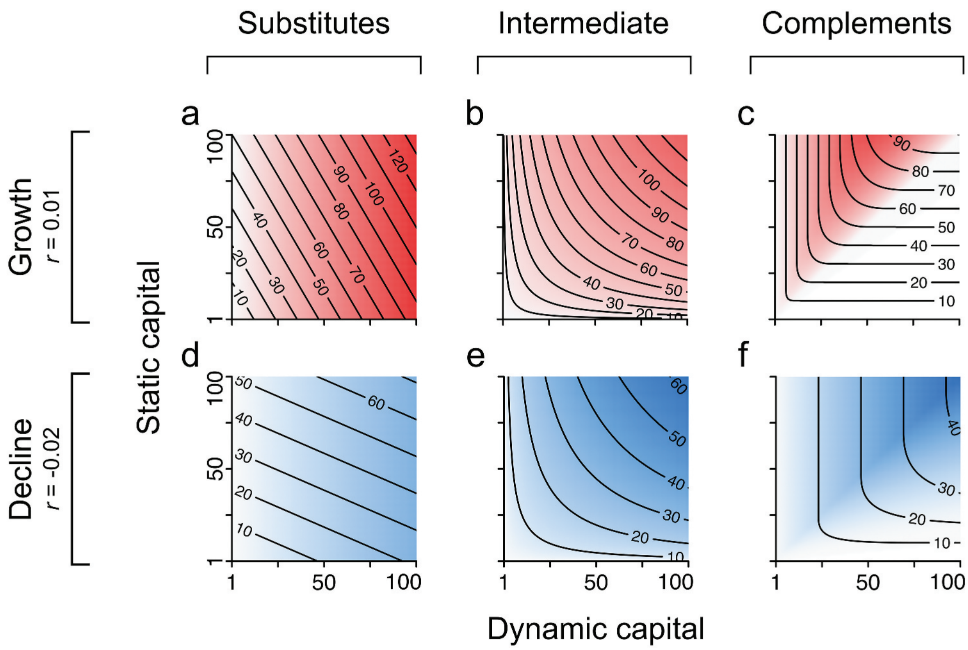

Figure 3. Expected average ES provision from a dynamic model where one capital grows (top row) or declines (bottom row) over time, over a period of 100 time steps. The amount of the 'dynamic capital' (*x*-axis; arbitrary units) changes exponentially over time with growth rate *r*, while the amount of the 'static capital' (*y*-axis; arbitrary units) remains constant over time. The amount of ES co-produced by each combination of the two capitals (arbitrary units) is indicated by the contour lines. The difference in ES provision between this model and a scenario where capitals are static (Figure 2) is indicated by the coloured shading (blue = less, white = same, red = more). The three columns illustrate three possible forms of the relationship between capitals and ES provision: perfect substitutes (left), perfect complements (right), and an intermediate scenario where capitals behave more like substitutes when both are present in similar amounts, but behave more like complements as the difference between them increases (middle).

a dynamic capital in sufficiently large quantities such that it does not decline past the 1:1 line during the management time frame.

3.2. One-way interaction between two capitals

In the 'one-way interaction' scenario, one capital (the 'driving capital') has an effect on the other 'responding' capital, with the magnitude of the effect proportional to the amount of both capitals present (Figure 4). This scenario represents systems where there are inherent trade-offs (negative effect) or synergies (positive effect) between different capitals, e.g. synthetic insecticides and native predators in agricultural systems, or visitor service infrastructure and naturalness of landscapes in recreation areas.

When the two capitals were perfect substitutes, less of the driving capital is needed to provide the same level of ES, relative to the static scenario (Figure 4a). This is functionally identical to the positive growth rate scenario (Figure 3a), except ES provision is impacted indirectly, via its effect on the responding capital, rather than directly. A negative interaction breaks dependence, even for a case of perfect substitutability, when levels of one capital are low – but balanced amounts of both capitals yield the best ES (Figure 4d).

When the two capitals were complements, a positive interaction led to increased ES provision, compared to the static scenario, and a weakening of the strict complementarity as the curvature of isolines resemble a more intermediate case (Figure 4c). Interestingly, when there is a negative 1-way interaction between capitals, there is an optimal minimum of the driving capital. Beyond that minimum threshold, increasing the rate of the driving capital requires additional investment in the responding capital to maintain ES provision (Figure 4f).

The intermediate scenario showed an intermediate pattern for the change in ES provision, especially with a positive interaction (Figure 4b). With a negative interaction, the outcome was more similar to that where the capitals were perfect complements, but with some substitutability for the responding capital indicated by some vertical curvature (Figure 4e).

3.2.1. Management implications – one-way interaction

When capitals are substitutes and the interaction is positive, the management implications are identical to the scenario with positive growth – investment in the driving capital provides a relatively greater benefit over time than the same investment in the responding capital – although the mechanism behind this outcome is different (Table 2). When there is

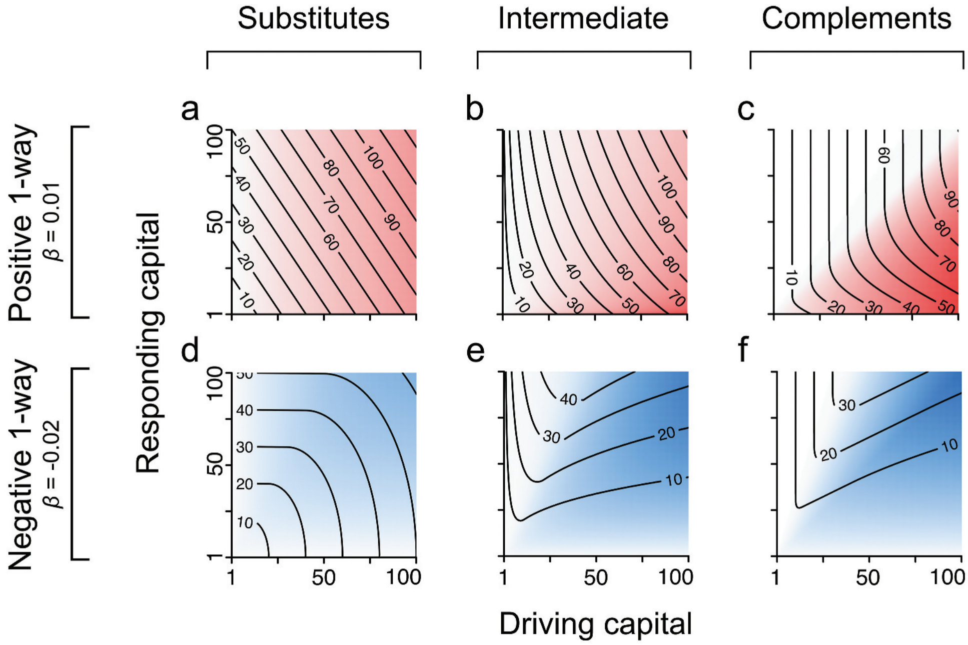

Figure 4. Expected average ES provision from a dynamic model with a one-way positive (top row) or negative (bottom row) interaction between capitals, over a period of 100 time steps. The amount of the 'responding capital' (*y*-axis; arbitrary units) changes over time as a function of the amount of the 'driving capital' (x-axis; arbitrary units) and parameter *β* which indicates the strength and direction of the interaction. The amount of ES co-produced by each combination of the two capitals (arbitrary units) is indicated by the contour lines. The difference in ES provision between this model and a scenario where capitals are static (Figure 2) is indicated by the coloured shading (blue = less, white = same, red = more). The three columns illustrate three possible forms of the relationship between capitals and ES provision: perfect substitutes (left), perfect complements (right), and an intermediate scenario where capitals behave more like substitutes when both are present in similar amounts, but behave more like complements as the difference between them increases (middle).

a negative interaction, losses in ES can be minimized by minimizing the amount of one of the two capitals, which minimizes the effects of the interaction on ES provision. This also means that the marginal effects on ES provision of investments in either capital are small when the amount of that capital is low (the contour lines intersect the axes at a 90° angle in Figure 4d): when a small amount is invested in the responding capital, it is quickly lost due to the interaction between capitals, and when a small amount is invested in the driving capital, the positive effect on ES provision is counteracted by its negative effect on the amount of the responding capital. The marginal effect of investment in the driving capital can even become negative if the decline in ES caused by loss of the responding capital due to the interaction is greater than the positive effect on ES provision by adding the driving capital.

When capitals are complements and the interaction is positive, the effect is again similar to positive growth, except now investments should be made in the driving capital so that its positive effect on the responding capital can be harnessed for greater ES provision over time. When capitals are complementary and the interaction is negative, if the amount of the driving capital is low, it is the limiting factor in ES production, regardless of the interaction, due to the complementary relationship between capitals. However, when the amount of the driving capital passes the point where it is no longer the limiting factor, further increases result in decreases in ES provision as a result of the negative interaction. Thus, the highest ES provision can be achieved by having the bare minimum of the driving capital necessary to produce the desired quantity of ES, while also increasing investment in the responding capital to compensate for its loss over time as a result of the negative interaction.

3.3. Two-way interaction between two capitals

n the 'two-way interaction' scenario, we modelled a system where both capitals have equal positive or negative effects on each other, and the magnitude of the effect is proportional to the amount of both capitals (Figure 5). As the behaviour of both capitals within the model is identical, we simply refer to them as 'capital 1' and 'capital 2'. This scenario may be relevant to understanding systems with bidirectional synergies and trade-offs between capitals, such as synergies between natural and man-made forms of coastal protection or human-wildlife conflicts related to tourism.

When both capitals had a positive effect on the other, ES provision intuitively is greater than the static model for a given level of capital investment.

When the two capitals were perfect substitutes (Figure 5a), the magnitude of increase in ES provision increased linearly with the sum of the initial amounts of the two capitals. When the two capitals were perfect complements, however, there is an optimal balance of investment in the two capitals, but we do not see strict complementarity as in the static case (Figure 5c). The intermediate fell in between these two extremes (Figure 5b).

When the interaction was negative, ES provision was less than the static model except along the axes, and qualitatively similar to the one-way interaction case (Figure 4). When the capitals were perfect substitutes, the highest levels of ES provision come from a balanced investment in the two capitals, but ES provision is still maintained close to this optimum without any investment in one of them (Figure 5d). When the capitals were perfect complements (Figure 5f), as well as in the intermediate case (Figure 5e), any increase in the more abundant capital resulted in a decrease in ES provision.

3.3.1. Management implications – two-way interaction

With a positive two-way interaction where capitals are substitutes, managers can continue to treat the two capitals as substitutes while enjoying increased ES provision relative to the static model for all possible management strategies (Table 2). With a positive two-way interaction where the capitals are complements, the two capitals begin to act to some degree as if they are substitutes. While the highest ES provision (for a given total amount of capitals) is still at an equal ratio of the two capitals, investment in one capital and not the other does produce gains in ES provision, albeit at a slower rate. With a negative two-way interaction, like with a negative one-way interaction, the greatest amount of ES is produced by maximizing one capital while minimizing the other. If the strength of the interaction in both directions is greater than the marginal effect of either capital on ES provision, the capital that is most abundant always has a positive marginal effect on ES provision, while the less abundant capital has a negative marginal effect. With a negative two-way interaction where capitals are complementary, this relationship is inverted so that the less abundant capital has a positive marginal effect on ES provision while the more abundant capital has a negative marginal effect. As in the static model, the highest ES provision (for a given total amount of capitals) is achieved by maintaining an equal ratio of both capitals, although the negative interaction will always result in a lower ES provision for a given combination of capitals.

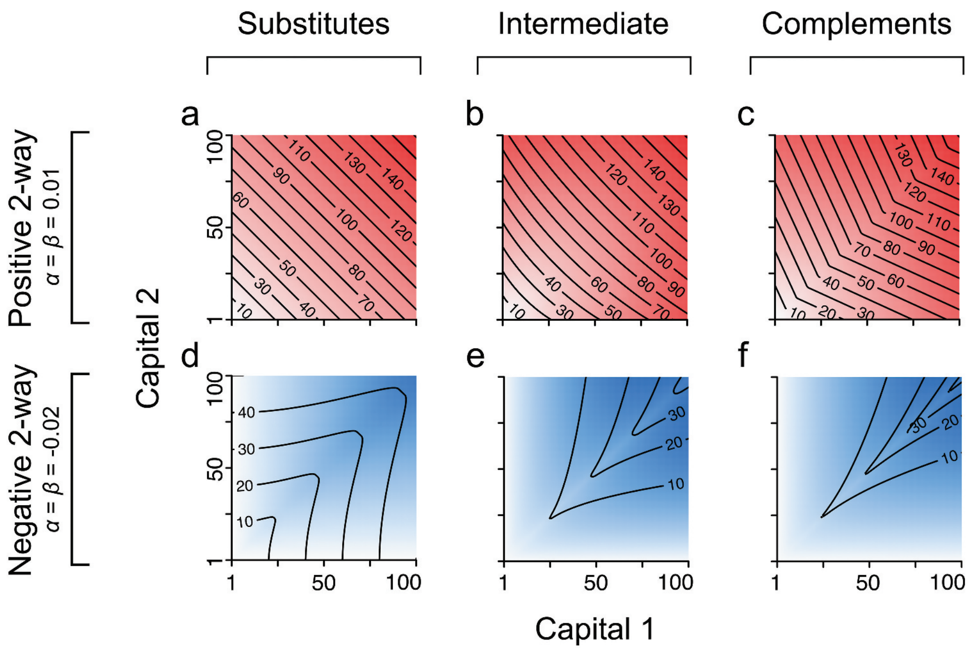

Figure 5. Expected average ES provision from a dynamic model with a two-way positive (top row) or negative (bottom row) interaction between capitals, over a period of 100 time steps. The amounts of both capitals (*x*- and *y*-axes; arbitrary units) change over time as a function of the amount of the other capital and parameters *α* and *β* which indicate the strength and direction of the interactions. The amount of ES co-produced by each combination of the two capitals (arbitrary units) is indicated by the contour lines. The difference in ES provision between this model and a scenario where capitals are static (Figure 2) is indicated by the coloured shading (blue = less, white = same, red = more). The three columns illustrate three possible forms of the relationship between capitals and ES provision: perfect substitutes (left), perfect complements (right), and an intermediate scenario where capitals behave more like substitutes when both are present in similar amounts, but behave more like complements as the difference between them increases (middle).

3.4. Example

In this section, we present an example of how our modelling framework might be used in a real-world decision-making context, using a farmer's decision about how to manage pollination as a case study. This example is not intended to draw conclusions about pollination, but rather to illustrate how a decision-maker might use the outputs from our model to make more informed ES management decisions. A similar process could be undertaken for any management decision involving a choice between natural and human-derived capitals for ES provision, such as those described in Table 1.

In this scenario, a farmer relies on insect pollination for crop production. The farmer can obtain pollination in two ways: (1) pay each year to bring in domesticated honeybees, or (2) restore nearby land as wild pollinator habitat, with each strategy having distinct advantages and disadvantages (Table 3). Honeybee pollination involves fixed annual costs to rent hives. The number of pollinators is linearly related to the number of hives. Wild pollinators, including non-bee taxa like flies and butterflies, can be more efficient and effective than honeybees at successfully pollinating a variety of crops (Garibaldi et al. 2013; Cusser et al. 2021), so the farmer may wish to use wild pollinators as much as possible. Additionally, management that benefits wild pollinators may enhance other synergistic ES, such as pest control (Egan et al. 2020), and diverse wild pollinator populations may be less vulnerable to stresses like disease, loss of forage resources, and pollution than managed bees, resulting in more resilient provision of pollination (Williams et al. 2019). On the other hand, if managed bees are lost due to localized stresses, more can quickly and easily be imported from elsewhere. In terms of flexibility, the pollination benefits from creating habitat for wild pollinators cannot be immediately enjoyed as newly-created habitat supports few pollinators; the number of pollinators increases over time as populations establish themselves (Blaauw et al. 2014). This means that the number of pollinators per unit area of habitat will be low in the first year of wild pollinator habitat but will grow over time until it reaches the carrying capacity of that habitat. Additionally, benefits of wild pollinators are more variable, depending on weather and other local conditions over which the farmer has no control, which may have an impact on farmer decision-making. Thus, honeybees are the more flexible and controllable option for providing pollination in the short-term, while investment in wild pollinator habitat may reduce the costs involved in providing pollination, and promote additional benefits, over the long-term.

In order to understand the advantages and disadvantages of each option, a farmer would ideally want to know how much pollination to expect from each potential management strategy over a certain period of time. Given that wild pollinators are expected to be more effective and resilient while managed bees are more flexible and easily controlled, an attractive management strategy might be to manage for both. However, the farmer also may have concerns about potential negative interactions between honeybees and wild pollinators. Some suggest honeybees compete with native pollinators (Goulson and Sparrow 2009; Thomson and Irwin 2016), meaning beehives could be detrimental to efforts to build wild pollinator populations. However, others have found that, despite a high degree of resource overlap, honeybees do not appear to negatively affect wild pollinators (Steffan-Dewenter and Tscharntke 2000; Roubik and Wolda 2001). To account for this uncertainty, we modelled this system twice, once with a strong negative effect of honeybees on native pollinators, and once with a much weaker negative effect.

Our model results show that, if long-term dynamics between the capitals are disregarded, the two capitals function as substitutes (Figure 6a). Initially, one unit of investment in wild pollinator habitat results in a smaller increase in pollination than one unit of investment in honeybees, so the greatest returns on investment are realized when all resources are directed towards honeybees.

Table 3. Potential advantages and disadvantages of managing for crop pollination using wild pollinators and honeybees.

	Wild pollinators	Honeybees
Advantages	• May provide more effective pollination. • Potential to support other synergistic ES. • May be more resilient to multiple stressors. • Under ideal conditions, populations will grow and maintain themselves with minimal management.	• Number can be increased or decreased as needed by hiring renting hives from commercial providers. • New hives can be brought in to replace any lost due to stresses.
Disadvantages	• Population size depends on habitat and can only be managed indirectly and slowly. • Amount of pollination may vary over time in unpredictable ways due to natural factors. • Pollinator habitat requires removing land from crop production.	• May be less effective at pollinating certain crops. • May be more sensitive to disease, pollution, loss of forage resources. • Ongoing costs to the farmer for hive rental.

If the dynamics of the capitals are considered, and the effect of honeybees on wild pollinators is assumed to be low (Figure 6b), the situation looks only slightly different from the static model; the highest returns on investment still occur when all investment is directed towards honeybees (though this effect is now tempered). We also begin to see a threshold effect, where small amounts of investment in wild pollinator habitat fail to substantially increase pollination, but increased investment in wild pollinator habitat, especially past a threshold level of investment, has a much stronger positive effect on the provision of pollination.

If the negative effect of honeybees on wild pollinators is stronger (Figure 6c), the threshold for investment shifts towards greater values of wild pollinator habitat, and two alternative strategies begin to emerge. Investing solely in honeybees continues to provide the highest return on investment (though this would not be the case if the growth rate of the wild pollinators were higher, or if the initial investment needed to establish pollinator habitat were lower), but it is also possible to attain relatively high levels of pollination through investing primarily in wild pollinator habitat (lower-right half of Figure 6c). As in the case where the interaction is weak, if all investment is currently directed towards honeybees, any investments in wild pollinator habitat will have negligible effects until a threshold (which is higher in this case) is passed. Finally, if pollination is already being provided primarily by wild pollinators or through a mix of wild pollinators and honeybees, increasing the amount of investment in honeybees will reduce pollination, as their negative effects on wild pollinator populations outweigh the pollination benefits that honeybees provide.

The model shows that, when the dynamic behaviours of the capitals are considered, the farmer can no longer simply invest in equivalent amounts of honeybees or pollinator habitat at will and expect to get the same outcomes. The relationships are no longer linear, and the marginal impact of investing in each type of capital changes depending on the type of management currently being employed. Although we cannot use the model to exactly predict the behaviour of the system or give an optimal value due to uncertainty about the strength of possible interactions, it illustrates a range of possible behaviours, some of which are not intuitive. This deeper understanding of possibilities can help guide adaptive management of the system so that the farmer is able to observe changes in the system over time and adjust management in a more appropriate way.

If already managing with honeybees, the farmer might want to move towards wild pollinators to take advantage of their more effective pollination and lower maintenance cost. However, depending on the strength of the interaction between honeybees and wild pollinators, there may be a threshold where a minimum amount of habitat must be created before there is any positive effect of added habitat. As the amount of pollination from wild pollinators increases, reducing the number of hives can actually increase pollination if the negative effect of the competition with wild pollinators was greater than the positive effect of adding hives.

A farmer that already has abundant wild pollinators should think carefully about using honeybees to further increase pollination as a strong interaction between honeybees and wild pollinators could mean that bringing in more honeybees actually reduces long-term pollination benefits. When the interaction is weaker, adding honeybees would increase pollination, but may not do so as much as would be expected if wild pollinators were not already present. In this case, the decision of whether to invest in honeybee hives should be based on how 'saturated'

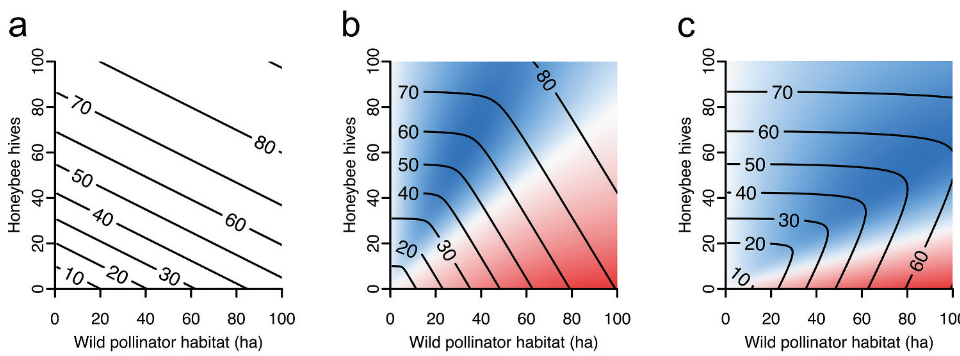

Figure 6. Average annual provision of pollination over 10 years (contour lines) for different combinations of investments in wild pollinator habitat (natural capital) and investments in honeybees (human-derived capital). Panel a shows the static model. Panel b shows a dynamic model where the effects of honeybees on wild pollinator populations is relatively low ($\beta = 1$). Panel c shows a dynamic model where the effects of honeybees on wild pollinator populations is higher ($\beta = 3$). For panels b and c, wild pollinator habitat grows over time with a growth rate $r = 0.25$. Coloured shading indicates, for each initial combination, whether ES provision was greater (red) or less (blue) than that provided by the static model, with darker shading indicating a greater difference.

the wild pollinator populations are; if more pollination is needed but so much of the land surrounding the farm is already managed as pollinator habitat that any further investments would be far away and provide few pollination benefits, it may make more sense to bring in beehives. However, if there are still feasible sites for pollinator habitat nearby, this may provide a higher return on investment.

Overall, this example highlights the importance of a dynamic perspective on ES co-production. Relatively simple dynamics, like a negative effect of honeybees on native pollinators, can lead to surprising behaviours like thresholds and other non-linear responses to ES drivers. Simply understanding the ES co-production function, e.g. that honeybees and native pollinators are substitutes, is insufficient to model the system's long-term dynamics and make well-informed management decisions.

4. Discussion

ES are produced by complex social-ecological systems, and all ES models make simplifying assumptions at some level. Typically, this simplification involves the assumption of linear relationships between system components and omission of potential interactions; these assumptions allows many drivers of ES provision to be studied simultaneously within a framework that remains straightforward to model and interpret (Smith et al. 2017; Martínez-López et al. 2019). In this paper, we alternatively reduce the number of potential drivers of ES provision to just two–one representing ecosystems and another representing man-made inputs – which allows us to maintain a more realistic level of complexity in the way we model the dynamics of ecosystems and man-made inputs, including the interactions between them.

Our results demonstrate that the amount of different capitals used to produce an ecosystem service, the degree to which the capitals substitute for or complement each other, and any potential dynamics or interactions between capitals can have meaningful impacts on the outcomes for ES provision. Our model provides a simple framework that managers could use to better account for these factors in their decision-making. As a first step, decision-makers could use Table 1 to find a scenario analogous to theirs, based on the types of dynamics and interactions they have observed on the ground or which have been described in the scientific literature for similar systems. Then, they could use the general management implications presented in Table 2 to determine if and how they could consider adjusting their management strategy to compensate. To quantitatively determine the outcome of their decision, more extensive on-the-ground research would be needed to confirm whether predicted interactions and parameters are in fact present in the system and to parameterize the model. Such a series of steps could be part of an adaptive management approach, where managers iteratively update their understanding of the system from monitoring the outcomes of management actions, and then adjust their management to align with this new knowledge (Birgé et al. 2016).

Our model also points to a need for further empirical work exploring the degree of substitutability or complementarity of specific capitals for the co-production of ecosystem services in real-world contexts, as this relationship had a substantial influence on the behaviour of the simplified systems we modelled. We focused our exploration on the boundary cases, where capitals were either highly substitutable or highly complementary, because we expected these to encompass the widest range of system behaviours and provide the clearest examples for characterizing possible outcomes. However, many ES may look more like our 'intermediate' scenarios, where substitutability between capitals declines as the amount of either capital increases relative to the other. In other cases there may be no effective anthropogenic substitute for natural capital, particularly for cultural ES such as education (Hutcheson et al. 2018) or cultural and spiritual identity tied to specific landscapes (Bélisle et al. 2021), although, even in these cases, contributions to people's well-being are still mediated by their cultural values and perceptions. More detailed knowledge of how substitutable particular capitals tend to be (or not) for different ES would help managers anticipate which systems are most likely to be impacted by the dynamics and interactions we identified, and what types of behaviour to look for.

4.1. Insights from the model

Our model illustrates how expected outcomes from ES management can be different when one accounts for long-term dynamics and interactions among capitals. Although the precise behaviour of the model varied across the different scenarios, we observed a number of more general patterns that may be useful for understanding and managing the systems that co-produce ES. These results may also be important for ES modellers, who often simplify ES models by eliminating these dynamics and interactions.

If the dynamics and interactions are weak enough, or slow enough compared to the time frame of a decision, they are unlikely to substantially affect the outcome in terms of ES provision. In these instances, decision-makers can choose a strategy based on the degree to which the different components complement or substitute for each other, as well as logistical concerns such as cost, flexibility, and ease of use. However, when dynamics and interactions are stronger, management that overlooks them can lead to surprises. For instance, in our pollination example, if managers know that honeybees and native pollinators are substitutes they might logically assume that if they invest in x honeybees and y native pollinators, they would provide $x + y$ pollination. This may be approximately accurate if the negative interaction between the two is weak, but if, as some research suggests, there is strong competition between honeybees and native pollinators (a strong negative interaction; Goulson and Sparrow 2009; Thomson and Irwin 2016), the farmer may obtain substantially less pollination than expected. This can be seen in our general model with negative interactions (Figure 4d-f).

As expected, positive growth in capitals or positive interactions between capitals led to more ES provision than a static model predicts, while negative growth or interactions led to less ES provision. The effects of the dynamics were not evenly distributed across the decision-space (as shown by the coloured shading in Figure 2), and by managing towards a certain part of this space, depending on the structure and dynamics of the system, decision-makers can either maximize the positive effects of positive dynamics or minimize the negative effects of negative dynamics.

Depending on the production function, there may even be combinations of capitals where ES provision is not affected at all by the dynamics of capitals. This is apparent in both the Cobb-Douglas case, where the marginal effect of each capital saturates, and in the Leontief case where the capitals are complements. In both cases, there are areas in the decision-space where one of the two capitals is the limiting factor for ES provision, and any changes in the other capital have little to no effect on overall ES provision. This means that any dynamics, either positive or negative, that act on the non-limiting capital have no effect on overall ES provision, except when they change the amount of that capital enough that it reaches the point where it becomes the limiting factor.

One general pattern we observed was that negative interactions tended to have the greatest impact on outcomes when both capitals were employed in approximately equal amounts. This could be of particular concern if managers try to gradually shift towards natural capital-based management, for example if they have limited resources to invest in natural capital or if they do not trust natural capital enough to fully commit to it. In such a case, introducing natural capital to a system dominated by technology could increase the effects of negative interactions, providing a lower level of ES than expected in the short term, at least until the amount of human-derived capitals is reduced. If managers assume that more capital will lead to more ES provision, this could cause them to wrongly conclude that the natural capital is ineffective. For example, habitat conservation to promote biological pest control may provide fewer benefits than expected in a landscape with high use of synthetic pesticides, if the pesticides impact both the pests and their predators (Tscharntke et al. 2016). Switching such a system from a management strategy based on human-derived capital to one based on natural capital may require a certain level of trust by managers to reduce the amount of human capital used before they are able to experience the full benefits of the natural capital.

4.2. Assumptions and limitations

Our modelling approach enables us to identify generalized patterns of how more complex relationships among drivers affect ES provision and to discuss the implications of these patterns for managers, but this also means that these patterns and implications should be interpreted carefully within the context of our simplifying assumptions. For example, what our model conceptualizes as single variables for natural and human-derived capitals actually encompass multiple drivers each, which may not necessarily all behave the same (e.g. Felipe-Lucia et al. 2018); ES are not provided in isolation, but rather multiple ES can share common drivers and interact with each other (e.g. Botzas-Coluni et al. 2021); drivers may show more complex dynamics than those we explored here, like feedbacks and threshold effects (e.g. Watson et al. 2021); and the distinction between natural and human-derived capitals is not necessarily clear-cut, as illustrated by the classification of honey bees as ‘human-derived capital’ in our pollination example. Adding any of these additional sources of complexity to our model could plausibly change the specific ES outcomes observed. Thus, our model is not necessarily intended to provide definitive conclusions about how specific types of dynamics will affect ES provision. Rather we developed a model to illustrate that, even with the simplest level of interactivity, these dynamics are important and affect outcomes under a range of plausible, though highly simplified, systems.

Our modelling framework also represents a conceptually simplified view of environmental decision-making, where decision-makers are limited to just two alternative strategies and where decisions are made based solely on the expected provision of a single ES. In reality, decisions may have impacts on multiple ES, different management strategies affect not only the amount of ES provided but also the timing of ES provision, the degree of certainty with which that provision can be predicted, and the amount of control managers have over ES provision, and a decision made now is constrained by past decisions (e.g. whether a decision-maker has been trained to use a particular technology) and in turn constrains future decisions (e.g. agricultural practices now impact the future provision of multiple cropland ES; Hoeffner et al. 2021). Beyond just the amount of ES provision, managers must also consider a system's resilience or ability to respond to future shocks and changes while maintaining desired ES benefits to people (Bennett et al. 2021). Our model outcomes and recommendations provide important information to decision-makers that they would not otherwise get from static models; however, they should be regarded as just one piece of the picture for decision-makers who, in light of these other considerations, may have incentives to make decisions that are less-than-optimal in terms of ES provision alone.

For example, one common argument in favour of ecosystem-based management is that natural capital is often multifunctional and can provide additional benefits beyond its primary function (Moberg and Rönnbäck 2003; Madureira and Andresen 2014), although it can also lead to disservices as well (Lyytimäki and Sipilä 2009). By increasing diversity and redundancy, natural capital can also enhance the resilience of ES provision and human wellbeing and reduce the risk of future shocks that undermine the functionality of the system (Biggs et al. 2012), while human-derived capitals generally require ongoing maintenance to maintain their function over time. Even though some human-derived capitals, such as urban stormwater infrastructure, are beginning to be designed for multiple benefits (Fletcher et al. 2015), many others, such as a water treatment plant or a pesticide, are designed to perform a single function as efficiently as possible. The multiple benefits provided by natural capital may make it a more attractive option than technology in some contexts. On the other hand, natural capital-based management strategies rely on complex ecosystems to provide benefits, which means that they can take more time to implement (Blaauw et al. 2014), can be less flexible to changes in demand (Holling and Meffe 1996), and can provide less predictable levels of benefits (Georgis and Gaugler 1991) than human-derived capital that performs similar functions. These logistical concerns may favour human-derived capital over natural capital in some contexts, even when both provide similar functions. While important, concerns about multifunctionality and manageability do not undermine our case for the importance of understanding the dynamics and interactions of different components: being able to more accurately estimate long-term ES provision helps decision-makers better evaluate all the costs and benefits of alternative management strategies.

Beyond multifunctionality, there is also evidence that relying more heavily on human-derived capitals for ES co-production leads to more externalities, impacting not just the focal ES but also the bundle of ES provided by the landscape. For example, more technology-intensive marine aquaculture systems were found to have more trade-offs with other ES, such as nursery habitat for squid and nutrient cycling (Outeiro et al. 2017). Future work could explore these broader impacts of management decisions with models of multiple ES, where ES are linked by shared capital drivers.

One aspect of a decision that is less easily evaluated in terms of costs and benefits is the replaceability of capitals (Bishop and Welsh 1992). Focusing management only on human-derived capitals, particularly those with negative environmental impacts, increases the risk of losing important forms of natural capital. Once lost, many types of natural capital, such as the topsoil from a field or a species of medicinal plant, are extremely difficult if not impossible to replace (Shanley and Luz 2003; Pimentel 2006). Although many human-derived capitals are more replaceable, others, such as traditional management knowledge and skills, are at risk of being permanently lost if not actively preserved and shared (Gómez-Baggethun et al. 2010). Losing irreplaceable capitals can also undermine the resilience of the system: even if these capitals are not needed now, they still serve as management options that may be useful in the future if conditions change, a benefit that has been conceptualized as 'maintenance of options' (Díaz et al. 2018). The irreplaceability of certain components may mean that some management strategies are unacceptable, even though they are logistically feasible and provide the desired amount of ES, if they would result in the loss of an irreplaceable component and constrain future management possibilities.

5. Conclusion

Even as environmentalists call for the conservation of natural capital that underpins ES provision, it is often assumed that technological developments will be able to compensate indefinitely for environmental degradation (Ayres et al. 2001). To ensure the sustainable future provision of the ES that support human wellbeing, a clearer understanding is needed of when and how much to rely on natural capitals and how much to use human-derived capitals for ecosystem service provision. Our modelling work illustrates how the substitutability of natural and human-derived capitals may be influenced both by how different capitals change over time and how they interact with each other. Understanding these dynamics is crucial for determining expected long-term ES provision and avoiding surprise outcomes.

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