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# Ecological and economic trade-offs between amount and spatial aggregation of conservation and the cost-effective design of coordination incentives

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#### **Abstract**

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To counter not only the continuous loss but also the fragmentation of species habitats, coordination incentives (CI) have been proposed to incentivise the spatial aggregation of conservation efforts. An important issue is the cost-effective design of these instruments. Two main types of CI, the agglomeration bonus and the agglomeration payment, are analysed with stylised models. Their ecological effects are assessed through a metapopulation simulation model. Rather than choosing the usual approach and analysing the joint ecological-economic model, I analyse the ecological and economic sub-models separately and join the results within an economic production theory framework in which production factors (here, the proportion and aggregation of conserved land parcels) are financed under a budget- or cost constraint and generate an output (here, metapopulation viability). This decomposition of the ecological-economic analyses allows highlighting the ecological and economic trade-offs between proportion and spatial aggregation of conservation and generating a more general understanding of the budget- and cost-effectiveness of CI. Results include, among others, that the agglomeration payment is never more budget- and cost-effective than the agglomeration bonus and that in the agglomeration bonus the budget-effective level of spatial aggregation is lower than the cost-effective level.

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#### **Highlights**

- Ecological-economic models of coordination incentives are presented
- The models are analysed within an economic production theory framework
- Scheme cost-effectiveness depends on ecological and economic parameters
- The agglomeration payment is never more cost-effective than the agglomeration bonus

#### **Key words**

agglomeration bonus, agglomeration payment, coordination incentives, cost-effectiveness, ecological-economic model, economic production theory,

#### 35 1 Introduction

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The loss and fragmentation of species habitats are the main direct drivers of the continuing loss of biodiversity world-wide (Banks-Leite et al. 2020). While habitat loss does not explicitly refer to spatial structure, habitat fragmentation considers that in the course of habitat loss remaining habitat patches become more isolated from each other, increasing the extinction risk of the remnant local populations and hindering the movement of individuals between habitat fragments (Hanski 1999).

The cause behind habitat loss and fragmentation is largely human land use (Powers and Jetz 2019), which is largely forestry (and in particular, deforestation) and (intensive) agriculture. Thus biodiversity conservation is in conflict with the societal goals of food and timber production (although it is also a requirement for food production, for instance in the form of pollination services), as well as the private profits of the owners of the land.

While the establishment of nature reserves is a primary approach to protecting and halting the decline of biodiversity, much of the world's biodiversity is on private lands and even the success of nature reserves hinges on the state of the private lands around them (Scott et al. 2001, Kamal et al. 2015). On private lands, biodiversity conservation measures can, in general, be implemented only on a voluntary basis, where the most common policy approach are conservation payments (de Vries and Hanley 2016), implemented under labels such as payments for ecosystem services (Engel et al. 2008, 2016), the conservation reserve program (CRP) in the United States (Hellerstein 2017), or agri-environment schemes in the European Union (Batáry et al. 2015).

Most of these payment schemes are spatially homogeneous, flat payments where for a given conservation measure each landowners receives the same payment per hectare. Considering that profit maximisation is a dominant component of farmers' decisions (Bartkowski and Bartke 2018, Schaub et al. 2023), farmers will, in good approximation, conserve land only if and only if the payment exceeds the forgone profit associated with the implementation of the conservation measure. The spatial location of conservation efforts is thus determined by the spatial distribution of the conservation costs (forgone profits), which are generally not known by the policy maker. Thus, while a conservation payment can increase the overall conserved area, thus addressing the loss of habitat, it cannot control the spatial allocation of habitat – which would be necessary to effectively counter the fragmentation of habitat.

To address this shortcoming of conservation payments, Parkhurst et al. (2002) proposed an agglomeration bonus (AB), in which the conservation of a land parcel not only earns the flat

payment but also an additional bonus if the land parcel is adjacent to other conserved land parcels (Parkhurst et al. 2002, Parkhurst and Shogren 2007, Banerjee et al. 2012, Albers et al. 2018, Panchalingam et al. 2019, Bareille et al. 2023).

A major alternative to the AB is the threshold payment (TP) in which a payment is only granted if the joint conservation effort in a defined zone exceeds a certain threshold (Grout 2009, Drechsler et al. 2010, Wätzold and Drechsler 2014, Zavalloni et al. 2019). So while the AB is paid per conserved neighbour and the payment to the landowner (sum of base payment and bonuses per conserved neighbours) can differ among land parcels, the TP is the same for all landowners in the defined area and paid if and only if the number of conserved land parcels in that region is large enough.

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A variant of the TP is the threshold bonus in which the threshold payment (here termed bonus) is added to an unconditional base payment. These outlined conservation schemes are subsumed under the label 'coordination incentives' (CI) (Nguyen et al. 2022).

CIs promise to conserve species more cost-effectively than flat payments (Albers et al. 2008, Hartig and Drechsler 2009, Drechsler et al. 2010, Dijk et al. 2017, Liu et al. 2019, Nguyen et al. 2022, Bareille et al. 2023), but their cost-effectiveness gain depends on ecological and economic conditions. A number of factors have been identified that affect the cost-effectiveness of CI, including the spatial variation and correlation of the conservation costs and the species dispersal range (Hartig and Drechsler, 2009, Drechsler et al. 2010, Wätzold and Drechsler 2014, Bareille et al. 2023).

The mentioned studies have some limitations that the present paper aims to relax. One is their reliance on a single ecological model for the assessment of the ecological benefit (species survival) of the analysed conservation schemes. In the latter three studies the ecological benefit was assessed by a simple function that was based on arguments of plausibility but had no further foundation in ecological theory. Hartig and Drechsler (2009) used a population model that is rooted in ecological theory but considered only three selected types of species, which restricts the generality of their results.

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The second limitation is that the two main variants, AB and TP have not yet been compared (note that the "agglomeration bonus" in Wätzold and Drechsler (2014) is in fact a threshold bonus *sensu* Nguyen et al. (2022)). Third, except for Wätzold and Drechsler (2014), either budget- or cost-

effectiveness has been considered, while there is no direct comparison between the two. Fourth, interactions between model parameters were considered only selectively.

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While the three last limitations could be addressed by appropriate extensions of the models and model analysis, to achieve a higher generality of the results (and a more intuitive understanding) I consider the introductory statement that loss and fragmentation (or their opposites: amount and spatial connectivity) of habitat are the main determinants of biodiversity. These two landscape features may be substitutable from the species' point if view, formally represented by an indifference function (IF), so that a reduction in the amount of habitat may be offset by an increase in spatial connectivity and vice versa (Drechsler and Wissel 1998).

115 Acknowledging the central role of amount and connectivity of habitat, the paper then explores the performance of two CI, the AB and the TP, with respect to these two landscape features. In particular I will show that there is a trade-off between habitat amount and connectivity, so that for given conservation budget (or total conservation cost) both can generally not be maximised simultaneously. The trade-off is formally expressed by a production possibility frontier (PPF)

120 (Polasky et al. 2008) which consists of the "efficient" combinations of habitat amount and connectivity, so that an increase in the one must be "paid for" by decrease in the other.

The shapes of IF and PPF are shown to depend on ecological and economic model parameters and to differ between the two considered types of CI, and on whether the provision of amount and connectivity of habitat is constrained by an agency's conservation budget or by the total cost (forgone economic profits) incurred by the conservation efforts. Discussion of the shapes of IF and PPF creates an understanding of the ecological and economic trade-offs between habitat amount and connectivity.

Understanding the shapes of IF and PPF directly translates into an understanding of the budget- and cost-effective levels (maximisation of ecological benefit under budget- or cost constraint) of the two CI. This is because the present problem can be viewed within economic production theory (Varian 2010, Wilkinson 2012) by identifying the ecological benefit as the output of two production factors, amount and connectivity of habitat, whose feasible levels are determined by a budget- or cost constraint, respectively. The cost-effective levels of the two production factors, as well as the associated CI scheme design parameters depend on the shapes of PPF and IF.

For didactic reasons, the paper will deviate slightly from the standard structure with Methods and Results but start with an outline of the analysis, the construction and discussion of PPFs and IFs, and their joint consideration in a cost-effectiveness analysis. Methodological details are provided in subsections of the major sections or in Appendices.

#### 2 Outline

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A fictitious model landscape is considered, structured as a square grid with  $N = 10 \times 10$  grid cells with each grid cell representing a land parcel. Boundary effects are avoided by the assumption of periodic boundary conditions. Each land parcel i can be managed for economic purposes ( $x_i = 0$ ) to earn an economic profit  $c_i$ , or for conservation ( $x_i = 1$ ) to receive a conservation payment  $p_i$ . Conservation forfeits the economic profit  $c_i$  which thus is identified as the opportunity cost of conservation, or henceforth: *conservation cost* – being aware that in reality there may be other costs associated with conservation like management costs or transaction costs.

The conservation costs are assumed normally distributed with mean one and standard deviation  $\sigma$ . By setting the mean cost to one, all costs such as the conservation budget below, are effectively scaled in units of the mean cost; implying that parameter  $\sigma$  is the relative standard deviation of the conservation costs. The costs are spatially correlated with a correlation length l which represents the typical dimension of the "hills" and "valleys" in the "cost landscape". The procedure for the correlated sampling uses a moving-window average, as described by Drechsler et al. (2021).

In the centre of the analysis are the two "production factors", amount and spatial connectivity of habitat. The former is measured here by the *proportion of conserved land parcels* in the model region,

$$q = \frac{1}{N} \sum_{i=1}^{N} x_i \tag{1}$$

and the latter by the average proportion of conserved land parcels in the neighbourhood of conserved land parcels,

$$r = \frac{\frac{1}{8} \sum_{i=1}^{N} \sum_{j \in M_i} x_i x_j}{\sum_{i=1}^{N} x_i} = \frac{\sum_{i=1}^{N} \sum_{j \in M_i} x_i x_j}{8qN}$$
(2)

Quantity r, henceforth termed the *spatial aggregation of conserved land parcels*, equals one if every conserved land parcel is fully surrounded by conserved land parcels, while it equals zero if none of the conserved land parcels has a conserved neighbour. Increasing r within its range of  $0 \le r \le 1$  represents increasing spatial aggregation of conserved land parcels.

A statistical relationship exists between quantities q and r. If the conserved land parcels are randomly distributed, if the proportion of conserved land parcels is q so will approximately be the expected proportion of conserved land parcels around a conserved land parcels. Values r >> q indicate a "non-trivial" spatial aggregation of conserved land parcels, while r << q indicates disaggregation.

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To construct production possibility frontiers (PPFs) I model the land-use patterns generated by the agglomeration bonus (AB) and the threshold payment (TP) for given conservation budget B and for given conservation cost C. Characterising each land-use pattern by its q and r, PPFs are defined by  $B(q, r) = B_0$  and  $C(q, r) = C_0$ , respectively. These two functions contain all combinations of q and r that lead to a given level of  $B_0$  and  $C_0$ , respectively.

Indifference functions (IFs) are constructed from the benefit function introduced by Drechsler et al. (2010) and a metapopulation model similar to that of Hartig and Drechsler (2009). Plotting the ecological benefit V as a function of q and r yields IFs in the form of  $V(q, r) = V_0$  that contain all combinations of q and r that lead to a chosen benefit level  $V_0$ . IFs and PPFs are overlaid, according to the economic production theory, to analyse scheme budget- and cost-effectiveness.

#### 3 Production possibility frontiers

#### 3.1 The costs and trade-off between proportion and aggregation of conserved land parcels

To understand the costs associated with the "provision" of proportion q and aggregation r of conserved land parcels for the species, consider the simple cost landscape in Table 1.

Table 1: Fictitious landscape of nine land parcels with spatially heterogeneous conservation costs.

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150	100	150
100	150	100

The aim is to conserve as many land parcels n for a given total cost implies that first (for small total cost levels) the land parcels with cost 100 are selected, before (for larger total cost levels) the ones with cost 150 are selected. This can be represented by a cost function C(n) = 100n for  $n \le 5$  and C(n) = 500 + 200(n - 5), with (stepwise) increasing marginal costs, associated with an over-linear increase in C.

The associated spatial aggregation r is zero if only land parcels in the four corners (or only the one in the centre) are conserved. If the five least costly land parcels (proportion q = 5/9) are conserved we have four land parcels with one conserved neighbour each and one land parcel with four conserved neighbours, leading to an aggregation of  $r = (4 \times 1/8 + 1 \times 4/8)/5 = 1/5$ . The total cost associated with this r is C = 500.

These five land parcels are obviously not very well connected, so r is quite small. To generate a higher r one should rather conserve a block of land parcels. Conserving, e.g., the square block of four land parcels in the upper left of the model landscape incurs the same total cost of C = 500 but generates an aggregation of  $r = (4 \times 3/8)/4 = 3/8$  which is almost twice the r of the previous selection. However, this maximisation of r comes at the "cost" that only four instead of five land parcels are conserved, so q = 4/9 compared to the previous q = 5/9. So for given cost C there is a trade-off between q and r.

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The reason for this trade-off is the "patch selection effect" coined by Drechsler et al. (2010) which highlights that if conservation costs vary spatially the conservation of adjacent land parcels requires that not always the least costly land parcels but at least some more costly ones are selected.

To summarise, q and r can generally not be maximised simultaneously, but there is, in the terminology of economic production theory, a "rate of transformation" between the two: in the above numerical example it equals  $\Delta r/\Delta q = (3/8 - 1/5)/(4/9 - 5/9) = -63/40$ . More generally, these rates of transformation are represented by a production possibility frontier (PPF) that contains all combinations of q and r that incur a given total cost C.

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#### 3.2 The land-use model with agglomeration bonus (AB)

#### 3.2.1 Methodology

Conservation of land parcels is induced by a payment  $p_i$  that may differ among land parcels. It consists of a base payment payment  $p_0$  and a bonus b that is paid for each conserved land parcel in the Moore neighbourhood  $M_i$ , consisting of the eight land parcels adjacent to land parcel i:

$$p_i = p_0 + b \sum_{j \in M_i} x_j \tag{3}$$

Conservation of land parcel i is profitable if the payment exceeds the cost:  $p_i > c_i$ . In line with the experimental study by Parkhurst and Shogren (2007), the land-use dynamics start with an economically used model landscape ( $x_i = 0$  for all i). The payment eq. (1) is offered and landowners decide on the most profitable land use. In that first time step there is no conservation in any neighbourhood  $M_i$ , so land parcels are conserved if and only if  $p_0 > c_i$ . For not too small base payments, some land parcels are conserved after the first time step, so the neighbourhoods of some land parcels will contain conserved land parcels. This may induce some more economically used land parcels to turn to conservation, and time step by time step a pattern of conserved land parcels emerges (note that in each time step no conserving landowner has an incentive to re-convert to economic use).

These land-use dynamics are simulated until a Nash equilibrium is reached in which no landowner has an incentive to change their land use. The time steps here may be regarded as the lengths of conservation contracts, or as "virtual" rounds in the development of a coordinated land-use plan. Strategic behaviour of the landowners, such that neighbours may be expected to conserve so that oneself conserves too, is ignored here, which is likely to underestimate the proportion (and possibly, aggregation) of conserved land parcels. To mimic effects of strategic behaviour and provide an upper bound on the level of conservation, I reverse the simulation and start from a landscape with all land parcels conserved. Analogous to above, in each time step the landowners observe the proportion of conserving neighbours and adapt their own land use. Some of them may convert to economic use. This is continued until there is no change any more. The two final land-use patterns represent the payoff- and risk-dominant solutions of the regional coordination problem confronting the landowners in an AB scheme (Parkhurst and Shogren 2007, Drechsler 2023, Drechsler in press).

In the following I disregard the peculiarities of the paths to the two final land-use patterns but consider these land-use patterns as static lower (for the initially economically used landscape) and upper (for the initially conserved landscape) bounds on the possible outcomes of an AB scheme. For each of them the budget (scaled by the number of land parcels) required to finance the final pattern of conserved land parcels is given by

$$B = \frac{1}{N} \sum_{i} p_{i} x_{i}$$
(4)

and the total cost incurred equals

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$$C = \sum_{i} c_{i} x_{i} \tag{5}$$

As supplementary quantities for further evaluations, I consider the average payment per conserved land parcel,

$$\pi = \frac{B}{q} = p_0 + \frac{8br}{q} \tag{6}$$

and the ratio between bonus and base payment,

$$\rho = \frac{b}{p_0} \,. \tag{7}$$

Similar to the example in section 3.1, each land-use pattern is associated with a level of q and r. To construct the PPF, I sample 100,000 cost landscapes with given cost variation  $\sigma$  and correlation length l, as well as a base payment  $p_0$  from the interval  $[1 - 3\sigma, 1]$  and a bonus b from the interval  $[0, \sigma]$ . To motivate these ranges, for b = 0, a base payment of  $1 - 3\sigma$  marks about the lower 0.1-percent quantile of the conservation costs and may be regarded as a reasonable lower bound; while for p = 1 and b = 0 about 50 percent of the land parcels will be conserved – a plausible upper bound. Preliminary analyses of the model revealed that for  $b = \sigma$  even a relatively small base payment around  $1 - 1.5\sigma$  will induce the majority of land parcels into conservation, suggesting  $b = \sigma$  as a plausible upper bound.

For each of the 100,000 samples, the land-use dynamics are simulated and the proportion q and aggregation r of the conserved land parcels calculated, as well as the budget B, the payment per land parcel  $\pi$  and the ratio of bonus and base payment  $\rho$ . As described in Appendix A, contour plots (or heat maps) B(q, r),  $\pi(q, r)$  and  $\rho(q, r)$  are constructed from the 100,000 data points. The values of B,  $\pi$  and  $\rho$ , respectively, are represented by a particular colour, so each colour represents all

combinations of q and r that lead to a given B,  $\pi$  and  $\rho$ , respectively, and represents a PPF. PPFs are established for nine economic scenarios, formed by systematically combining  $\sigma \in \{0.05, 0.15, 0.3\}$  and  $l \in \{0, 2, 4\}$ .

#### 3.2.2 Results

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Figure 1 shows, for the AB, the conservation budget B required to finance the two production factors q and r for the "lower bound" (simulation starts with economically used landscape). As a first observation, not all combinations of q and r were obtained in the 100,000 simulations of the land-use dynamics. As explained in section 2, only combinations with r not much smaller than q are observed. Any aggregation of conserved land parcels, either due to a positive spatial correlation in the conservation costs or a non-zero bonus b will increase r relative to q, filling the area above the diagonal in Fig. 1.

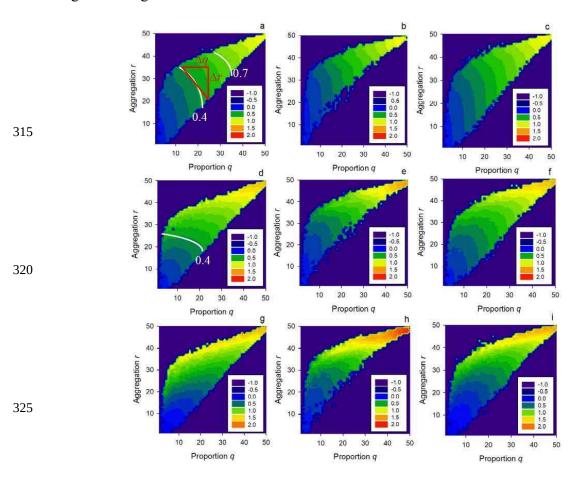


Figure 1: Conservation budget B for the agglomeration bonus, by colour scale, as a function of the proportion q and spatial aggregation r of conserved land parcels. Simulation started from an economically used landscape. Negative values (dark blue) indicate that the combination of q and r was not observed in those 100,000 samples. Upper, middle and lower panels: cost variation  $\sigma = 0$ , 05, 0.15, 0.3; left, middle and right panels: cost correlation l = 0, 2, 4.

As defined, the PPFs contain the points in *q-r* space that are associated with the same budget level (the same colour). Examples are the white lines in Figs. 1a and 1b which represent budget levels of 0.4 and 0.7, respectively, and contain all combinations of *q* and *r* that are associated with the respective budget level (precisely, the colour scale is continuous. However, plotting *B* on a continuous colour scale would complicate the detection of the PPFs which in the present outline are visible along the discrete colour changes; between these, one may imagine all other PPFs in parallel; also note that for the following interpretations of the figure it is not essential to know the exact budget levels associated with each colour).

The slopes of the lines represent the marginal rates of transformation between q and r, formally given by the ratio  $\Delta q/\Delta r$ , which means that an increase in q by some amount  $\Delta q$  has to come with a reduction in r by  $\Delta r$  to stay within the budget (red coloured example in Fig. 1a). The steeper the slope the more of r must be sacrificed to offset an increase in q, indicating that increases in q are relatively costly, while increases in r are relatively cheap.

That the slopes in Fig. 1 become shallower with increasing cost variation  $\sigma$  thus indicates that spatial aggregation becomes relatively more costly. The reason is the patch selection effect discussed in section 3.1 (that the spatial aggregation reduces the degrees of freedom for choosing the least costly land parcels, so aggregation is costly) and this effect becomes more pronounced as the cost variation increases.

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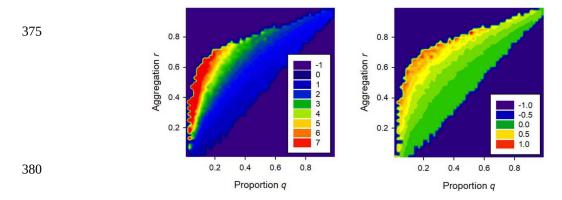
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Interestingly, at  $\sigma = 0.3$  (panels g-i) the slopes of the PPFs are even slightly positive, implying that the budget *decreases* with increasing proportion q. The reason for this unexpected finding will be presented in the two following paragraphs. An increasing  $\sigma$  further reduces the budget required for small q and r and increases the budget required for large q and r (compare the white PPF in Fig. 1d with the corresponding one in Fig. 1a). This is plausible, because for small q and r only the least costly land parcels need to be conserved whose costs decline with increasing  $\sigma$ , while for large q and r also the high-cost land parcels need to be conserved whose costs increase with increasing  $\sigma$ . The level of spatial correlation l has only a small effect on the shapes of the PPFs.

For the design of an AB scheme it is also helpful to know how the scheme parameters are associated with the inputs q and r. According to Fig. 2a, very high payments  $\pi$  (note that the mean cost in the landscape equals one, so a value of  $\pi = 5$ , e.g., means the payment is five times larger

than the mean cost) need to be offered to obtain a high aggregation r together with a low proportion q of conserved land parcels. The reason is that while a moderate aggregation is obtained just because of statistical reasons (as argued above: the more land parcels are conserved the more conserved neighbours they will have), an aggregation much higher than that statistical level can only be induced by very high bonus levels (Fig. 2b) which are in the end responsible for those high payments  $\pi$ .



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Figure 2: Payment levels  $\pi$  (panel a) and ratio  $\rho$  of bonus and base payment (panel b), by colour scale, associated with given levels of proportion q and spatial aggregation r of conserved land parcels. The magnitude and correlation of the conservation cost variation are  $\sigma = 0.3$  and l = 0 (exemplary for other levels of  $\sigma$  and l). Other details is in Fig. 1.

These circumstances also explain the above unexpected finding that at high cost variation (Figs. 1g–i) the PPFs have positive slopes, so the budget B decreases with increasing proportion q: The payment  $\pi$  declines less strongly than does q increase, so  $B = q\pi$  altogether declines.

Figure 1 shows the budget B(q, r) for the final land-use pattern after the simulation started with all land parcels in economic use. The simulation starting with all land parcels initially *conserved* leads to (very nearly) identical values B(q, r). The reason is that although the latter simulation leads, for given base payment and bonus, to higher q and r, the associated budget is – not quite unexpectedly – higher, too. Due to the similar outcomes of both simulation schedules, below I only consider the former one with all land parcels in economic use initially.

Next to the budget B, the total conservation cost C incurred by the conservation efforts is of interest (Fig. 3). Compared to Fig. 1, the slopes of the PPFs are much steeper and much less sensitive to the cost variation  $\sigma$ , indicating that spatial aggregation is relatively "inexpensive". The reason for the difference to Fig. 1 is that high spatial aggregation requires high bonuses and budgets (Figs. 1 and 2) while costs increase less strongly with increasing aggregation. This difference is obviously

associated with a substantial producer surplus (difference between payment and cost,  $p_i - c_i$ ) for the landowners.

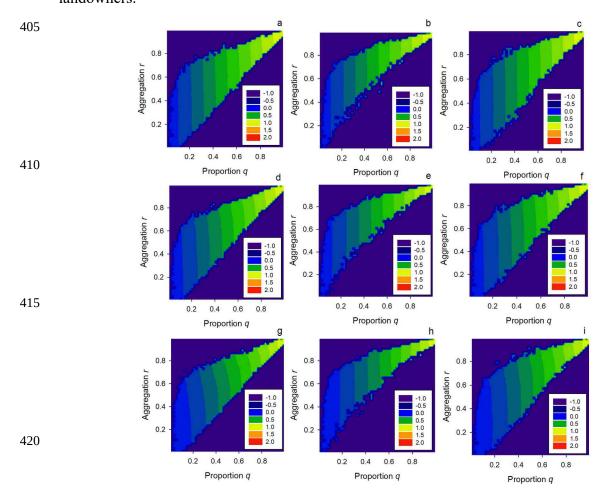


Figure 3: Total conservation cost C for the agglomeration bonus, by colour scale, as a function of the proportion q and spatial aggregation r of conserved land parcels. Simulation started from an economically used landscape. Negative values (dark blue) indicate that the combination of q and r was not observed in those 100,000 samples. Upper, middle and lower panels: cost variation  $\sigma = 0$ , 05, 0.15, 0.3; left, middle and right panels: cost correlation l = 0, 2, 4.

#### 3.3 The land-use model with threshold payment (TP)

## 3.3.1 Methodology

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Drechsler et al. (2010) proposed an "agglomeration payment" (a threshold payment sensu Nguyen et al. (2022) in which landowners receive payments p if their conserved land parcel is located within some rectangular section ("zone") of the landscape and if the proportion of conserved land parcels in that zone meets or exceeds some "density threshold" k). The model landowners choose the location of the zone whose size is prescribed by the conservation agency (other than in

Drechsler et al. (2010) where the size was be chosen by the landowners) to maximise their joint surplus, i.e. the difference between payment and conservation cost over all conserving landowners.

Other than Drechsler et al. (2010) I do not assumed that landowners transfer surpluses to induce other landowners (with high conservation costs) into conservation. So for a land-use pattern to be feasible (with all conserved land parcels generating a non-negative profit) it is not sufficient that the payment exceeds the average cost of all conserved land parcels but it must exceed the cost of the most costly land parcel.

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For simplicity, only square-shaped zones are considered with side length  $a \in \{4, 5, ..., 10\}$ , where the lower bound of a = 4 represents a square of size of about one sixth of the model landscape, while with the upper bound of a = 10 the entire landscape is covered. For the density threshold k all values from the interval [0, 1] are considered.

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The associated conservation budget B equals  $pka^2$ , where p is the most costly of the  $ka^2$  least costly land parcels in the zone. The total conservation cost C is the sum of the costs over all conserved land parcels (cf. eq. (5)). Model landscapes are generated, and the proportion q and aggregation r of conserved land parcels calculated as described in section 3.2.1.

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#### 3.3.2 Results

Figure 4 shows the conservation budget B required to finance the two inputs, proportion q and spatial aggregation r of conserved land parcels. The slopes of the PPFs (rates of transformation) are quite steep, so that aggregation is relatively inexpensive and the budget increases mainly with the proportion of conserved land parcels. The steepness of the PPFs slightly declines with increasing cost variation (the above-mentioned patch selection effect). The cost correlation l has only a minor effect.

The associated scheme parameters a (prescribed size of the conservation zone) and k (density

threshold) are shown in Fig. 5. As argued above, equality of q and r is, at least under uncorrelated costs, a statistical necessity, and can be achieved without restricting the size of the zone. To deviate and reach higher ratios r/q between aggregation and proportion of conserved land parcels, the size of the zone must be reduced (Fig. 5a) and the density threshold k increased (Fig. 5b). Finally, the

of the zone must be reduced (Fig. 5a) and the density threshold k increased (Fig. 5b). Finally, the results for the total conservation costs C (Fig. 6) are very similar to those obtained for the budget B in Fig. 4.

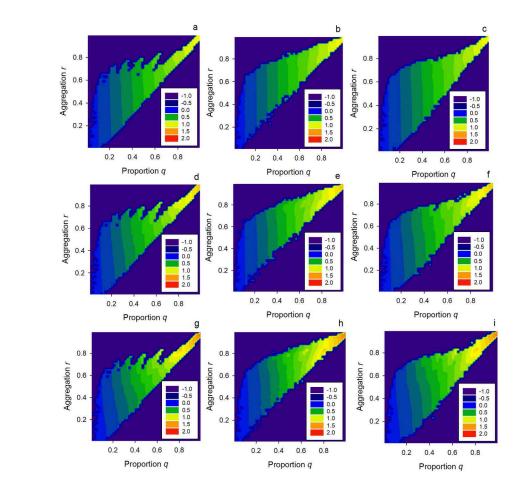


Figure 4: Conservation budget B for the agglomeration payment, by colour scale, as a function of the proportion q and spatial aggregation r of conserved land parcels. Negative values (dark blue) indicate that the combination of q and r was not observed on those 100,000 samples. Upper, middle and lower panels: cost variation  $\sigma = 0$ , 05, 0.15, 0.3; left, middle and right panels: cost correlation l = 0, 2, 4.

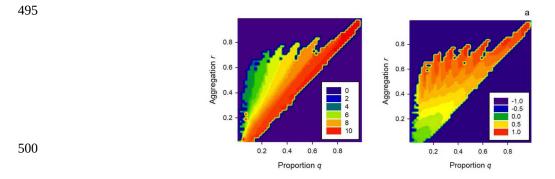


Figure 5: Prescribed sizes of the conservation zone, a (panel a), and density threshold k (panel b), by colour scale, associated with given levels of proportion q and spatial aggregation r of conserved land parcels. The magnitude and correlation of the conservation cost variation are  $\sigma = 0.3$  and l = 0 (exemplary for other levels of  $\sigma$  and l). Other details is in Fig. 4.

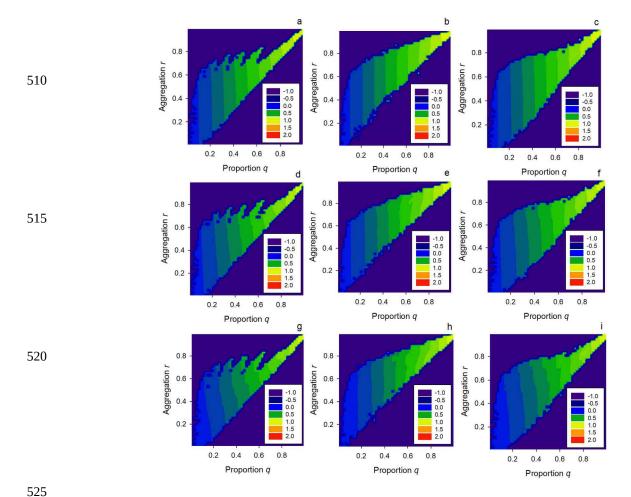


Figure 6: Total conservation cost C for the agglomeration payment, by colour scale, as a function of the proportion q and spatial aggregation r of conserved land parcels. Negative values (dark blue) indicate that the combination of q and r was not observed on those 100,000 samples. Upper, middle and lower panels: cost variation  $\sigma = 0$ , 05, 0.15, 0.3; left, middle and right panels: cost correlation l = 0, 2, 4.

#### 4 The indifference functions

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Indifference functions are established for two different models. The first is the benefit function proposed by Drechsler et al. (2010) (and adopted by Wätzold and Drechsler (2014) and Bareille et al. (2023)):

$$V = \sum_{i} \sum_{j} x_{i} x_{j} \exp\{-d_{ij} / d\}$$
 (8)

where d is the species dispersal range and  $d_{ij}$  is the Euclidean distance between land parcels i and j (taking periodic boundary conditions into account: each pair (i, j) is counted only once and the

smallest possible distance  $d_{ij}$  is chosen, so that for instance the distance between the two land parcels in the upper right and upper left corners of the  $10 \times 10$  model region is not 10 - 1 = 9 but 1).

One can see that V of eq. (8) increases with increasing proportion q of conserved land parcels and (since the "weight factor"  $\exp\{-d_{ij}/d\}$  increases with increasing between-land-parcel distances  $d_{ij}$ ) with increasing spatial aggregation r.

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To construct an IF from eq. (8), 100,000 land-use patterns  $\{x_i\}_{i=1,\dots,N}$  are sampled. Three different sampling algorithms are used to create landscapes with different amounts and spatial distributions of conserved landscapes – which all lead to very similar results (Online Appendix A). For each sampled land-use pattern the values of q, r and V are determined and contour plots V(q, r) constructed as described in Online Appendix A. The result is shown in Fig. 7. Each colour (theoretically on a continuum) represents a particular level of V as shown in the legends. One can see that the benefit increases with increasing proportion q and increasing spatial aggregation r of conserved land parcels (within each panel) and with increasing species dispersal range d (panels from left to right).

Indifference functions include points of equal V, i.e. equal colour. The IFs in Fig. 7 are (nearly) straight lines with negative slope, indicating that a reduction in q can/must be offset by an increase in r (or vice versa) to maintain a given level of V. In economic production theory this ratio of  $\Delta r/\Delta q$  is termed the (marginal) rate of substitution.

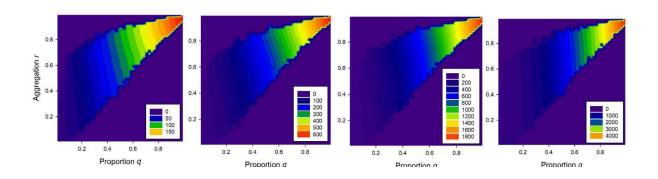


Figure 7: Ecological benefit V of eq. (3), by colour scale, as a function of the proportion (q) and spatial aggregation (r) of conserved land parcels. Zero values (dark blue) indicate that the combination of q and r was not observed on the 100,000 samples. Panels from left to right: species dispersal range d = 0.5, 1.0, 2.0, 5.0.

The slopes become slightly more negative as d increases, indicating that a large reduction in r can be offset by a small increase in q. In other words, the ecological benefit is relatively insensitive to a change in r, which is easily explained by the fact that species with a large dispersal range obviously do not strongly rely on the spatial aggregation of its habitat.

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The second model considered for the construction of IFs is the metapopulation model by Ovaskainen and Hanski (2001). Here each conserved land parcel forms a habitat patch that can be inhabited by a local population. Local populations go extinct at some rate e and individuals emigrate from local populations at some rate e; the ratio  $\lambda = m/e$  is termed henceforth the "emigration-extinction ratio".

The species has a dispersal range d. Analogous to eq.(8), the probability of a dispersing individual reaching a target patch is given by  $\exp\{-d_{ij}/d\}$ , so distant patches (with large  $d_{ij}$ ) are reached with a smaller probability and species with a large dispersal range d can reach distant patches better than species with a small d. The metapopulation dynamics are simulated (Online Appendix B) until a steady state is reached. The expected number of land parcels occupied by a local population in that steady state is taken as the (static) ecological benefit V associated with a given land-use pattern.

In the same manner as for eq. (8), 100,000 land-use patterns are sampled, V determined and IFs constructed (Fig. 8). Their general behaviour is similar to that of the IFs in Fig. 7, so that the IFs are (rather) straight lines with negative slope whose negativity amplifies with increasing species dispersal range d (exploring which kinds of ecological benefit functions or models lead to non-linear IFs may be a matter of future research).

However, some important differences exist to Fig. 7. First, the slopes in Fig.8 are much more sensitive to d and cover the entire range from nearly horizontal to nearly vertical. And second, the slopes are not only determined by the species dispersal range but also by the emigration-extinction ratio  $\lambda$  of the species.

#### 5 The cost-effective design of coordination incentives

According to economic production theory, the output is maximised under the given budget or cost constraint if the rate of transformation (slope of the PPF) equals the rate of substitution (slope of the IF), which geometrically is the point where the IF is in contact with the PPF.

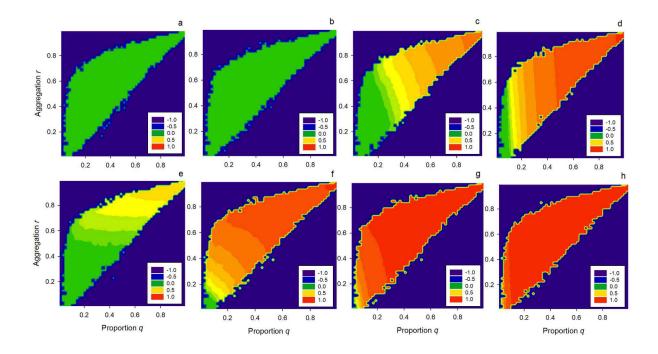
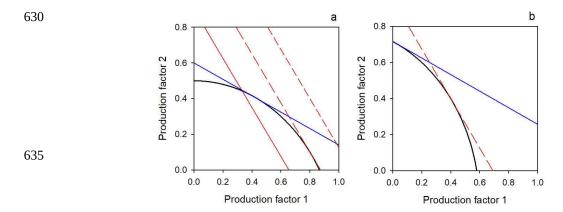


Figure 8: Metapopulation viability V (eq. (B3)), by colour scale, as a function of the proportion q and spatial aggregation r of conserved land parcels. Negative values (dark blue) indicate that the combination of q and r was not observed on the 100,000 samples. Upper panels and lower panels, respectively: emigration-extinction rate  $\lambda = 0.2$ , 2; panels from left to right: species dispersal range d = 0.5, 1, 2, 5. Results for  $\lambda = 0.1$ , 0.5, 1 and 5 are shown in Fig. C3 of Online Appendix C.

Some fictitious examples are shown in Fig. 9. In panel a the maximum obtainable output for IFs (red coloured lines) is given by the long-dashed line. Due to the negative slope of the IF (which indicates that production factor 2 must be increased considerable to offset a reduction in production factor 1), it is cost-effective to choose production factor 1 rather large and production factor 2 rather small. In contrast, if the IF has a shallow slope it is cost-effective to choose production factor 1 small and production factor 2 large. Altogether, an increasing negativity of the IF's slope "favours" high levels of production factor 1 and low levels of production factor 2. The opposite is observed when the (negative) slope of the PPF is increased (Fig. 9b): the cost-effective level of production factor 1 decreases and that of production factor 2 increases.

Identifying production factors 1 and 2 with the proportion q and spatial aggregation r of conserved land parcels, respectively, leads to the following conclusions. Increasing cost variation  $\sigma$  reduces the negativity of the PPF's slope (Figs. 1, 3, 4, 6), so a comparatively large r and a comparatively small q are budget- and cost-effective, induced by relatively large bonuses (in the AB) or thresholds (in the TP). An increasing dispersal range d (and in the case of the benefit representing the survival

probability of a metapopulation model: an increasing emigration-extinction ratio  $\lambda$ ) increases the negativity of the IF's slope (Figs. 7, 8), so a comparatively large q and a comparatively small r are budget- and cost-effective.



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Figure 9: Fictitious examples of production possibility frontiers (PPF, black lines) and indifference functions (IF, red and blue lines). The PPFs contain all combinations of levels of Input 1 and Input 2 that can be afforded for the given budget (or total cost), and the IF contains all combinations of input levels that lead to a given output level. The red lines in panel a represent different levels of output, the red and blue lines in each panel represent different shapes of IF, and panels a and b show different shapes of PPFs.

An interesting interaction can be observed between cost variation and species dispersal range for budget-effectiveness in the AB. As Figs. 1g–h show, for large cost variation the PPF has a pronounced edge towards the upper-right. Imagining straight IFs with different slopes around that edge reveals that all these IFs touch the PPF at very similar levels of *q* and *r*. This indicates that at a large cost variation the budget-effective levels of *q* and *r* (and thus, the cost-effective levels of base payment and bonus) are almost independent of the species dispersal range.

After both coordination incentives have been analysed separately, in a final step I compare them. Referring to the discussion of budget- and cost-effectiveness above, one can observe that under budget constraint the PPFs of the TP (Fig. 4) are much steeper than those of the AB (Fig. 1), indicating that higher levels of r and lower levels of q are budget-effective; while under cost constraint the PPFs of AB and TP are similar.

To compare the budget- and cost-effectiveness of the two schemes I subtract, for each combination of q and r, the associated budget (cost) of the AB from that of the TP. Figures 10 and 11 show that for any (q, r) combination (with very few exceptions in Fig. 11) the budget and total cost in the TP

are higher than or equal to those in the AB. While the budget differences can be substantial (relative to the budget levels observed in Figs. 1 and 4) the cost differences are rather minor, so one may regard both schemes as approximately equally cost-effective. Higher budgets in the TP are observed especially for the generation of very high levels of r (Fig 10).

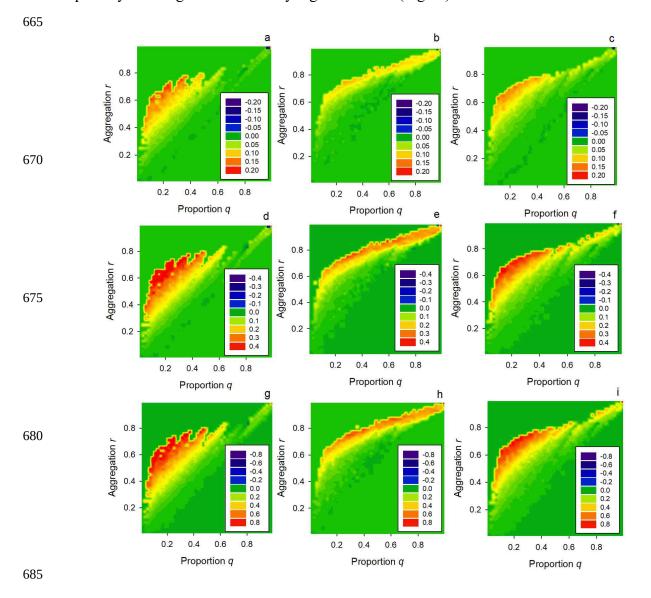


Figure 10: Differences between the budgets B of the threshold payment and the agglomeration bonus, by colour scale, associated with given levels of proportion q and aggregation r of conserved land parcels. Green colour represents equality of the budget, but (for technical reasons) also those combinations of q and r (cf. Figs. 1 and 4) that were not attained in the 100,000 sampled land-use patterns.

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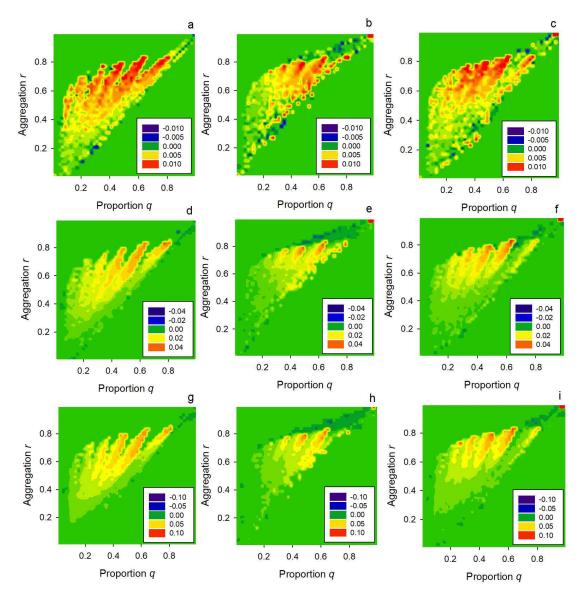


Figure 11: Differences between the total costs C incurred by the agglomeration payment and the agglomeration bonus, by colour scale, to generate given levels of proportion q and aggregation r of conserved land parcels. Green colour represents equality of the budget, but (for technical reasons) also those combinations of q and r (cf. Figs. 3 and 6) that were not attained in the 100,000 sampled land-use patterns.

#### **6 Discussion**

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An ecological-economic model is presented to analyse economic and ecological trade-offs between the amount (proportion) and the spatial connectivity (aggregation) of habitat, both of which are essential for the survival of many species. The economic model considers spatially heterogeneous conservation costs and two alternative economic coordination incentives, the agglomeration bonus (AB) and the threshold payment (TP), to conserve land in a spatially aggregated manner. Both the

total cost of conservation (foregone economic revenues) and the size of the conservation budget required to finance the payments to the landowners are considered.

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Conserved land serves as habitat for species that are sensitive both to amount and connectivity of the habitat. The ecological benefit, i.e. effect of the land-use pattern on the species, is measured by an ad-hoc function and, alternatively, by the survival of a metapopulation in the model region. The metapopulation model is based on the metapopulation concept widely used in landscape ecology which assumes that individual habitat patches can inhabit local species populations that can go extinct, while unoccupied habitat patches can become colonised by neighbouring local populations, where the size if the neighbourhood depends on the species' dispersal ability. The classical model by Hanski (1999), adopted in the present analysis, assumes that the probability of an individual crossing a particular distance declines exponentially with that distance increasing, where the rate of decline is inversely proportional to the species dispersal ability.

Rather than analysing the full ecological-economic model I focus on the two key features of the land-use pattern, the proportion q and aggregation r of conserved land parcels and (i) construct production possibility frontiers (PPFs) for q and r that show their levels that can be delivered under a given budget or cost constraint; and (ii) indifference functions (IFs) that contain all levels of q and r that generate a given level of ecological benefit.

The PPFs and IFs are interpreted within the framework of economic production theory to analyse trade-offs between the two land-use features and the budget- and cost-effective design of the two coordination incentives. The main results are:

- 1. A decreasing species dispersal range makes the IFs shallower, meaning that the dependence of the ecological benefit on r becomes comparatively more pronounced and that or q becomes comparatively less pronounced. This implies that higher bonuses (AB) and higher thresholds (TP) become budget- and cost-effective, confirming and explaining a finding of Wätzold and Drechsler (2014), that the TP (termed agglomeration payment by the authors) becomes more cost-effective relative to a spatially homogeneous payment (with zero bonus or threshold).
- 2. In the considered metapopulation model the slope of the IF is not only determined by the species dispersal ranges but increases with increasing emigration-extinction ratio. The metapopulation model further generated a much wider range of IF slopes when the dispersal range was varied in contrast to the ecological benefit function of Wätzold and Drechsler (2014) that always produced

very steep slopes and is thus likely to underestimate the importance of *r* for species survival. And
hence, it is likely to underestimate the budget- and cost-effective levels of bonus or threshold in the AB and TP, respectively.

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- 3. Increasing variation of the conservation costs makes the PPFs shallower, meaning that q becomes comparatively less and r becomes comparatively more expensive, both with respect to total cost and budget. This implies that lower bonuses (AB) and lower thresholds (TP) become budget- and cost-effective, confirming and explaining the finding of Wätzold and Drechsler (2014), that the TP becomes less cost-effective relative to a homogeneous payment. When budget-effectiveness is considered in the AB, the partly positive slopes of the PPFs at high cost variation (Fig. 1g) imply that for given r the required budget declines with increasing q; or conversely, for given q the ereation of r levels around q (that are induced by homogeneous payments; ef. Fig. 3) requires higher budgets than the creation of higher r levels (induced by the AB). This means that here the agglomeration bonus is more budget-effective than the homogeneous payment. The edged shapes of the PPFs further imply that the point of contact between PPF and IF is relatively independent of the slope of the IF, so that this result is largely independent of the species dispersal rate.
- 4. The shape of the PPF is relatively independent of the correlation length of the conservation costs, which among the things implies that there can be no or only a weak interaction between that length and the species dispersal range. The reason is that the species only observes the land-use pattern (q and r) and not the conditions (cost distribution and scheme design) that led to its establishment.
- 5. In the TP the PPFs are rather straight. Together with the straightness of the IFs this implies that only the two "corner solutions" exist with the density threshold either maximal or minimal (zero) explaining with much higher generality the finding of Wätzold and Drechsler (2014) that a mixture of homogenous payment and TP is never more budget- or cost-effective than either the homogenous payment or the TP.
- 6. For the TP, the PPFs with respect to budget and cost are relatively similar, explaining why Wätzold and Drechsler (2014) did not find strong difference between budget- and cost-effectiveness. For the AB, in contrast, the PPFs with respect to budget are much shallower than those with respect to cost, indicating that r becomes comparatively more costly. The reason is that high levels of r require high bonuses, implying that the budget-effective bonus level is smaller than the cost-effective bonus level.

7. The budget associated with any level of q and r in the TP has at least the magnitude of that in the AB – with particularly high exceedance for high levels of r, so here the AB is much more budget-effective than the TP. In contrast, the cost differences between TP and AB for given q and r are rather small, so both schemes are about equally cost-effective. The larger budgets required in the TP may be explained by higher producer rents. Although both schemes involve producer rents, in the TP all landowners receive the same payment (equal to the cost of the most costly conserved land parcel) while in the AB the payments differ among land parcels and are high only for those conserved land parcels that are really surrounded by conserved land parcels – so that the budget in the AB is invested in a more targeted manner. A more targeted investment of the budget in the TP seems to be achieved in the coalition-forming approaches of Zavalloni et al. (2019) and Barielle et al. (2023).

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Altogether, the present analysis synthesises previous results about coordination incentives and adds a number of new insights. In particular, the two main types of coordination incentive, the AB and the TP were considered and compared, both with respect to budget- and cost-effectiveness, and the consideration of the ecological benefit was enriched by considering a metapopulation model.

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This comprehensiveness was much facilitated by analysing the ecological-economic model within the framework of economic production theory. For instance, budget- and cost-effectiveness of each payment scheme, and the two coordination incentives with respect to their budget- and cost-effectiveness, could be compared efficiently without explicitly referring to the ecological model (represented by the IFs). Conversely, the analysis could be enriched on the ecological dimension by including a simple but theory-founded metapopulation model, without explicitly considering the budget- and cost functions (PPF).

This approach increases the generality (and hopefully intuitive understanding) of the results, so that
implications of economic conditions could be derived without reference to the ecological
dimension, and implications of ecological aspects could be derived without reference to the
economic dimension of the problem. This does not deny the limitations of a rather simple model as
the present one (so that, e.g., on the economic dimension the decision behaviour of the landowners
is rather simple, and on the ecological dimension only a single species is considered), but due to the
decomposition into the ecological and economic dimensions, assumptions on the one dimension

have less impact on results about the respective other dimension.

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