Spatial Economic Analysis

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/rsea20

Valuing biodiversity and resilience: an application to pollinator diversity in the Stockholm region

Gustav Engström , Åsa Gren , Chuan-Zhong Li & Chandra Kiran B. Krishnamurthy

To cite this article: Gustav Engström , Åsa Gren , Chuan-Zhong Li & Chandra Kiran B. Krishnamurthy (2020) Valuing biodiversity and resilience: an application to pollinator diversity in the Stockholm region, Spatial Economic Analysis, 15:3, 238-261, DOI: 10.1080/17421772.2020.1784988

To link to this article: https://doi.org/10.1080/17421772.2020.1784988

SPATIAL ECONOMIC ANALYSIS
2020, VOL. 15, NO. 3, 238–261
https://doi.org/10.1080/17421772.2020.1784988

Routledge
Taylor & Francis Group

Regional Studies Association

Valuing biodiversity and resilience: an application to pollinator diversity in the Stockholm region

Gustav Engström[a], Åsa Gren[b], Chuan-Zhong Li[c] and
Chandra Kiran B. Krishnamurthy[d]

ABSTRACT
This paper characterizes the value of biodiversity and ecosystem resilience by formalizing a stochastic dynamic bioeconomic model of pollinator diversity under climate changes, with an application to oil rapeseed production in the Stockholm region of Sweden. It studies the optimal provision of semi-natural habitat for two different pollinator bee species: bumble bees and solitary wild bees. It is found that, despite being less effective, solitary bees hold considerable resilience value due to the differences in how the two species respond to temperature shocks. The paper also discusses the role of spatial aspects, in particular the reduced pollination effectiveness due to spatially uneven allocation of semi-natural habitats. It is found that spatial unevenness leads to an increase in the habitat provision, with an attendant reduction in the resilience value of solitary bees.

KEYWORDS
climate change, bioeconomic model, semi-natural habitat, pollination service, resilience value

JEL C61, Q20 (Q24), Q57
HISTORY Received 31 January 2019; in revised form 3 June 2020

INTRODUCTION

We live in a world of change, characterized by complex adaptive social–ecological systems in which resilience, defined as an ecosystem's ability to maintain its basic functions and controls under disturbances (Holling, 1973; Walker & Salt, 2012), becomes crucial. It is thus important to assess explicitly how to build, maintain and increase resilience of ecological systems to ensure the continued provision of ecosystem services central to human welfare (Folke et al., 2011).

CONTACT
[a] The Beijer Institute for Ecological Economics, Royal Swedish Academy of Sciences, Stockholm, Sweden; and Global Environmental Dynamics and the Biosphere, Royal Swedish Academy of Sciences, Stockholm, Sweden.
[b] The Beijer Institute for Ecological Economics, Royal Swedish Academy of Sciences, Stockholm, Sweden; and The Stockholm Resilience Center, Stockholm University, Sweden.
[c] **(Corresponding author)** chuanzhong.li@nek.uu.se
The Beijer Institute for Ecological Economics, Royal Swedish Academy of Sciences, Stockholm, Sweden; Department of Economics, Uppsala University, Uppsala, Sweden; and School of Economics, Sichuan University, Chengdu, China.
[d] The Beijer Institute for Ecological Economics, Royal Swedish Academy of Sciences, Stockholm, Sweden; Department of Forest Economics, Swedish University of Agricultural Sciences, Umeå, Sweden; and Center for Environmental and Resource Economics, Umeå, Sweden.

Supplemental data for this article can be accessed at https://doi.org/10.1080/17421772.2020.1784988

The significance of biodiversity in an ecosystem service and resilience context has been extensively discussed (e.g., Balvanera et al., 2006; European Union, 2015). This includes the functional aspect of biodiversity, that is, the identity, abundance and range of species traits, which are also considered to be of key importance to understanding the effects of biodiversity on many ecosystem services (Díaz et al., 2007). A decline in biodiversity can lead to a decline, sometimes dramatic, in ecosystem service provision, unless alternative species capable of providing a very similar service are available. Thus, building on the notion of redundancy, sustaining diversity within functional groups is important. This aspect of biodiversity, referred to as response diversity, has been much less studied (cf. Jansson & Polasky, 2010) despite its salience in building resilience.

Before resilience can be managed, either for the services derived from biodiversity or for biodiversity itself, it should be quantified. A common approach has been to attach economic values to individual species or other elements of ecosystems (cf. Brock & Xepapadeas, 2003; Li et al., 2018). In the recent literature, researchers have also developed methods to assess the accounting prices of the underlying stocks that generate resilience services (cf. Li et al., 2016; Matsushita et al., 2017; Mäler & Li, 2010; Walker et al., 2010). Matsushita et al. (2017), for example, investigate the shadow value of resilience in complex natural land as pollinator habitat, along the lines of Mäler and Li (2010) and Walker et al. (2010). In view of the fact that a potentially significant component of the value of biodiversity lies in its ability to maintain and build resilience, there is a need to develop tools and methods that complement commonly used approaches to the valuation of biodiversity, allowing one to account for the resilience value of biodiversity.

While the effects of climate change on specific species of plants and insects has been investigated extensively (for a review, see Pudasaini et al., 2015), few studies attempt to look at trade-offs between different species in a resilience context and none, to our knowledge, has applied a bioeconomic modelling framework explicitly quantifying key trade-offs involved. The challenge of meeting rapidly increasing food demand through crop production, which depends upon a whole host of ecosystem services including pollination, means that the task of valuing resilience using biodiversity as a proxy acquires even greater importance. In this context there is a pressing need to better understand the complex interactions between climate, crops and biodiversity (FAO, 2008, 2011).

This paper is concerned with the role of the diversity of wild pollinator bees underpinning oil rapeseed production in a Northern European setting. We are interested in assessing the effects of changes in land use of key pollinator habitats (semi-natural habitats – SNHs) along with those of climate change, which is anticipated to significantly affect key pollinators. We focus on two wild pollinator species, bumble and solitary bees, which belong to the same functional group, but, due to differences in life traits, respond differently to both climate change and access to SNHs.[1] These aspects indicate certain trade-offs in play with regards to rapeseed production: larger semi-natural areas, while beneficial from a pollination potential perspective, lead to lower production today. In addition, functional aspects of biodiversity also matter for this choice: solitary bees and bumble bees contribute differently to pollination and are affected differently by different aspects of climate change. Consequently, there is scope for preservation of both bee species in an optimally managed regime, despite their differential pollinating potential.

In any case, many aspects of management are of interest here, including the value of resilience services provided by species diversity, in a functionally heterogeneous context. To explore these and other aspects, we develop a stochastic dynamic bioeconomic model to determine the optimal level of SNHs, which serve as a habitat for both pollinating bee species, in connection to the oil seed rapeseed (OSR) fields. The essential links between temperature, bee population dynamics and the pollination potential of the two pollinator species groups are all taken into account. We calibrate the model to oil rapeseed production in Sweden, drawing on parameters and insights from the Swedish literature. Since the population of bees in the landscape we consider is not saturated, the two bee population dynamics are considered to evolve independently of one another.

Using the model, we simulate the optimal pattern of SNHs, the optimal mix of the two pollinator species groups and the optimal value function of oil rapeseed production. We also discuss how the marginal value of pollinator stocks for resilience services may be derived.

The results indicate that while the solitary bees may appear at a first glance to be redundant in the presence of the bumble bees, they have a sizeable resilience value under the risk of temperature shocks. As the model parameters are subject to uncertainty, we also conduct sensitivity tests under different assumptions regarding temperature evolution. We find, among other things, that an increase in the stochastic variation in temperature has a negative effect on the optimal value function, but a weakly positive effect on the steady state of the bee stocks. Persistence in temperature, on the other hand, is found to have a positive effect on the value function and bee stocks, but a negative effect on the provision of SNH. Concerning the value of solitary bees for resilience services, we find that the smaller the bumble bee stock, the greater the value of the solitary bees for their resilience services. In view of the fact that spatial aspects are integral to the analysis (e.g., since flying distance of the two bees differ), we explore the extent to which our insights differ under different spatial patterns of land uses. To keep the analysis tractable, we make use of an empirically observed relationship for bees: a more even distribution of SNH over a landscape leads to a better harvest, meaning that we use the evenness of the SNH distribution as our spatial dimension. The simulation results indicate that increased unevenness substantially reduces the optimal value function and leads to greater provision of SNH, to compensate for the reduced pollination potential from its uneven distribution.

The paper is structured as follows. The next section provides the ecological background to the dynamics of the two pollinator bee species. The third section lays out the model framework and details, while the fourth section discusses the parameters of the model. The fifth section presents the main results and provides a discussion of the effects of changes in key parameters. The sixth section concludes with a discussion of the implications of the findings.

BACKGROUND AND ECOLOGICAL ASPECTS

More than 75% of the world's crop plants rely on pollination by animal vectors, and the annual value of global crops directly affected by pollinators has been estimated at US$235–577 billion (FAO, 2016). The analysis will be located in the Nordic region (Stockholm region, to be more specific), and focused on wild pollinators, in view of their significantly greater effectiveness in pollinating (Garibaldi et al., 2013). More specifically, we focus on two wild pollinator groups relevant in a Northern European landscape context: (1) bumble bees, represented by the bumble bee species *Bombus terrestris*; and (2) solitary bees, represented by the pollinator species *Osmia bicornis* (prev. *rufa*). These two pollinator groups are of significant importance as pollinators of mass flowering crops in these landscapes and thus to the crop producing potential. The two bee species groups also contribute greatly to the pollination of wild flora (Linkowski et al., 2004). Both groups are potentially effective pollinators of oil rapeseed (a crop of increasing global significance; OECD & FAO, 2016) and, in this aspect, can be said to belong to the same functional group.

Although both wild pollinator species (*B. terrestris* and *O. bicornis*) are pollen-seeking pollinators, which are typically stated to be several times more effective than domesticated honey bees (*Apis mellifera*) (e.g., Stanley et al., 2013), there are no studies directly comparing the potential differences in pollination potential between the two species in focus here. In order to quantify the differences in pollination potential, we assume that body size can be used as an indicator for pollination efficiency, thereby assuming that the larger pollinator species, *B. terrestris* (bumble bee), is a more effective pollinator due to its larger body size. This assumption is based on the reasoning that the ability of these types of pollinators to 'buzz pollinate', that is, to shake loose additional pollen by vibrating their wings, should become more effective with increasing body size (De Luca et al., 2019). It therefore follows, based on an average body size of 11–17 mm of a *B. terrestris* worker and an average body size of 8–10 mm of a male *O. bicornis*, that *B. terrestris* is, roughly, doubly as effective.[2] Another difference in life traits between the two pollinator groups is flying distance, with an advantage for the bumble bees due to their ability to fly longer distances when foraging (Knight et al., 2005).

Effects of temperature increase on the two pollinator groups and host plants

In view of the observational evidence that many ecosystems are particularly affected by temperature increases (IPCC, 2007), we will focus only on the effects of temperature increase as the basis for our climate change scenario. The effects of climate change upon ecosystems in general can be categorized into direct and indirect effects. A substantial body of work has emerged around phenological effects (indirect effects) of climate change, such as shifts in flowering time and insect emergence and potential temporal mismatches between the two, with severe demographic consequences for the species involved (e.g., Bartomeus et al., 2011; Burkle et al., 2013). Flowering phenology in Northern ecosystems is largely determined by snowmelt timing and the accumulation of daily (or monthly) mean air temperature of the preceding months (Diekmann, 1996). In contrast, the emergence of overwintered bumble bees is determined by the daily maximum ambient temperature at local hibernating points (Alford, 1969). In any case, early-flowering plants are anticipated to advance their flowering during a warm spring, whereas bumble bee queen emergence may remain unaffected by spring temperatures, causing a mismatch between emergence of the bumble bee queens and their food sources,[3] with significant adverse implications for wild bee populations.[4]

However, relatively little research has addressed physiological effects (or direct effects), although these effects are likely to have essential consequences for plant–pollinator interactions (Scaven & Rafferty, 2013). While Deutsch et al. (2008) point out that the direct effect of temperature increases on insect species at higher latitudes may actually enhance their performance, temperature changes may also have negative effects, for example, through change in the duration of development in insects. If development is remarkably accelerated due to warm temperature, multivoltine organisms, such as *B. terrestris*, might use the saved time for one or more additional generations in the growing season (Robinet & Roques, 2010). In contrast, univoltine species, such as *O. bicornis*, may face the problem of reaching their overwintering stage too early and might be exposed to unsuitable temperatures.[5] In any case, it is evident that climate change-induced temperature increases can lead to very different implications for the two bee pollinator groups (Table 1).

Parameterization of ecological effects

Table 1 presents the relevant direct and indirect effects of temperature increase on the two pollinator groups, represented by *B. terrestris* and *O. bicornis*. It is important to note that studies from a production function perspective, on the interrelationship between direct and indirect effects of temperature increase and pollinator density in the landscape, are missing. The relationship between other drivers of change, for example, land-use change and pollinator density, on the other hand, is well studied (e.g., Steffan-Dewenter et al., 2002). To better assess the potential impacts of climate change on food provisioning and to design more sustainable management strategies for food production, better information on the quantitative effects of climate change on essential parameters such as pollination potential is needed. While mechanisms counteracting the negative effect of temperature increase on the survival of univoltine species such as the *O. bicornis* have been identified, the degree to which they assist in responding to climate change is unknown.[6]

Another parameter potentially affecting the value of oil rapeseed production is pollination efficiency. To better assess the economic implications of change in the populations of the two pollinator groups, better knowledge regarding the degree to which the two pollinator groups differ in pollination efficiency is needed. To our knowledge the bulk of this type of information is on the

Table 1. Effects of temperature increase on bumble and solitary bees.

	Pollinator species	
	Bombus terrestris	**Osmia bicornis**
Direct effect (physiological)		
Effect on the duration of development due to increased temperatures	The multivoltine *B. terrestris* can balance this effect by additional generations in the growing season	The univoltine *O. bicornis* cannot compensate with additional generations
Level of effect	No effect	22.5°C in a hut results in a 16.1% rate of adult mortality
Indirect effect (phenological)		
Mismatch with key plant species *Salix* (willow)	The impregnated *B. terrestris* queens need pollen for their eggs. They emerge early in the season when *Salix* is the major pollen source	The *O. bicornis* females are not as dependent on *Salix* for their pollen needs due to the later emergence in the season
Level of effect	50% drop in pollination	No effect

Note: Uni(multi)-voltine species have one (more than one) brood of offspring per year; *prepupal* refers to the stage between the larval and the pupal stages of an insect; and *adult eclusion* refers to the emergence of an adult insect from a pupa or a larvae from an egg. A 'hut' refers to the dwelling of wild bees.

difference in efficiency between wild and domesticated pollinators (e.g., Garibaldi et al., 2013; Javorek et al., 2002). A partial list of other potentially relevant parameters to assess in this context includes sensitivity to parasites under temperature increase, response to elevated CO_2 and response to change in precipitation pattern.[7]

THE MODEL FRAMEWORK

We consider a dynamic stochastic general equilibrium bioeconomic model with three variables that evolve over time (i.e., stock variables): temperature and the stock of the two wild pollinator species, represented by bumble and solitary bees, available for pollination services. To focus on the role of the two pollinator species, we abstract away from detailed modelling of various subspecies. For tractability, we consider the simplest spatial representation in our benchmark model, a representative area located in a field from which the bees can reach any location in an OSR field. Subsequently, we discuss a simple way of assessing the effect of spatial distribution of the SNH, inspired by very suggestive findings from observational studies of bee behaviour. Using the well-known and widely used Camargo evenness index, we assume that the pollination potential is increasing in the evenness of distribution of the SNHs, with more uneven distributions (e.g., concentrated at fewer points) having lower pollination potential than more even distributions (e.g., uniformly spherical patches equidistant from one another).

As to the model details, we consider that, at time period t, the control variable is the area devoted to semi-natural land, x_t (with $1 - x_t$ as the area devoted to the rapeseed crop production, normalizing area of the field to unity),[8] with T_t, B_t, S_t, respectively, standing for temperature, stock (density, to be precise, in view of the area normalization) of bumble bees and solitary bees.[9]

Time $t = 0, 1, 2, \dots, \infty$ is discrete. The timing of action is intuitive and conventional: the farmer observes the stock of bees at time period t, and makes a decision regarding the area to be set aside for this time period which, in turn, will determine stock of both bee groups in the next period. Thus, each year's decision regarding the area to be set aside is based upon known stocks of the two groups of bees, while uncertainty surrounds the effects of this year's area set-aside decision upon stock regeneration. More precisely, the farmer bases his decision of the amount of land to be set aside, x_t, upon the stock of bees, (B_t, S_t), at time t, where the effects of x_t upon B_{t+1} and S_{t+1} are random, depending upon the realized temperature and other factors. Since uncertainty intervenes between the farmer's decision for period t and that for period $t+1$, the farmer does not directly choose B_{t+1} and S_{t+1}, unlike in many resource economics frameworks.

We assume that the dynamics of temperature are exogenous and follow a simple AR(1) process:

$$T_{t+1} = \mu + \rho T_t + \epsilon_t, \tag{1}$$

with the initial temperature normalized to $T_0 = 0$. With the intercept parameter μ and the persistence parameter ρ, we have the mean temperature $\mu/(1-\rho)$. The term ε_t is a stochastic variable assumed to be drawn from a distribution with zero mean and constant variance, and is i.i.d over time. The year is conceived as beginning in March (early spring) when the bees normally awaken. Over the summer, they live on SNHs and provide pollination services over the rapeseed fields. The provision of semi-natural area at year t affects the stocks of bees next year, which evolve according to the following transition equations:

$$B_{t+1} = f(x_t, T_{t+1})B_t^{\alpha} \tag{2a}$$

$$S_{t+1} = g(x_t, T_{t+1})S_t^{\alpha}, \tag{2b}$$

where $\alpha \in (0, 1)$ denotes the exponent on the growth function, which is of the power function form. The productivity functions, $f(\cdot)$ and $g(\cdot)$, are defined with respect to the current choice of SNH, x_t, and the realized temperature in the next time period, T_{t+1}.[10]

Note that our functional forms for the bee stocks in equation (2) suggest that the bee population development proceeds independently for the two bee types. The reason is that the concentration of bees in the landscape we are modelling is not considered to be saturated, meaning that the two bee types are regarded not to be in competition. This is in contrast to the case of two interacting crop species that compete for nutrients, as modelled by Brock and Xepapadeas (2003).

From the second section, it is known that bumble bees are more vulnerable to spring temperature than solitary bees. If the spring is very warm, bumble bees (i.e., the queens) awaken before the blossoming of the flowers (their main food source), due to which their mortality rate is likely to be high. In addition, bumble bees are more dependent on semi-natural areas, with a requirement of at least 2% of total cultivable area (Westphal et al., 2003). Thus, both productivity functions are related positively to the share of SNH and negatively to temperature (Pyke et al., 2016). More specifically, we assume the following functional forms:

$$f(x_t, T_{t+1}) = A_b(1 - \exp(-\theta_b x_t))^c \exp(-\gamma_b T_{t+1}) \tag{3}$$

$$g(x_t, T_{t+1}) = A_s(1 - \exp(-\theta_s x_t)) \exp(-\gamma_s T_{t+1}) \tag{4}$$

where $A_b, A_s, \theta_b, \theta_s, \gamma_b, \gamma_s$ and c are all positive parameters, with parameters for solitary and bumble bees differentiated by the subscripts s, b, respectively. To capture the adverse effect of temperature increases upon the growth of bees, we use a net-of-damage function approach, which, following Golosov et al. (2014), is assumed to be exponential: $\exp(-\gamma_i T_{t+1})$, $i = b, s$.

With current (starting) period temperature normalized to $T_0 = 0$, we have the reference level $\exp(-\gamma_i T_0) = 1$, while $\exp(-\gamma_i T_t) < 0$ for $T_t > 0$. This implies that a higher temperature increase would cause more damage, but as long as the increase is finite, this net-of-damage function will remain positive. Also, we do not assume any damage for some modest cooling with $T_t < 0$ and treat this as if it were $T_t = 0$. Note that while the parameter A_i, $i = b, s$, denotes the abundance scales of the bee groups, θ_i represent the effect of semi-natural area on the birth rate of the bee groups. The parameter c appears only for the bumble bee group in equation (2) to reflect the crucial dependence of bumble bees on some ‘minimum’ level of the semi-natural shares (of 2%, see above). With $c > 0$, the expression $(1 - \exp(-\theta_b x_t))^c$ represents a convex–concave relationship with respect to x_t, with its value being virtually zero at very low shares of semi-natural area (it is first convex, and turns concave when x rises). To reflect the fact that bumble bees are more vulnerable than solitary bees (as detailed in the second section), we set $\gamma_b > \gamma_s$.

We turn next to the farmer’s objective function, which is the profit from harvest:

$$\Pi(x_t, B_t, S_t) = p_t(1 - x_t)H(B_t, S_t). \tag{5}$$

where $H \in (0, 1)$ is a harvest potential function depending positively on the stock of the bees inherited from the previous period; and p_t denotes the maximum economic value of the products derived from a unit area of the rapeseed field (say 1 ha) under perfectly ideal pollination conditions.

This formulation also illustrates the inter-temporal tension in many resource extraction problems: the myopic solution of $x_t = 0$, while clearly optimal for the current period, equally certainly reduces the stock of bees in the next period, leading to reduced future yield. This is the standard consumption–savings trade-off faced by an economic agent: reduced saving today leads to less capital accumulation and reduced output tomorrow, where in our case saving and output are represented by the semi-natural area set aside and stock of bees.

The dependence of harvest upon pollination is represented by the generalized logistic function:

$$H(B, S) = \frac{1}{1 + A_h \exp(-r(B + wS))}, \tag{6}$$

with $A_h, r > 0$. As detailed in the second section, bumble bees are larger in size and can fly farther into the wildflower field from the habitat, and thus have a larger pollination potential than solitary bees. Since both bee types provide the same service, pollination, $Z := B_t + wS_t$ from equation (6) may be considered the total pollination service provided by both bee types, with $w \in (0, 1)$ a scaling factor that converts a solitary bee into some equivalent number of bumble bees (from the perspective of pollination service).[11] Clearly, H is increasing in the pollination service provided by the effective stock of bees, which in turn are decreasing in the change in temperature T, as detailed above. Thus, the profit function is decreasing in temperature T, and increasing in the bee stocks B_t and S_t.

We note that r, which is the ‘growth rate’ (or slope) of the harvest function, is a key parameter, with larger values of r leading to increased harvest for the same quantity of pollination service. In our subsequent spatial explorations, we assume that the evenness index determines r, with more uneven distributions of the SNH leading to reduced values of r. The parameter A_h is related to the benchmark pollination level in the absence of bees. For example, if $A_h = 4$, then the basic pollination potential (from wind and birds) becomes $H(B, S) = 1/(1 + 4) = 0.20$.

The discounted present value of the income streams at the start of the planning horizon is:

$$V_0 = \max_{(x_t)} E_0\left[\sum_{t=0}^{\infty} \beta^t p_t(1 - x_t)H(B_t, S_t)\right], \tag{7}$$

where $\beta \in (0, 1)$ is the discount factor; and E_0 the expectation of the discounted sum of future profits conditional on the information available at time period 0. We are now interested in optimizing the objective functional (equation 7) subject to the state transition equations (1) and (2). The Bellman equation for the associated dynamic programme then reads:

$$V(B_t, S_t, T_t) = \max_{(x_t)} [p_t(1 - x_t)H(B_t, S_t) + \beta E_t[V(B', S', T')]], \tag{8}$$

with a prime denoting variable corresponding to the next time period, $t + 1$ (Stokey et al., 1989, p. 11). Together with the state transition equations (1) and (2), the first-order optimality condition (see section A1 in the supplemental data online) enables one to determine the optimal feedback decision rule:

$$x_t^* = x(B_t, S_t, T_t), \tag{9}$$

and the optimal value function, $V(B_t, S_t, T_t)$, at any time $t = 0, 1, 2, \ldots, \infty$.

With the optimal decision rule and the value function, we can study the marginal value of bumble and solitary bees, $V_B'(B_t, S_t, T_t)$ and $V_S'(B_t, S_t, T_t)$, respectively, as well as the marginal cost of a temperature change $V_T'(B_t, S_t, T_t)$. In particular, we are interested in the value contribution of solitary bees including their resilience services. Due to the stochastic nature of our problem, it is not possible to derive the optimal time sequence at the start of the planning horizon as the deterministic case. The best we can do is to apply the optimal decision rule to assess the expected value $E_t[V(B', S', T')]$ and to simulate the possible sequences of the future states $(B_{t+n}, S_{t+n}, T_{t+n})$ for $n = 1, 2, \ldots, \infty$, with all available information at time t. Using the simulated time sequences, we will examine the asymptotic probability distribution of the bee stocks and to what extent they depend on the model parameters.[12]

MODEL PARAMETERIZATION

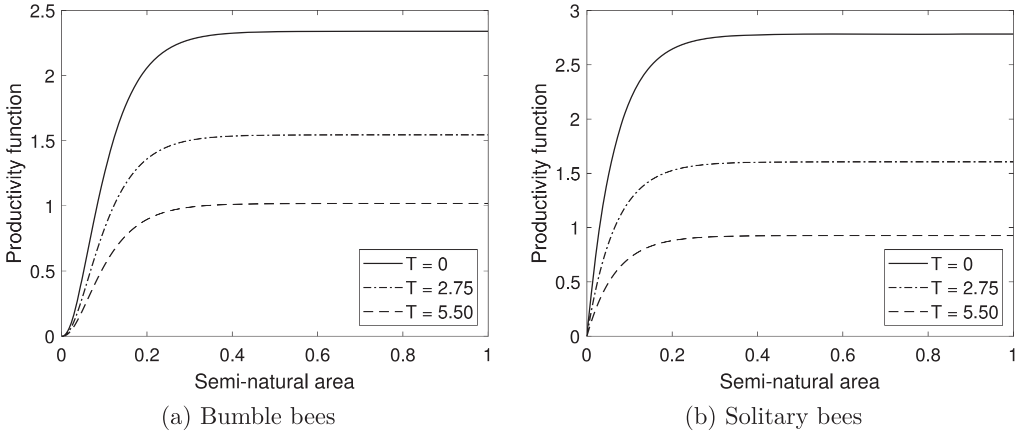
Concerning the temperature dynamics (1), we estimate a de-meaned version of the model:

$$(T_{t+1} - \bar{T}) = \rho(T_t - \bar{T}) + \epsilon_t, \tag{10}$$

using the annual average time-series data for the Stockholm region with $\bar{T}$ as the overall mean (SMHI, 2006). The relevant estimates are $\hat{\rho} = 0.26$ for the persistence parameter ρ and $\hat{\sigma} = 0.96$ for the standard deviation of the error term ε_t. For the stock transition equations (equation 2), however, there are little empirical data available for econometric estimation of the parameters. First, the density of the bees, namely the number of bees disposable for pollinating a unit of the rapeseed field, remains unknown, although there are rough estimates on the visit frequency at selected sites (Öckinger & Smith, 2007). Thus, we rely on other data sources to infer model parameters. The computations based upon the literature suggest that it appears reasonable to assume that about 4000 bumble bees are available for pollination service under current climatic conditions.[13] As solitary bees are more abundant, we assume them to have twice the bumble bee population, meaning that $B_0 = 4000$ and $S_0 = 8000$/ha.

Next, we parameterize the productivity functions $f(\cdot)$ and $g(\cdot)$ in equations (3) and (4) for the bumble bee and solitary bee groups. As previously discussed, both groups are potentially effective pollinators of oil rapeseed, belonging to the same functional group, but exhibiting differences in many important life-traits and will react differently to climate change.[14] Based on figures provided in Kudo et al. (2004),[15] we believe that the climate damage parameters can be reasonably approximated to be $\gamma_b = 0.25$ and $\gamma_s = 0.20$ for the bumble bees and solitary bees, respectively. For these parameter values, following an increase in the annual mean temperature by 1°C, mortality rate increases by 25% for bumble bees and reduces by 20% for solitary bees, which appears to be reasonable for the Northern European landscape context. Finally, due to the lack of detailed knowledge on the effectiveness of semi-natural areas for self-regeneration of the two bee groups, we calibrate them to be identical, with $\theta_b = \theta_s = 15$ and $A_b = 2.34$, $A_s = 2.78$ (in thousands). This parameter choice implies that over 90% of the attainable pollination effectiveness is reached for both bee types for semi-natural area below 40%.

Figure 1 depicts the two effectiveness functions under different temperature increase assumptions. Note that for bumble bees, the curve is strictly convex (and close to zero) at levels of semi-natural area below 2%, whereas this is not the case for solitary bees.



(a) Bumble bees (b) Solitary bees

Figure 1. Productivity functions for the two bee types.

To calibrate the harvest potential function in equation (6), we first set $A_b = 4$ leading to $H(0, 0) = 0.2$, indicating that, even without the bees, wildflower plants would be pollinated anyway by the wind and by birds. Due to the solitary bees' smaller body size and flight capacity, we set $w = 0.5$, meaning that that two solitary bees are functionally (in pollination service) equivalent to one bumble bee. The pollination coefficient r is set to be 0.5, meaning that over 97% of the land would be pollinated even without solitary bees, with about 10, 000 bumble bees/ha (i.e., one bee/m^2) (Figure 2).

We now move to the economic parameters of the model. In our quantitative analysis, we consider 2019 (say, March) as the start of the planning period and consider annual time increments. The time discount factor is set to $\beta = 0.95$ with an annual pure rate of time preference of 5% in the benchmark scenario. The growth function exponent is set to $\alpha = 0.75$ in the transition equations (equation 2). For the maximum attainable rapeseed value per hectare of the crop land, we assume that $p_t = 1$ (thousands of euros), which is exogenously given. Since 2005, rapeseed yield has largely been between 2.0 and 2.5 tonnes/ha (Peltonen-Sainio et al., 2007), and its price has been about €450 per tonne in Europe (Carré & Pouzet, 2014). These statistics imply that

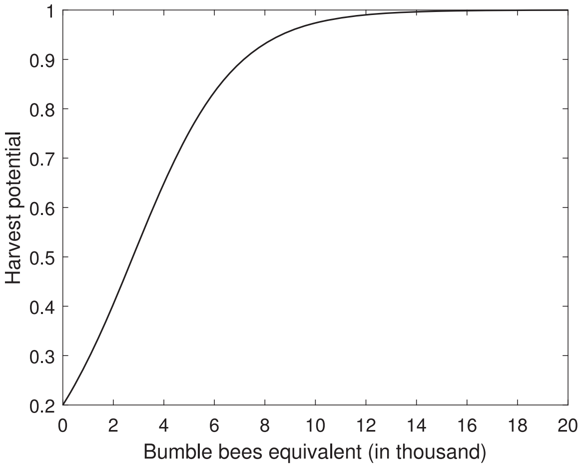


Figure 2. Harvest potential function.

Table 2. Model parameters.

B_0	S_0	A_b	A_s	θ_b	θ_s	γ_b	γ_s	A_h	r
4	10	2.34	2.78	15	15	0.25	0.20	4	0.5
α	β	w	ρ	σ					
0.75	0.95	0.5	0.26	0.96					

the production value of rapeseed ranges from €900 to €1125/ha, which underlies our approximation with $p_t = 1$. Table 2 summarizes all parameters used in our analysis.

QUANTITATIVE RESULTS AND DISCUSSION

Simulation

In this section we apply the value function iteration method (cf. Ljungqvist & Sargent, 2018) to analyse the bioeconomic model to characterize the optimal plans, the pollinator stock dynamics and their shadow values for pollination services. With a discount factor $\beta \in (0, 1)$, the contraction mapping theorem ensures convergence of the value function iteration procedure. We provide very brief description of the simulation framework, with more details provided in section A2 in the supplemental data online.

In brief, we first construct a discrete representation for the temperature variable in equation (1) using the Gaussian-quadrature approach, choosing a nine-state Markov chain for temperature based upon the estimated parameters. Next, we choose a grid of admissible values for the stock of the two pollinator groups, which, together with the Markov temperature state T, represents a three-dimensional array over which the value function is sought. Finally, for each grid node we compute a value function and, using value iteration, continue until convergence to obtain the unique value function.

Benchmark results

The computed value function (in thousands of euros) is depicted in a three-dimensional diagram in Figure 3, conditional on the initial temperature $T = 0$ (see section B in the supplemental data online for graphs of the value functions for other temperatures). The optimal value function increases, as expected, in both bee stocks, but at a decreasing rate. Note that the surface is expected to be lower for a higher initial temperature.

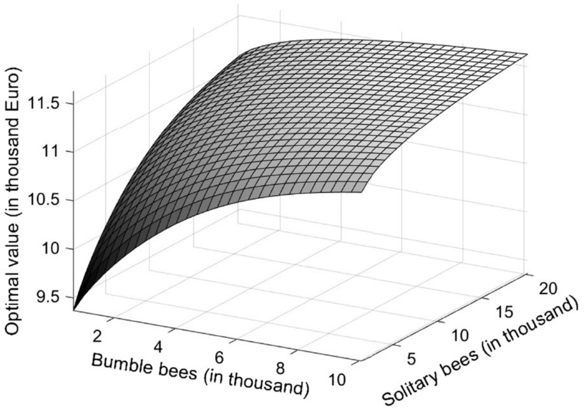
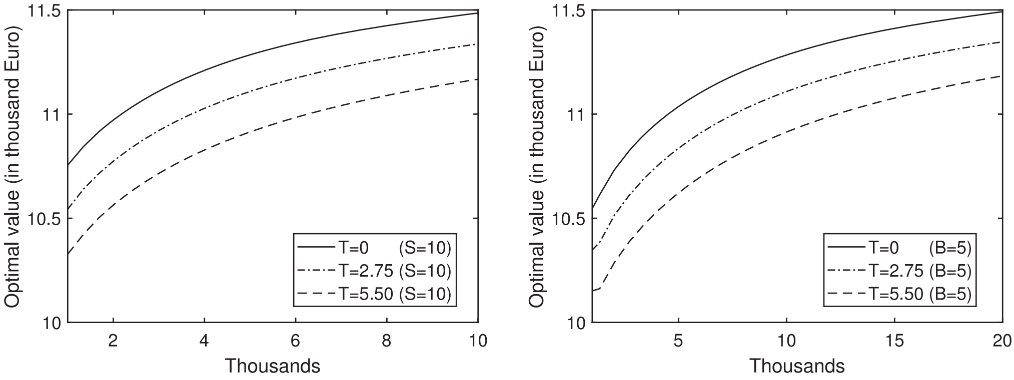
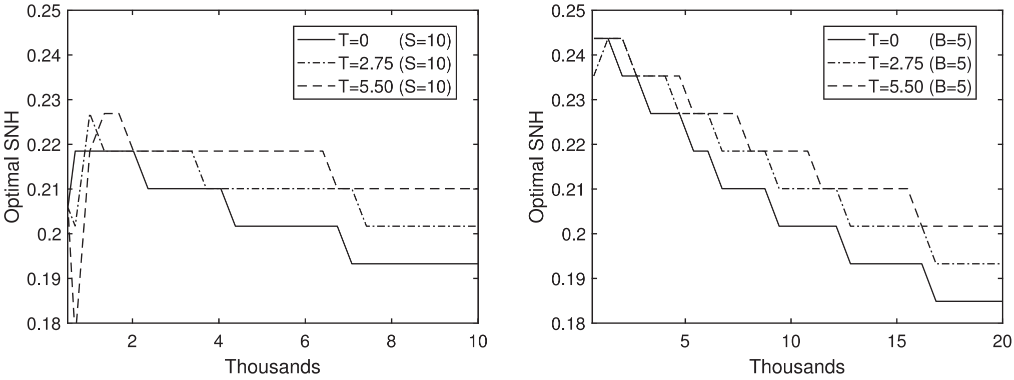


Figure 3. Value function conditional on initial temperature ($T = 0$).



(a) Value function in bumble bees (b) Value function in solitary bees



(c) Policy function in bumble bees (d) Policy function in solitary bees

Figure 4. Optimal value and decision functions under different conditions.

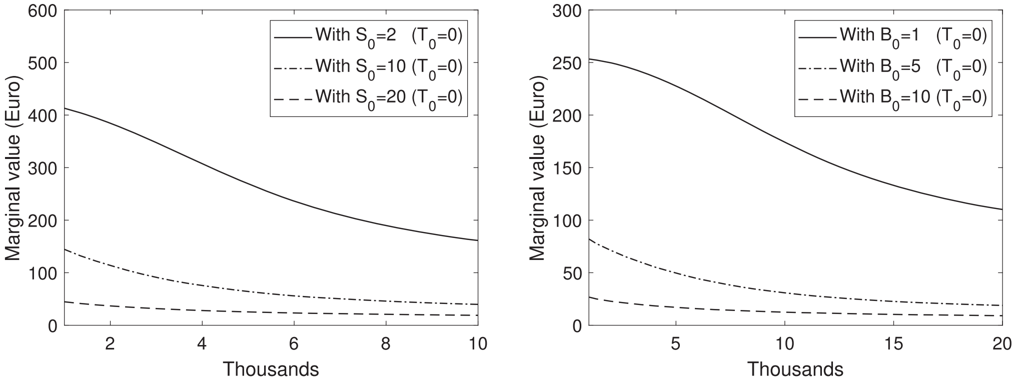
To visualize the effect of changes in both temperature and the bee stocks, we depict the optimal value and decision functions on the optimal SNH with respect to only one bee species at a time, in two-dimensional diagrams, conditional on the stock of the other bee species, in Figure 4 (three-dimensional diagrams for the policy functions are provided in section B in the supplemental appendix for selected temperatures). The graphs in the upper panels of Figure 4 indicate that the optimal (conditional) value function $V(B_t, S_t, T_t)$ in equation (A2) in the supplemental data online is increasing for both bee stocks, that is, in the number of bumble bees (conditional on 10,000 solitary bees/ha) and solitary bees (conditional on 5000 bumble bees/ha), but decreasing in temperature. These results are consistent with our theory that the value function is associated positively with bee stocks but negatively with temperature increases.

For the optimal decision rule $x_t^* = x(B_t, S_t, T_t)$, however, we cannot a priori say anything as regards comparative statics. Both stocks have a direct effect on the harvest via equation (6) and they also affect the future value functions indirectly via their contribution to the future population (see equation 2). Due to the difference in their functional service, they may have different effects on the optimal set-aside of a semi-natural area. As shown in the lower panel of Figure 4, the optimal semi-natural area needed would, in general, decrease in the prevailing bumble bee stock except at very low bee stocks. In response to a temperature increase, we anticipate that optimal semi-natural area will increase, at least partly to compensate for the resulting damage. At very low stocks, we find no regular pattern for the optimal semi-natural area preserved, which we surmise is due to the specific bumble bee productivity functional form. Above a certain stock level (such as $B = 1.3$), semi-natural area and bee stocks become substitutes in the production of future bees, whereas they might be complements below the threshold (at least for certain temperature levels). A reasonable explanation is that at a very low stock level, greater semi-natural area is needed for building up the bee stock, and this is particularly the case with the risk of climate damage.

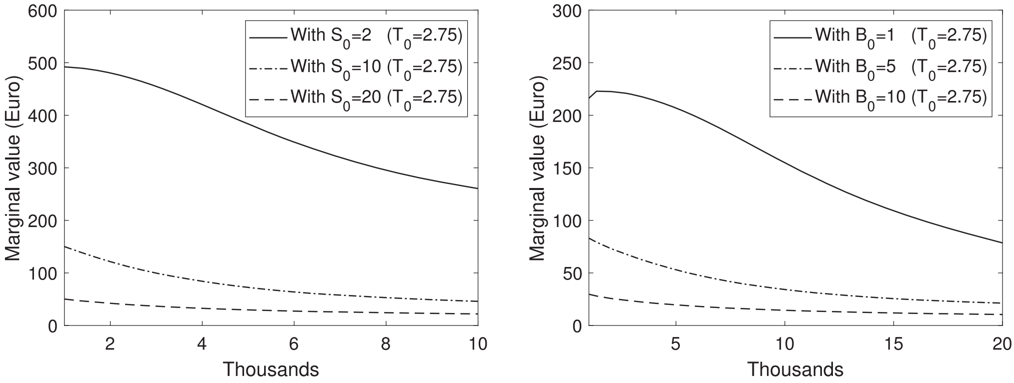
We are interested in the marginal value of the bee stocks under different conditions. The upper panels in Figure 5 depict the marginal value functions conditional on the benchmark temperature level $T_0 = 0$, while the lower panels depict this function conditional on $T_0 = 2.75$. These figures indicate that the marginal value of each bee group is larger conditional on a smaller stock of the other bee group, but as expected, decreases in its own stock level. Comparing the upper and lower panels, we can see that the marginal value function for bumbles conditional on a higher temperature ($T_0 = 2.75$) is larger than evaluated at $T_0 = 0$, especially for the lower stock of solitary bees. One possible interpretation is that a higher temperature implies a lower future bumble bee stock, and the resulting scarcity leads to this species becoming more valuable. However, this is not necessarily the case for solitary bees. The reason for this may be the complicated interaction between the effects of the temperature and the bee stock. From equation (8), we can, for instance, derive the marginal value function for solitary bees as:

$$V_S(B, S, T) = p(1 - x^*)H_S(B, S) + \beta E_t\left[V_{S'}(B', S', T') \cdot \frac{\partial S'}{\partial S}\right], \tag{11}$$

in which we implicitly invoked the envelope theorem. How a change in the current temperature T affects this entity is not entirely clear, due to two opposing effects. On the one hand, a rise in



(a) Marginal value function in bumble bees (b) Marginal value function in solitary bees



(c) Marginal value function in bumble bees (d) Marginal value function in solitary bees

Figure 5. Marginal value functions under different conditions.

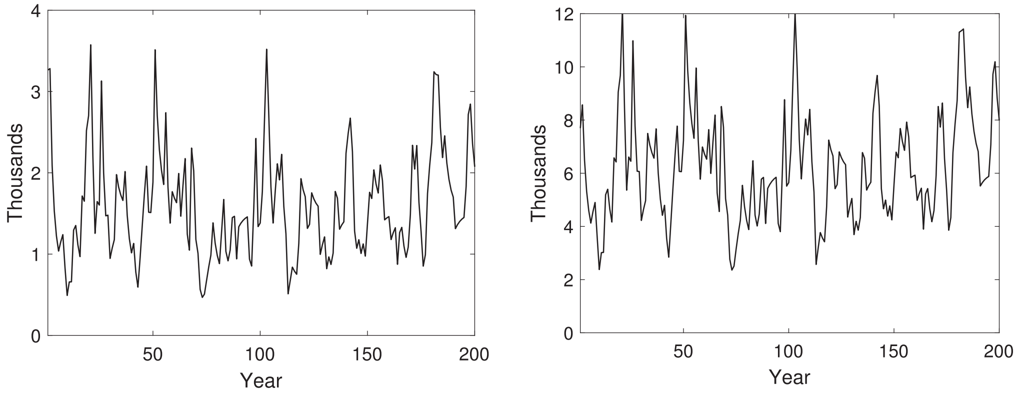
temperature today and tomorrow (T and T', respectively) is likely to lead to a lower bee stock level (S') and, consequently, to an increase in the future marginal value $V_{S'}(B', S', T')$. On the other hand, such a change will also lower the overall level of the optimal value function $V(B', S', T')$ and consequently the marginal value function $V_{S'}(B', S', T')$ – acting as a 'scale' or 'output' effect. Moreover, a rise in T will also lower marginal bee productivity, $\partial S'/\partial S$ in equation (11) (via equation 2), thereby lowering the marginal value function. Therefore, we cannot assess the sign of the cross-derivative $V_{ST}(B, S, T)$ purely from theory. Based on our simulations, however, the scale or output effect appears to dominate, implying that a higher temperature may reduce not only the optimal value (the present value of the whole profit stream) but also the marginal value of the bees. In the worst-case scenario, if a very high temperature is likely to completely eliminate bees in future, then the current bee stock would be valued the least, as they can only pollinate today, with no possibility of future regeneration.

It is important to emphasize that any framework that accounts for the value of pollination service relative to output is likely to face competing effects, in particular since the output price is considered exogenous (as is very likely for any specific location for easily traded commodity crops). In this sense, these insights indicate the importance of using frameworks which help better understand the drivers of decisions regarding ecosystem provision. It also indicates that, to the extent the social value of pollination is larger than private values (due, for example, to factors as simple as pollination services being shared across farmers or other service users), there is likely scope for policy to promote provision of pollination service.

It is also worth mentioning that the optimal decision rule (in equation 9) $x_t^* = x(B_t, S_t, T_t)$ only provides a contingent plan at time t as the future temperature and the resulting stocks remain unknown as of time zero. Unlike the deterministic model setting, it is not possible here to determine an optimal time sequence for the control and state variables (Miranda & Fackler, 2004). The best we can do is to simulate different likely development scenarios based upon the transition matrix. The simulation results indicate that, in most cases, the optimal semi-natural area is negatively related to the existing bee stocks (Figure 6 shows one realization). The mean of the stochastic steady state for bumble bees becomes about 1600 individuals/ha, with a standard error of about 600. The corresponding figures for solitary bees are 6000 and 2000. For the share of optimal semi-natural area, the mean and standard error are about 0.2469 and 0.0133, respectively. As no costs are incurred on annual changes in x, it varies considerably from year to year.

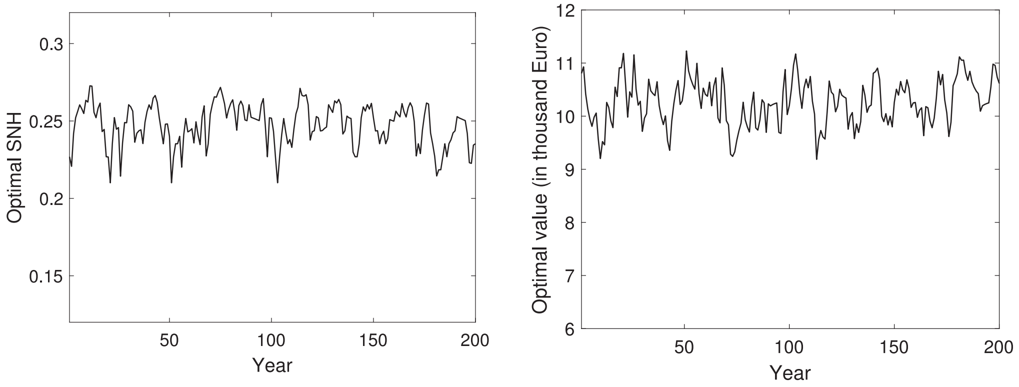
We now turn to valuing resilience services from solitary bees for rapeseed production. As touched upon in the introduction, in the notion of Holling (1973), resilience measures the capacity of an ecosystem to maintain its basic functions and controls under stochastic disturbances. To operationalize this concept for economic analysis, Mäler (2008), Mäler and Li (2010) and Walker et al. (2010) define resilience as a stock variable and analyse its marginal value for mitigating the expected loss from potential regime shifts.[16] Among the different applications of this approach, that conducted by Matsushita et al. (2017) is most relevant to the present study. In their study, the crop in concern is buckwheat (in Japan) and honey bees are the main pollinator species. Their resilience stock is the forest surrounding the crop field and the change in its area may induce honey bee stocks to undergo abrupt changes. Their empirical estimates suggest a resilience value per km^2 of the neighbouring forest of up to 50% of the productive value per hectare of the buckwheat land.

Our study uses a structural model with the semi-natural area share as an endogenous variable, meaning the approach in Matsushita et al. (2017) is not applicable. The main concern is to optimize the provision of pollination services from the vulnerable but otherwise more effective bumble bees, and the solitary bees that are more tolerant to temperature shocks but less effective pollinators. With a sufficiently large population of bumble bees, the solitary bees may become redundant, but with larger temperature uncertainty, the solitary bees may acquire greater value. Therefore, we



(a) Bumble bee stock over time

(b) Solitary bee stock over time



(c) Optimal SNH area

(d) Optimal value function

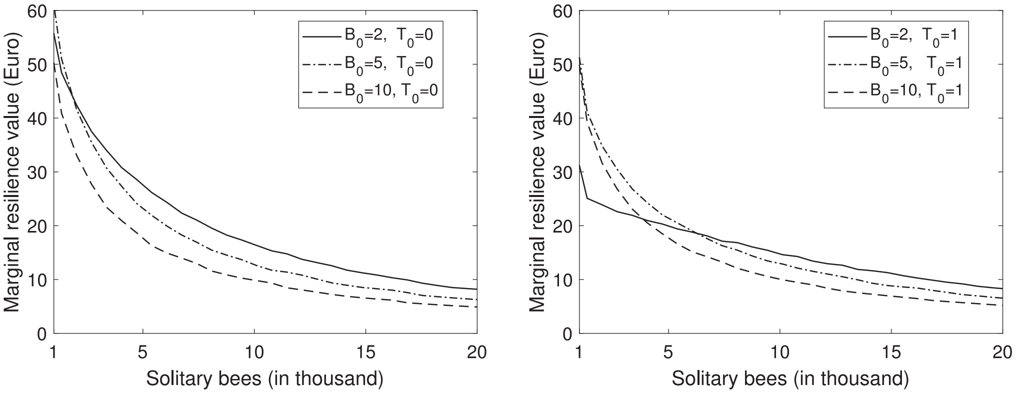
Figure 6. Simulated stocks and decision variables.

consider the stock of solitary bees as our resilience stock. Another difference is that we use standard stochastic temperature disturbances in a dynamic stochastic general equilibrium (DSGE) model framework, with no explicit regime shift risk. As a result, the resilience value in our study is defined as the marginal contribution of solitary bees to the reduction in the expected economic loss caused by the stochastic temperature.

Let $V(B, S, T|\mu, \sigma, \rho)$ denote the optimal value function conditional on the stochastic temperature dynamics equation, and let $\hat{V}(B, S, T)$ denote the ideal value function without any stochastic temperature disturbance. The difference $\hat{V}(B, S, T) - V(B, S, T\mu, \sigma, \rho)$ then defines the loss in value caused by the stochastic temperatures, that is, the risk premium that the farm owner would be willing to pay to eliminate the uncertainty. For a given bumble bee stock B and temperature T, we thus define the marginal value of solitary bees for their resilience service by:

$$MRV(S|B, T) = \frac{-\partial \hat{V}(B, S, T) - V(B, S, T|\mu, \sigma, \rho)}{\partial S} \tag{12}$$

Conditional on a ‘good’ state, with a lower temperature T, we expect that $\hat{V}(B, S, T) > V(B, S, T|\mu, \sigma, \rho)$ as the stochastic disturbance would more likely drive the system to worse states than better ones. In this case, we expect the marginal resilience value to be positive, namely, more solitary bees can always mitigate the expected value loss, $\hat{V}(B, S, T) - V(B, S, T\mu, \sigma, \rho)$, caused by the stochastic temperature disturbances.[17]



(a) Initial temperature T=0 (b) Initial temperature T=1

Figure 7. Marginal resilience value under different initial temperatures.

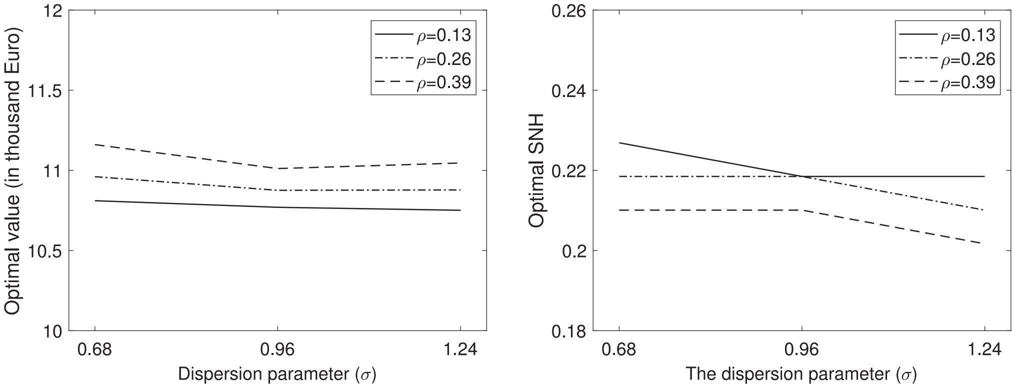
Conditional on different bumble bee stocks and temperatures, we have computed the marginal resilience value of solitary bees as depicted in Figure 7. These results indicate that the marginal resilience value of solitary bees is decreasing in its own stock, in the stock of bumble bees, and, somewhat surprisingly, in temperature.[18] We can see from the left panel that, for any given solitary bee stock, its marginal resilience value appears to decrease in the number of bumble bees. Evaluated at $B = 2$ and $S = 5$ (in thousands), for example, the marginal value of resilience services is about €26.2/1000 solitary bees; the corresponding value becomes about €21.9 when $B = 5$. These results suggest that with a negative shock in the stock of bumble bees, the otherwise seemingly redundant solitary bees may have a relatively large value. The results highlight the benefits of functional diversity for resilience.

Figure 7(b) readily shows that the marginal resilience values with a higher initial temperature $T = 1$ become lower than those with a lower one with $T = 0$, as in Figure 7(a). The reason for this is that, starting with a somewhat higher (counterfactual) temperature, the expected loss caused by the stochastic disturbances $\hat{V}(B, S, T) - V(B, S, T|\mu, \sigma, \rho)$ becomes smaller, reducing the marginal benefit from solitary bees.

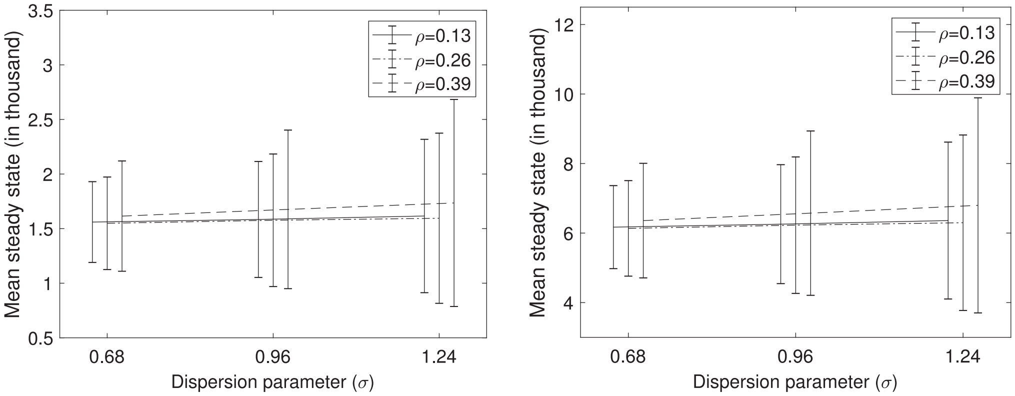
Sensitivity analysis

In this section, we study the effect of some counter-actual changes in the climate parameters such as the standard deviation, σ, of the error term (ε_t) and the persistence parameter ρ in equation (1). Three different combinations of σ and ρ are considered (yielding a total of nine scenarios, one for each combination of σ and ρ), where σ takes values 0.68, 0.96 (the base case), and 1.24, while ρ takes values 0.13, 0.26 (the base case), and 0.39. The results are depicted in Figure 8, evaluated at bee stocks of $B = 3.7$, $S = 7.4$ and temperature $T = 0$. From Figure 8(a), we can see that the optimal value increases in the persistence parameter ρ conditional on dispersion σ. The reason for this is that a larger value of ρ provides more information regarding temperature evolution, leading to an increase in the value function.

For a given value of ρ, the value function seems to weakly decrease in the dispersion parameter σ. This result is intuitive, since the harvest potential function is concave in the bee stocks, which in turn depend upon the temperature variable (meaning that increases in variance of T should lead to reduced harvest potential). The magnitude of change, however, is rather small across the three dispersion measures. The reason for this result lies in the specification of the exponential net-of-damage function in the bee productivity functions in equations (3) and (4). In the absence of any temperature increase with $T = 0$, we have a zero damage with a net-of-damage



(a) Value function (b) Semi-natural habitat



(c) Bumble bees (d) Solitary bees

Figure 8. Sensitivity to parameters in the temperature equation.

$\exp(-\gamma T) = 1$. With a temperature increase, it is obvious that $\exp(-\gamma T) < 1$ with reduced bee productivity. However, we do not assume any damage for temperature decreases below zero and any negative temperatures are clustered in the $T = 0$ category (a truncation effect).[19] In such a setting, greater dispersion might even benefit bee productivity due to the increase in the probability of the $T = 0$ cluster including temperature decreases, which may result in smaller loss in the optimal value function than expected.

Figure 8(b) indicates that the optimal SNH area decreases in both persistence, ρ, and dispersion,σ. For a given level of dispersion, greater persistence may provide better information for planning and thus reduce the need for more SNH provision. The effect of temperature variability can be attributed to the same off-setting trends as for the optimal value function. Figure 8(c, d) indicates that the mean steady-state stocks of both bee species modestly increase in both σ and ρ. The standard deviations of the stochastic steady states, however, increase in ρ, as indicated by the height of the vertical error bars. To summarize our explorations here, greater persistence in temperature may lead to a lower optimal SNH provision, but some higher mean steady-state bee stocks; higher levels of temperature variability lead to modest decrease in the optimal SNH area (in particular for the increase from 0.96 to 1.24) and some higher mean steady-state bee stocks.

With regard to resilience, we have also conducted a similar analysis (figures not shown). We find, among other things, that an increase in σ from the benchmark level of 0.96 to 1.24 would reduce the marginal resilience value of solitary bees (per thousand) from €26.6 to €23.3 (for $\rho = 0.26$, $B = 2$ and $S = 5$). When ρ increases from 0.26 to 0.39 (with $\sigma = 0.96$, $B = 2$ and

$S = 5$), we find that the marginal resilience value reduces from €26.6 to €23.8. It seems that the more uncertain the temperature shocks and the larger the persistence parameter are, the less the solitary bees are valued for their resilience services.

Scale and spatial effect

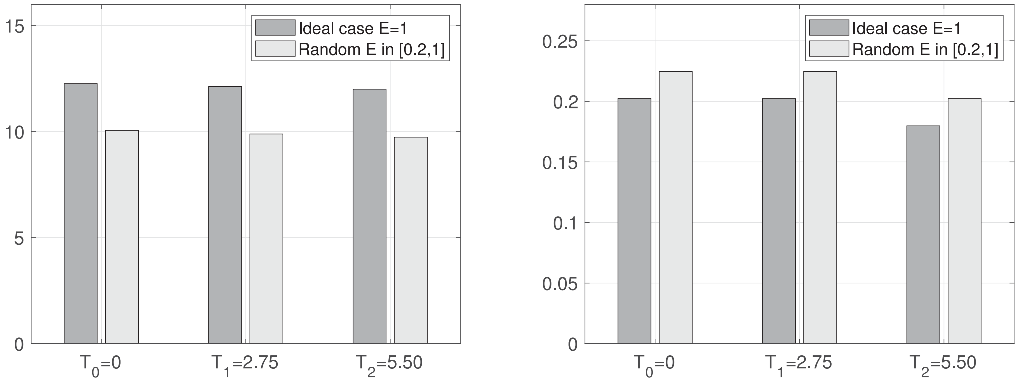
In our analysis above, we have implicitly assumed an ideal spatial allocation of the SNH in relation to the OSR field. For small-scale OSR management, such as within a circle of field with a radius of 750 m, this assumption is likely to be very reasonable, as both pollination groups would likely have similar dispersal abilities (i.e., foraging ranges) within the circle (Gathmann & Tscharntke, 2002; Holzschuh et al., 2016; Steffan-Dewenter et al., 2002). For larger scales, for example, a circle with a radius of 3000 m, Steffan-Dewenter et al. (2002) show that the correlation between the percentage of SNH area and the pollinators' visit frequency at random sampling sites becomes considerably weaker. An important reason for this is that the bees tend to forage in the proximity of the SNH and they are less likely to fly longer distance in the OSR field – particularly true of the smaller solitary bees. Thus, unless the large OSR field is perfectly homogeneous, as can occur when it may be considered as consisting of multiple small scale fields, the spatial allocation of the SNH is likely to affect the pollination potential even with the same stock of bees.

Within the scope of our study, which is the first of its kind in the literature, we will not attempt to optimize the patch size and spatial allocation of the SNH. Instead, we simply illustrate the spatial issues involved by taking the advantage of the well-known Camargo (1993) evenness index (cf. Tuomisto, 2012) and its effect on the pollination potential parameter r in equation (6). Consider N spatially distributed, identically sized (say, 750 × 750 m) grid cells, and let x_i denote the percentage of SNH area in the i^{th} cell relative to the whole management area. Figure B1 in Appendix B in the supplemental data online, drawn for $N = 9$ grid cells and a SNH of 10%, readily shows that the left panel with the same percentage of SNH in each grid cell is more homogeneous than the right panel where it is concentrated in the same corner cell. From the Camargo evenness index:

$$E = 1 - \sum_{i=1}^{N} \sum_{j=i+1}^{N} \frac{|x_i - x_j|}{N},$$

we see that $E = 1$ for the left panel with an even SNH distribution and $E = 0.2$ for the concentrated one. In reality, there may be infinitely many intermediate cases with different cluster formations of the SNH. In any case, it seems reasonable to assume a positive link between the evenness index and pollination potential, meaning that (increased) unevenness of the distribution of SNH in a field reduces bee pollination potential. This, in turn, will imply smaller value of r in equation (6) with increased unevenness (with $E < 1$), in comparison to the ideal case (with $E = 1$).

As a crude approximation, assume that $r = 0.25 + 0.25E$, then we have $r = 0.3$ for $E = 0.2$, and $r = 0.5$ for $E = 1$ (as in our ideal case). In order to evaluate the effect of evenness on the choice of SNH area, we proceed as follows: draw random samples (from some underlying super-population) of the OSR field with E randomly distributed over [0.2, 1]; compute the value of r for each draw, using which we compute the value function and the optimal SNH provision. These simulation results are then averaged and analysed. We present the results of these simulations in Figure 9, for different temperature conditions (with given initial pollinator stocks $B = 3.7$ and $S = 7.4$ in thousands). It is evident that unevenness reduces the value function due to the negative effect on the harvest potential function H. Consequently, there is an increase in the optimal SNH to combat the effect of reduced harvest potential. Even with unevenness in the distribution of the SNH area, however, it may still pay to enhance the SNH to accommodate larger bee stocks, which lead to an increase in the probability that the bees visit distant parts of



(a) Value function (in thousand Euro)

(b) Optimal semi-natural area

Figure 9. Effect of spatial evenness.

the OSR field. Concerning resilience values, we have conducted a similar analysis and find that the marginal resilience value of solitary bees (in thousands) falls from €26.2 (as shown above for the ideal case) to €21.6/ha due to a spatial pattern shift of the SNH from the perfectly even case to the uneven one.

DISCUSSION AND CONCLUSIONS

Empirical evidence shows that the stock of bumble bees has been declining across Europe and the main reasons for the decline appears to be the loss of habitat and forage availability due to agricultural intensification. This may have severe ecological and commercial consequences, given that bumble bees are very effective pollinators of a range of wildflowers and crops. This paper formalizes a stylized bioeconomic model to study the optimal provision of SNH for bees and to assess the economic consequences of SNH provision under climate change. In particular, we assess the economic value of biodiversity and resilience in a two-species model framework involving both bumble bees and solitary wild bees, with special reference to the production of rapeseed in the Stockholm region.

Using this model, we evaluate the effects of exogenous climate change, accommodating both stochastic temperature shocks and persistence patterns over time. We describe the dynamics of the two pollinator groups as a power production function, where the bee population productivity depends on the SNH area and temperature changes. We close the model with a link between species density and profit via a postulated harvest potential function. To the best of our knowledge, this is the first bioeconomic model where pollination services from wild bee stocks are explicitly taken into account.

Using annual temperature data for the Stockholm region, we estimate a dynamic temperature equation as an AR(1) process and discretize the continuous stochastic process with a nine-state Markov chain. Concerning the productivity function for bee stocks, we use the best available estimates from the ecological literature to calibrate both the damage resulting from a temperature rise on the bee stocks and the benefit of SNH areas. For bumble bees, for example, we introduced a soft threshold on SNH at about 2% of the total crop field from which the stock of the bee species may effectively grow. Bumble bees, while more effective at pollinating than solitary bees (due to their large body size and higher foraging capacity), were also considered more vulnerable to a temperature increase.

Based on the calibrated model, we conducted a number of explorations to examine, among other things, optimal choice of the SNH area, stock dynamics of the two pollinator groups, and the optimal value functions. For the base scenario, with current temperature conditions, we find that, except at a very low level of solitary bee stocks, the optimal SNH is negatively related to the current bee stocks, that is, lower bee stocks entail increased SNH for increased bee reproduction. With a temperature increase, the optimal response is to increase the SNH to offset the damaging effect of increased temperature. Without conversion frictions, our simulated optimal SNH is considerably responsive to the bee stock and temperature changes.

We find that the resilience value of the solitary bees, in terms of mitigating the reduction in the value of rapeseed production resulting from climate change-driven uncertainty may be substantial. The exact magnitude of resilience value of solitary bees depends on the size of the two bee stocks as well as temperature. We also analysed counterfactual scenarios with increased temperature dispersion and persistence of temperature. Increased dispersion led to a reduced value function and increased SNH provision, while increases in persistence led to the converse effect, an increased value function and reduced SNH provision.

We also analysed the effect of the spatial distribution of SNH provision. Reasoning that an even distribution of SNHs is likely to be advantageous from a pollination perspective, we evaluated the effect of departing from the ideal case of a perfectly even spatial distribution. We also quantified the possible suboptimality arising from unevenness in the distribution of SNH. In the interests of simplicity, we use the well-known Camargo evenness index and link it to the potential loss in the harvest potential, and thereby the present discounted value of future profits. Unevenness in SNH distribution, as can be anticipated, does lead to a degree of loss in the harvest potential. Nonetheless, even with an uneven distribution of SNH, our previous insight that the solitary bees can have considerable resilience value still holds.

The analysis in this paper is centred around a stylized model, with an emphasis on tractability and intuition. Consequently, we abstracted away from many potentially important aspects related to the problem. To illustrate, some parts of pollination services are presumably collective, meaning that they affect more than the single decision maker assumed here, in addition to providing other services at large. To this extent, there is an externality in terms of pollination services, and a consideration of these aspects may be a fruitful direction of future research. In addition, spatial aspects related to optimal path size and location are known to be of some importance and were not considered in our analysis. The analysis also did not consider the question of imperfect stock observability, and frictions involved in changing land uses. In any case, dynamic models incorporating one or more of these possibly important aspects are an important avenue for future research. In view of the fact that accurate functional relationships between temperature and bee population dynamics are not yet readily available, our numerical results are to be viewed as providing a rigorous basis for a discussion of the economic value of biodiversity and resilience, rather than as a definitive assessment of it.

ACKNOWLEDGEMENTS

The authors are grateful to two anonymous reviewers and the editors for helpful comments and suggestions. The usual disclaimer applies.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

FUNDING

Gustav Engström and Chandra Kiran Krishnamurthy gratefully acknowledge financial support from the Ragnar Söderbergs Stiftelse.

NOTES

[1] To the best of our knowledge, the literature concerned with bioeconomic modeling of pollinators is very sparse. The only related literature we could find targets the role of honey bees and the problem of beekeeping as a way of securing crop production (Champetier et al., 2015; Rucker et al., 2012).

[2] We compare the body size of the *B. terrestris* worker with the male *O. bicorins* since the male *bicorins* perform the majority of the pollination within the species (Seidelmann, 2006).

[3] Kudo et al. (2004) found that early-flowering plants in Japan advanced their flowering during a warm spring, whereas bumble bees queen emergence appeared unaffected by spring temperatures. Due to the fact that many wild bees in Northern European countries feed on early spring plants similar to those examined in the Japanese study (Linkowski et al., 2004), a similar mismatch may be expected. A similar finding was reported for spring wildflowers at a temperate deciduous forest in the United States (Motten, 1986).

[4] Further evidence for this hypothesis is provided by developments anticipated regarding *Salix*, one of the most important pollen and nectar sources for newly emerging bees, particularly bumble bees, in Northern Europe. Linkowski et al. (2004) and Post et al. (2008) have shown that for grey willow (*Salix glauca*) all phenological events monitored occurred earlier on warmed plots, and that warming reduced the aggregate life history of this *Salix* species by 22 days on average, thus indicating that *Salix* is among the plant species that will express earlier flowering phenology in response to temperature increase.

[5] For *O. bicornis*, long pre-wintering periods as adults has been showed to lead to elevated fat body depletion and decreased overwintering survival (Radmacher, 2012).

[6] The mechanism in question is the extension of the prepupal phase of the univoltine *O. bicornis*. Recent research has shown that an extension of the prepupal phase could be a suitable mechanism that allows the adjustment of adult eclosion under warmer conditions that could aid the bees to cope better with the consequences of climate change in this aspect.

[7] Future research also needs to consider insect herbivore phenotypic and genotypic flexibility, their responses to global change parameters operating in concert, and an awareness that some patterns may only become apparent in the longer term.

[8] The formulation assumes that land can be costlessly switched between semi-natural and agricultural area every year. While clearly a simplification, we believe this to be a plausible approximation in our agricultural setting, of a single farmer with a marginally irrigated seasonal crop with only moderate specialization required. This assumption helps keep our model tractable, since adding frictions to conversion may need semi-natural area to be an additional state variable.

[9] We note that all stocks are assumed perfectly observable in our model. Clearly, this is a simplification, since in reality it is difficult for the farmer to observe the exact size of the two bee species in circulation on his plot of land. However, typically bee population is likely determined by simple factors that are beneficial for bees and strongly correlated to their population levels. To the extent an experienced farmer can gauge these factors, it is very likely that the services provided by the bee population can be consistently estimated by the farmer. Examples of such factors would thus be the amount of semi-natural land (for nesting), but also the size of the rapeseed field (for food). We leave an exploration of the effects of uncertainty in bee stock (reported as being substantial for fisheries in Sethi et al., 2005) estimates for future research.

[10] We note that these equations are stochastic, depending upon the state T_t which is stochastic. In view of the fact that f, g (see equations 3 and 4) are both positive and finite numbers (and can be shown to be bounded above and below), it can be shown that for any given time path for T, there is a finite steady-state stock (density) of both bee types (bumble and solitary). Under mild conditions, it can then be established that there is a non-degenerate unique invariant distribution for the two bee types (which is the equivalent to the 'steady state' in the deterministic setting) for any stationary choice of the path for x_t.

[11] To illustrate, if $w = 1/2$, $B_t = 100$ and $S_t = 100$, then the total pollination capacity is equivalent to that obtained with $100 + 1/2*100 = 150$ bumble bees.

[12] In stochastic dynamic models, the stock variables converge to a steady-state probability distribution, which is the equivalent of a 'steady state' in deterministic settings.

[13] According to The Bumblebee Conservation Trust (2017) and Cueva del Castillo et al. (2015), the nest size for bumble bees depends on the exact species, but most form colonies of between 50 and 400 individuals per nest (20–1700 in extreme cases). With a dozen of such nests over 1 ha of the field, 11-15 nests/ha (cf. Osborne et al., 2008), the figure of 4000 we use can be arrived at.

[14] In particular, a warmer spring season may enable the bumble bees to feed an extra generation, but a warmer spring may also increase the mortality rate of these bees by up to 50%. Although there is no exact trade-off information available, the net effect seems to be negative. In comparison, the solitary bees do not suffer from the early spring temperature as they awaken later in the spring. On the other hand, the mortality rate of this group may become considerably higher for temperature increases.

[15] This study indicates that for a temperature increase from 17.5 to 22.5°C, the mortality rate of solitary bees increases from 16% to 25%, and for a temperature change from 22.5 to 27.5°C, the mortality rate would rise rapidly to 100%.

[16] For more on optimal resource management with regime shift risks, see Baggio and Fackler (2016) and Ren and Polasky (2014).

[17] Consistent with the literature, the marginal resilience value would be negative if the initial state is a worse one and shocks can increase the chance for the system to shift to better states.

[18] The value of resilience may not be monotonic (Baumgärtner & Strunz, 2014; Li et al., 2016).

[19] This may not be realistic for large temperature reductions, but for simplicity, we focus on the damage of warming rather than the unlikely benefits of cooling.

ORCID

Gustav Engström http://orcid.org/0000-0002-7588-3595

REFERENCES

Alford, D. (1969). A study of the hibernation of bumblebees (Hymenoptera: Bombidae) in southern England. *The Journal of Animal Ecology*, *38*(1), 149–170. https://doi.org/10.2307/2743

Baggio, M., & Fackler, P. L. (2016). Optimal management with reversible regime shifts. *Journal of Economic Behavior & Organization*, *132*, 124–136. https://doi.org/10.1016/j.jebo.2016.04.016

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., & Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, *9* (10), 1146–1156. https://doi.org/10.1111/j.1461-0248.2006.00963.x

Bartomeus, I., Ascher, J. S., Wagner, D., Danforth, B. N., Colla, S., Kornbluth, S., & Winfree, R. (2011). Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proceedings of the National Academy of Sciences*, *108*(51), 20645–20649. https://doi.org/10.1073/pnas.1115559108

Baumgärtner, S., & Strunz, S. (2014). The economic insurance value of ecosystem resilience. *Ecological Economics*, *101*, 21–32. https://doi.org/10.1016/j.ecolecon.2014.02.012

Brock, W. A., & Xepapadeas, A. (2003). Valuing biodiversity from an economic perspective: A unified economic, ecological, and genetic approach. *American Economic Review*, *93*(5), 1597–1614. https://doi.org/10.1257/000282803322655464

The Bumblebee Conservation Trust. (2017). Bumblebee nests. Technical report, The Bumblebee Conservation Trust. Archived from the original on 22 September 2017.

Burkle, L. A., Marlin, J. C., & Knight, T. M. (2013). Plant–pollinator interactions over 120 years: Loss of species, co-occurrence, and function. *Science*, *339*(6127), 1611–1615. https://doi.org/10.1126/science.1232728

Camargo, J. (1993). Must dominance increase with the number of subordinate species in competitive interactions? *Journal of Theoretical Biology*, *161*(4), 537–542. https://doi.org/10.1006/jtbi.1993.1072

Carré, P., & Pouzet, A. (2014). Rapeseed market, worldwide and in Europe. *OCL*, *21*(1), D102. https://doi.org/10.1051/ocl/2013054

Champetier, A., Sumner, D. A., & Wilen, J. E. (2015). The bioeconomics of honey bees and pollination. *Environmental and Resource Economics*, *60*(1), 143–164. https://doi.org/10.1007/s10640-014-9761-4

Cueva del Castillo, R., Sanabria-Urbán, S., & Serrano-Meneses, M. A. (2015). Trade-offs in the evolution of bumblebee colony and body size: A comparative analysis. *Ecology and Evolution*, *5*(18), 3914–3926. https://doi.org/10.1002/ece3.1659

De Luca, P. A., Buchmann, S., Galen, C., Mason, A. C., & Vallejo-Marín, M. (2019). Does body size predict the buzz-pollination frequencies used by bees? *Ecology and Evolution*, *9*(8), 4875–4887. https://doi.org/10.1002/ece3.5092

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, *105*(18), 6668–6672. https://doi.org/10.1073/pnas.0709472105

Díaz, S., Lavorel, S., Chapin, F. S., Tecco, P. A., Gurvich, D. E., & Grigulis, K. (2007). Functional diversity—at the crossroads between ecosystem functioning and environmental filters. In J. G. Canadell, D. Pataki, & L. Pitelka (Eds.), *Terrestrial ecosystems in a changing world* (pp. 81–91). The IGBP Series. Springer-Verlag.

Diekmann, M. (1996). Relationship between flowering phenology of perennial herbs and meteorological data in deciduous forests of Sweden. *Canadian Journal of Botany*, *74*(4), 528–537. https://doi.org/10.1139/b96-067

European Union. (2015). Science for environment policy. ecosystem services and the environment. In-depth Report 11 produced for the European Commission, DG Environment by the Science Communication Unit, UWE. http://ec.europa.eu/science-environment-policy

FAO. (2008). Climate change and biodiversity for food and agriculture. Technical background document from the expert consultation held on 13 to 14 February 2008. Food and Agriculture Organization of the United Nations.

FAO. (2011). Potential effect of climate change on crop pollination. http://www.fao.org/fileadmin/templates/agphome/documents/Biodiversity-pollination/Climate_Pollination_17_web__2_.pdf

FAO. (2016). Pollinators vital to our food supply under threat. http://www.fao.org/news/story/en/item/384726/icode/

Folke, C., Jansson, Å, Rockström, J., Olsson, P., Carpenter, S. R., Chapin, F. S., Crépin, A.-S., Daily, G., Danell, K., Ebbesson, J., Elmqvist, T., Galaz, V., Moberg, F., Nilsson, M., Österblom, H., Ostrom, E., Persson, Å., Peterson, G., Polasky, S., … Westley, F. (2011). Reconnecting to the biosphere. *Ambio*, *40*(7), 719. https://doi.org/10.1007/s13280-011-0184-y

Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., Kremen, C., Carvalheiro, L. G., Harder, L. D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N. P., Dudenhoffer, J. H., Freitas, B. M., Ghazoul, J., Greenleaf, S., … Klein, A. M. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, *339*(6127), 1608–1611. https://doi.org/10.1126/science.1230200

Gathmann, A., & Tscharntke, T. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology*, *71*(5), 757–764. https://doi.org/10.1046/j.1365-2656.2002.00641.x

Golosov, M., Hassler, J., Krusell, P., & Tsyvinski, A. (2014). Optimal taxes on fossil fuel in general equilibrium. *Econometrica*, *82*(1), 41–88. https://doi.org/10.3982/ECTA10217

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, *4*(1), 1–23. https://doi.org/10.1146/annurev.es.04.110173.000245

Holzschuh, A., Dainese, M., González-Varo, J. P., Mudri-Stojnić, S., Riedinger, V., Rundlöf, M., Scheper, J., Wickens, J. B., Wickens, V. J., Bommarco, R., Kleijn, D., Potts, S. G., Roberts, S. P. M., Smith, H. G., Vilà, M., Vujić, A., Steffan-Dewenter, I., & Novotny, V. (2016). Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecology Letters*, *19*(10), 1228–1236. https://doi.org/10.1111/ele.12657

IPCC. (2007). Climate change 2007: Synthesis report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. http://www.fao.org/3/a-BO098e.pdf

Jansson, Å, & Polasky, S. (2010). Quantifying biodiversity for building resilience for food security in urban landscapes: Getting down to business. *Ecology and Society*, *15*(3). https://doi.org/10.5751/ES-03520-150320

Javorek, S., Mackenzie, K., & Vander Kloet, S. (2002). Comparative pollination effectiveness among bees (Hymenoptera: Apoidea) on lowbush blueberry (Ericaceae: Vaccinium angustifolium). *Annals of the Entomological Society of America*, *95*(3), 345–351. https://doi.org/10.1603/0013-8746(2002)095[0345:CPEABH]2.0.CO;2

Knight, M. E., Martin, A. P., Bishop, S., Osborne, J. L., Hale, R. J., Sanderson, R. A., & Goulson, D. (2005). An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology*, *14*(6), 1811–1820. https://doi.org/10.1111/j.1365-294X.2005.02540.x

Kudo, G., Nishikawa, Y., Kasagi, T., & Kosuge, S. (2004). Does seed production of spring ephemerals decrease when spring comes early? *Ecological Research*, *19*(2), 255–259. https://doi.org/10.1111/j.1440-1703.2003.00630.x

Li, C.-Z., Crépin, A.-S., & Folke, C. (2018). The economics of resilience. *International Review of Environmental and Resource Economics*, *11*(4), 309–353. https://doi.org/10.1561/101.00000096

Li, C.-Z., Villasante, S., & Zhu, X. (2016). Regime shifts and resilience in fisheries management: A case study of the Argentinean hake fishery. *Environmental and Resource Economics*, *65*(3), 623–637. https://doi.org/10.1007/s10640-016-0038-y

Linkowski, W., Cederberg, B., & Nilsson, L. (2004). Vildbin och fragmentering. *Kunskapssammanställning om situationen för de viktigaste pollinatörerna i det svenska jordbrukslandskapet. Svenska Vildbiprojektet vid ArtDatabanken, SLU & Avdelningen för växtekologi, Uppsala Universitet*.

Ljungqvist, L., & Sargent, T. J. (2018). *Recursive macroeconomic theory*. MIT press.

Mäler, K.-G. (2008). Sustainable development and resilience in ecosystems. *Environmental and Resource Economics*, *39*(1), 17–24. https://doi.org/10.1007/s10640-007-9175-7

Mäler, K.-G., & Li, C.-Z. (2010). Measuring sustainability under regime shift uncertainty: A resilience pricing approach. *Environment and Development Economics*, *15*(6), 707–719. https://doi.org/10.1017/S1355770X10000318

Matsushita, K., Taki, H., Yamane, F., & Asano, K. (2017). Shadow value of ecosystem resilience in complex natural land as a wild pollinator habitat. *American Journal of Agricultural Economics*, *100*(3), 829–843. https://doi.org/10.1093/ajae/aax075

Miranda, M. J., & Fackler, P. L. (2004). *Applied computational economics and finance*. MIT Press.

Motten, A. F. (1986). Pollination ecology of the spring wildflower community of a temperate deciduous forest. *Ecological Monographs*, *56*(1), 21–42. https://doi.org/10.2307/2937269

Öckinger, E., & Smith, H. G. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, *44*(1), 50–59. https://doi.org/10.1111/j.1365-2664.2006.01250.x

OECD and FAO. (2016). The Organisation for Economic Co-operation and Development/ Food and Agricultural Organization of the United Nations. Oilseed and oilseed products. Snapshot. OECD-FAO AGRICULTURAL OUTLOOK 2016-2025, Food and Agriculture Organization of the United Nations. http://www.fao.org/3/a-BO098e.pdf

Osborne, J. L., Martin, A. P., Shortall, C. R., Todd, A. D., Goulson, D., Knight, M. E., Hale, R. J., & Sanderson, R. A. (2008). Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *Journal of Applied Ecology*, *45*(3), 784–792. https://doi.org/10.1111/j.1365-2664.2007.01359.x

Peltonen-Sainio, P., Jauhiainen, L., & Hannukkala, A. (2007). Declining rapeseed yields in Finland: How, why and what next? *The Journal of Agricultural Science*, *145*(6), 587–598. https://doi.org/10.1017/S0021859607007381

Post, E. S., Pedersen, C., Wilmers, C. C., & Forchhammer, M. C. (2008). Phenological sequences reveal aggregate life history response to climatic warming. *Ecology*, *89*(2), 363–370. https://doi.org/10.1890/06-2138.1

Pudasaini, R., Chalise, M., Poudel, P. R., Pudasaini, K., & Aryal, P. (2015). Effect of climate change on insect pollinator: a review. *Participatory Community Assessment for Priority Problem Diagnosis in Bajura District, Nepal: What Matters Most–Poverty or Climate Change?* 289.

Pyke, G. H., Thomson, J. D., Inouye, D. W., & Miller, T. J. (2016). Effects of climate change on phonologies and distributions of bumble bees and the plants they visit. *Ecosphere*, *7*(3), 1–19.

Radmacher, S. (2012). *Temperature effects on the development in the solitary bee Osmia bicornis (Hymenoptera, Megachilidae) – Development time, brain microstructure, and cognitive abilities* [Doctoral thesis]. Fakultät für Biologie und vorklinische Medizin der Universität Regensburg.

Ren, B., & Polasky, S. (2014). The optimal management of renewable resources under the risk of potential regime shift. *Journal of Economic Dynamics and Control*, *40*, 195–212. https://doi.org/10.1016/j.jedc.2014.01.006

Robinet, C., & Roques, A. (2010). Direct impacts of recent climate warming on insect populations. *Integrative Zoology*, *5*(2), 132–142. https://doi.org/10.1111/j.1749-4877.2010.00196.x

Rucker, R. R., Thurman, W. N., & Burgett, M. (2012). Honey bee pollination markets and the internalization of reciprocal benefits. *American Journal of Agricultural Economics*, *94*(4), 956–977. https://doi.org/10.1093/ajae/aas031

Scaven, V. L., & Rafferty, N. E. (2013). Physiological effects of climate warming on flowering plants and insect pollinators and potential consequences for their interactions. *Current Zoology*, *59*(3), 418–426. https://doi.org/10.1093/czoolo/59.3.418

Seidelmann, K. (2006). Open-cell parasitism shapes maternal investment patterns in the red mason bee *Osmia rufa*. *Behavioral Ecology*, *17*(5), 839–848. https://doi.org/10.1093/beheco/arl017

Sethi, G., Costello, C., Fisher, A., Hanemann, M., & Karp, L. (2005). Fishery management under multiple uncertainty. *Journal of Environmental Economics and Management*, *50*(2), 300–318. https://doi.org/10.1016/j.jeem.2004.11.005

SMHI. (2006). 250 years of weather observations at the Stockholm Observatory. Technical report, Svenska Meteorologiska och Hydrologiska institut. https://www.smhi.se/polopoly_fs/1.17736!/webbNr27_eng_ver.pdf

Stanley, D. A., Gunning, D., & Stout, J. C. (2013). Pollinators and pollination of oilseed rape crops (*Brassica napus* L.) in Ireland: Ecological and economic incentives for pollinator conservation. *Journal of Insect Conservation*, *17*(6), 1181–1189. https://doi.org/10.1007/s10841-013-9599-z

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., & Tscharntke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, *83*(5), 1421–1432. https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2

Stokey, N. L., Lucas, R. R., & Prescott, E. (1989). *Recursive methods in economic dynamics*. Harvard University Press.

Tuomisto, H. (2012). An updated consumer's guide to evenness and related indices. *Oikos*, *121*(8), 1203–1218. https://doi.org/10.1111/j.1600-0706.2011.19897.x

Walker, B., Pearson, L., Harris, M., Maler, K.-G., Li, C.-Z., Biggs, R., & Baynes, T. (2010). Incorporating resilience in the assessment of inclusive wealth: An example from south east Australia. *Environmental and Resource Economics*, *45*(2), 183–202. https://doi.org/10.1007/s10640-009-9311-7

Walker, B., & Salt, D. (2012). *Resilience thinking: Sustaining ecosystems and people in a changing world*. Island Press.

Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2003). Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, *6*(11), 961–965. https://doi.org/10.1046/j.1461-0248.2003.00523.x