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Cost-effectiveness of strategies to establish a European bison metapopulation in the Carpathians

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Summary

1. Where populations are confined to fragmented, human-dominated landscapes, preventing declines and extirpations will often rely on metapopulation management. Spatially-explicit population viability analyses provide tools to evaluate how well the local management efforts can be combined to conserve metapopulations across large areas. Yet, metapopulation models have rarely been combined with tools to assess the cost-effectiveness of different conservation strategies.

2. European bison *Bison bonasus* only occur in small, fragmented populations, making their long-term survival dependent on establishing a metapopulation across eastern Europe. We parameterized a European bison metapopulation model based on time-series of bison demography and a habitat suitability map to assess the viability of bison populations in the Carpathians and the relative cost-effectiveness of (i) reintroductions, (ii) wildlife overpasses and (iii) anti-poaching measures in establishing a viable bison metapopulation.

3. Our results suggest that the Carpathians could support a viable metapopulation of European bison provided that active efforts are taken to safeguard bison and connect isolated herds. With such steps, our model forecasts that bison numbers could increase substantially over the next 100 years as local populations increase and bison recolonize parts of the Carpathians.

4. Reintroductions appear to be the most cost-effective approach for establishing a viable bison metapopulation among our scenarios, especially when coupled with wildlife overpasses to improve connectivity among herds. The most promising region for a bison metapopulation in the Carpathians was south-eastern Poland, Ukraine and northern Romania. We identified several candidate regions for reintroductions and wildlife overpasses, especially in the border region of Romania and Ukraine. Site-specific assessments of both habitat suitability, and the costs and benefits of a large bison population, should target those regions.

5. *Synthesis and applications*. Our results highlight how careful conservation planning can identify solutions to preserve large mammals in human-dominated landscapes. Choosing the most effective option from a range of management strategies is a central challenge for wildlife managers. We have shown that incorporating cost-effectiveness analyses into metapopulation models can elucidate the relative value (gain per unit cost) of different conservation management options, allowing decision makers to choose cost-effective options to preserve large mammals. Our model projections also provide hope for establishing a viable free-ranging European bison population in the Carpathians, one of the last relatively wild areas in Europe.

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Introduction

Population declines and extirpations now occur at rates several times faster than the species losses they often foreshadow but are often overlooked in the wider biodiversity crisis (Ceballos & Ehrlich 2002; Gaston & Fuller 2008). With about 75% of the planet's land surface already transformed by humans (Ellis & Ramankutty 2008), habitat conversion is clearly the largest driver of these population declines and the extinction debts they incur (Rogers *et al.* 2009). Large mammals are particularly at risk from habitat conversion as they often require large tracts of intact habitat (Maehr, Noss & Larkin 2001; Morrison *et al.* 2007). As a result, many large carnivores and herbivores today only persist in small, fragmented populations (Woodroffe 2000; Gordon & Loison 2009).

Over-exploitation represents a second formidable threat to large mammals as they are attractive targets for poachers seeking meat, trophies or medicinal animal parts. Large mammals are also persecuted because they conflict with land use (Morrison *et al.* 2007; Gordon & Loison 2009). Due to slow reproductive rates, large mammals lack demographic resiliency; consequently, they are particularly vulnerable to poaching and the loss of only a few individuals can doom small populations (Milner-Gulland & Bennett 2003; Linkie *et al.* 2006). Moreover, over-exploitation and poaching tend to be widespread in times of political and institutional instability, as during armed conflicts or revolutions (Jedrzejewska *et al.* 1997; Stephens *et al.* 2001; Dudley *et al.* 2002).

The collapse of the Soviet Union in 1991 is an example of such an event. As states moved from central-planning to market-oriented economies, corruption increased (TI, 2010), law enforcement was weakened, the infrastructure for nature protection eroded and illegal resource use increased (Henry & Douhovnikoff 2008; Kuemmerle *et al.* 2009). Poaching also increased substantially causing, for example, population collapses in saiga antelopes *Saiga tatarica* (Milner-Gulland *et al.* 2001) and Siberian tigers *Panthera tigris altaica* (Carroll & Miquelle 2006). This is worrying, because eastern Europe and the former Soviet Union are among the few regions in the world where large mammals still roam freely (Morrison *et al.* 2007). Several species persist there that were extirpated long-ago from most of the western Europe (DeVries 1995; Breitenmoser 1998).

Although poaching threatens large mammal populations in regions of eastern Europe, the post-socialist period has also brought a decreasing intensity of land use and declining rural populations (Ioffe, Nefedova & Zaslavsky 2004; Müller *et al.* 2009). Millions of hectares of farmland were abandoned as the region's agricultural sectors collapsed and farmland was privatized (EBRD & FAO, 2008; Kuemmerle *et al.* 2008). As vast areas essentially rewild, some large mammals are extending their range westward in response (Enserink & Vogel 2006). Recent land use changes could afford substantial opportunities to conserve large mammals and restore their ecological roles. However, the fate of currently unused farmland remains uncertain and competing land use claims are likely (Verburg & Overmars 2009). To capitalize on this unique conservation opportunity, we urgently need to understand how recent threats like poaching interact with the opportunities afforded by newly available habitats to affect the persistence of large mammal populations.

European bison *Bison bonasus* L. only occur now in eastern Europe (Pucek *et al.* 2004; Krasinska & Krasinski 2007). The species were extirpated from the wild during the early 20th century with only about 50 bison surviving in zoos. Thanks to captive breeding followed by a reintroduction programme, today roughly 2600 wild bison are distributed in about 30 herds across eastern Europe (Krasinska & Krasinski 2007; Raczyński 2008). Despite these important conservation achievements, European bison face an uncertain future. All contemporary herds are small (only six herds exceed 100 bison) and isolated (Perzanowski, Olech & Kozak 2004; Pucek *et al.* 2004). Genetic diversity of the European bison population is low, with 90% of the combined gene pool provided by only seven founders (Pucek *et al.* 2004; Tokarska *et al.* 2009). The resulting effective population size of free-ranging bison appears to be too small to ensure long-term viability (Olech & Perzanowski 2002; Perzanowski & Olech 2007). In addition, poaching and trophy hunting have increased during the post-socialist period, especially in Ukraine where herds have declined substantially or been extirpated (Parnikoza *et al.* 2009).

The long-term persistence of European bison depends upon increasing the size of more herds to greater than 100 animals and connecting herds to establish a large bison metapopulation of several thousand animals (Pucek *et al.* 2004). To meet these conservation goals we need to know what determines the viability of contemporary bison herds, how local poaching affects metapopulation viability, which areas are becoming suitable for re-establishing herds and where active reintroductions should occur to link existing herds. Spatial metapopulation viability analysis is well-equipped to answer such questions (Akçakaya 2000) and has been used to assess population viability in large mammals (e.g. Carroll & Miquelle 2006; Hamel *et al.* 2006; Linkie *et al.* 2006). Metapopulation models can also provide important insights into the cost-effectiveness of different conservation management strategies, for example, to design reserve networks (Moilanen & Cabeza 2002; Haight & Travis 2008), to minimize habitat protection costs (Haight *et al.* 2002a) or to optimize population management (Haight *et al.* 2002b; Lindsey *et al.* 2005). Yet, no study to date has analysed how different conservation strategies could affect the metapopulation viability of European bison, or any other large mammal, in eastern Europe.

Here, we analyse the cost-effectiveness of different conservation management options on the viability of European bison populations in the Carpathians in eastern Europe. The Carpathians are among the few regions that could support a wild bison metapopulation (Perzanowski, Olech & Kozak 2004; Perzanowski & Olech 2007) as they provide ample habitat, much of which is currently unoccupied (Kuemmerle *et al.* 2010b). Our first goal was thus to assess European bison metapopulation viability in the Carpathians given current habitat patterns and herds. Our second goal was to compare the cost-effectiveness of three conservation management activities: (i) reintroductions; (ii) enhancing dispersal ability and (iii) anti-poaching measures, on European bison metapopulation viability.

Materials and methods

THE CARPATHIANS

The Carpathians of Central Europe extend over seven countries (Czech Republic, Poland, Slovakia, Hungary, Ukraine, Romania and Serbia), and are Europe's largest mountain range (210 000 km^2, Fig. 1). Gentle slopes dominate the topography with elevations ranging from $\sim$100 to 2665 m. The climate is temperate-continental with strong altitudinal gradients in mean annual temperature (9 °C in the plains to <0 °C on mountain peaks) and precipitation (<500 to >2000 mm). There are four distinct zones of potential natural vegetation: foothills (<600 m) dominated by beech *Fagus sylvatica*, hornbeam *Carpinus betulus* and oak *Quercus spp*; montane mixed forests with beech and fir *Abies alba* (600 to 1100 m in the north/1400 m in the south), subalpine coniferous forests (up to 1500 m/1800 m) with Norway spruce *Picea abies*, stone pine *Pinus cembra*; and alpine vegetation above the treeline (Webster, Holt & Avis 2001). Centuries of land use have created a mosaic landscape of forests, pastures and croplands. Yet, land use intensity remains relatively low so the region still harbours substantial old growth and semi-natural forests and high biodiversity (UNEP, 2007).

The Carpathians provide habitat for viable populations of all European large carnivores (brown bear *Ursus arctos*, wolf *Canis lupus* and lynx *Lynx lynx*, UNEP, 2007) as well as several large ungulates such as red deer *Cervus elaphus*, fallow deer *Dama dama*, roe deer *Capreolus capreolus* and wild boar *Sus scrofa*. European bison were reintroduced in the Carpathians during the 1960s, and in 2009 the region harboured five free-ranging herds (Pucek *et al.* 2004; Krasinska & Krasinski 2007): a western and eastern herd in the Polish Bieszczady Mountains (each $\sim$150 animals), one herd in the Slovak Poloniny National Park (9), one herd in the northern Ukrainian Skole district ($\sim$15), and one herd in the southern Ukrainian Bukovyna region ($\sim$80) (Fig. 1).

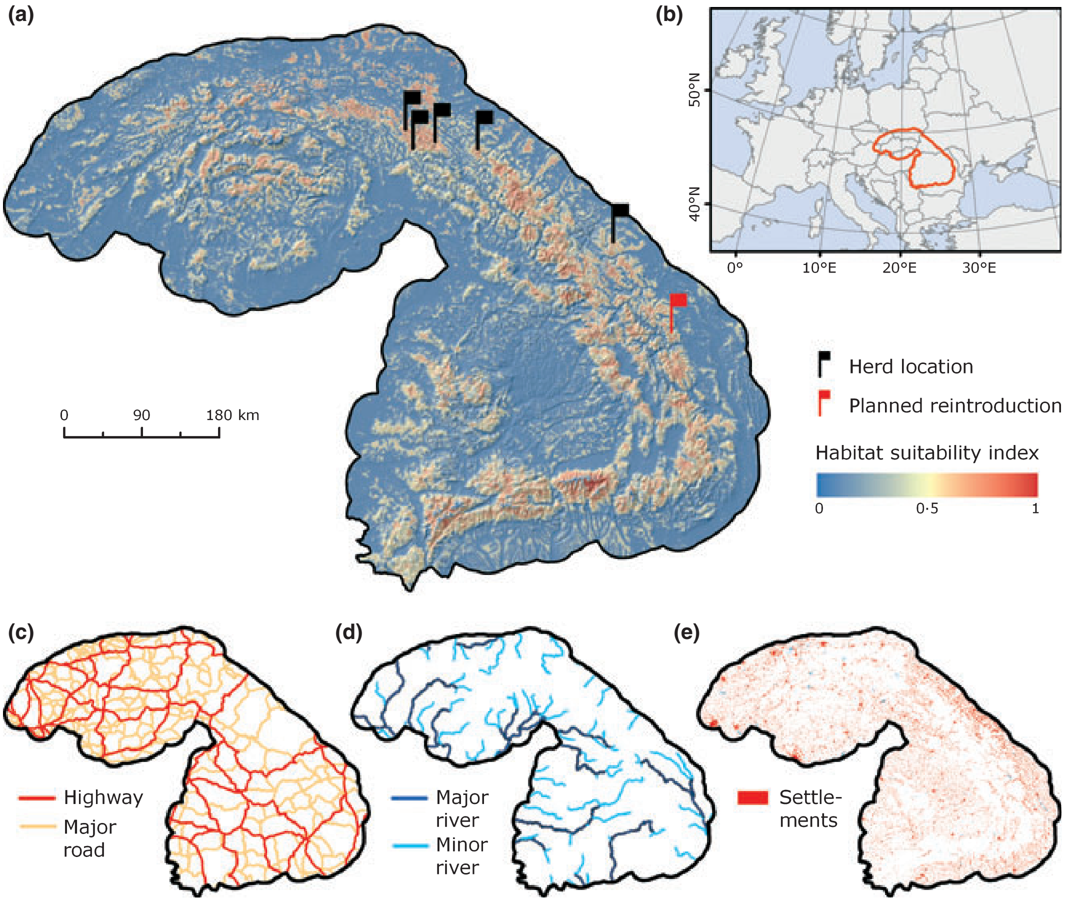

Fig. 1. (a) European bison habitat suitability map (Kuemmerle *et al.* 2010a) and contemporary bison herds in the Carpathians. (b) Location of the Carpathians in Europe. Dispersal barriers: highways and major roads (c), rivers (d) and settlements (e).

As elsewhere in eastern Europe, the collapse of socialism reduced land use intensity and rural populations, allowing some areas of the Carpathians to rewild (Baur *et al.* 2006; Kuemmerle *et al.* 2008). All Carpathian countries except Ukraine recently joined the European Union, requiring them to enlarge protected area networks substantially (http://www.natura.org, UNEP, 2007). Together, these trends may represent unique opportunities to conserve large mammals and establish a Carpathian metapopulation of European bison.

METAPOPULATION MODEL

To analyse metapopulation viability of European bison in the Carpathians, we used the software RAMAS GIS 5.0. First, the programme analyses habitat structure to derive patches that can harbour populations and to characterize species' dispersal ability. Secondly, a demographic matrix model is linked to each patch, allowing for spatial structure in population viability analyses and spatial variability in population dynamics (Akçakaya 2000, 2005).

We adopted the ecoregion defined by the Carpathian Ecoregion Initiative (Webster, Holt & Avis 2001), buffered by 30 km to include adjacent forests, but excluded the Serbian Carpathians as no bison exist there and the Danube River prevents dispersal. Habitat suitability (HS, scaled between 0 and 1) data were available from our previous research (Fig. 1b, Kuemmerle *et al.* 2010a). High-quality bison habitat in the Carpathians is characterized by a landscape mosaic including high forest cover, interspersed grasslands and low human impacts. We aggregated the HS map from its original 100 m resolution to 500 m using a median filter.

RAMAS GIS uses the continuous HS map to delineate a landscape that distinguishes patches of suitable habitat (i.e. with the potential to host a population) from background unsuitable habitat (i.e. matrix). We used HS thresholds of 0.5 and 0.6 representing the 25th and 50th percentile of the HS values within the contemporary bison ranges, respectively, to identify patches of suitable habitat. We clustered suitable cells into a single population if they were less than 2 km apart (see Appendix S1 Supporting Information). We derived separate patch maps for both spatial resolutions (100 and 500 m grain). To model the permeability of the background matrix for European bison dispersal (i.e. movements between two separate populations), we modelled a cost surface that incorporated both matrix quality and dispersal barriers (Akçakaya 2005) such as settlements, water bodies and major roads (Fig. 1c–e, see Appendix S1 Supporting Information).

To model bison population dynamics, we developed an age-structured matrix model (Caswell 2001) with annual time steps. We focused on the female segment of the population because: (i) male survival exerts only a minor influence on population viability of large ungulates (Gaillard *et al.* 2000); (ii) only about 50% of all male European bison participate in breeding (Daleszczyk & Bunevich 2009) and (iii) the sex ratio in larger herds is even (Krasinska & Krasinski 2007; Mysterud *et al.* 2007). Ungulate life cycles can be well-described by age-classes (Gaillard *et al.* 2000). We used a Leslie matrix model with 20 age-classes divided among calves (year 1), juveniles (2,3) and prime-aged adults (4,..., 20), as well as a senescent adult class (21 and older). Average vital rates for these four sets of age-classes were available from previous studies (Krasinski 1978; Gill 1998; Krasinska & Krasinski 2007; Daleszczyk & Bunevich 2009) (Table 1). Using the matrix model, we estimated λ and conducted elasticity analyses to identify key determinants of population growth (see Appendix S1 Supporting Information).

Table 1. Parameter estimates used in the spatial population viability analysis. All vital rates relate to the female segment of the European bison population (see Krasinska & Krasinski 2007; Mysterud *et al.* 2007; Daleszczyk & Bunevich 2009)

Parameter	Mean estimate	SD
Fecundity	0.2000	0.0920
Calf survival rate	0.9330	0.1176
Juvenile survival rate	0.9770	0.0293
Adult (reproductive) survival rate	0.9831	0.0125
Adult (senescent) survival rate	0.9500	0.0125
Carrying capacity	0.2 km^{-2}	–
$R_{\max}$	1.19	–

Density dependence in vital rates of ungulates is well-documented (McCullough 1975; Gaillard *et al.* 2000) and has been observed in both European (Mysterud *et al.* 2007) and American bison *Bison bison* (Plumb *et al.* 2009). We estimated carrying capacity (K) at 0.4 bison km^{-2} (=0.2 females km^{-2}) for the Carpathians, and included habitat quality when calculating K (see Appendix S1 Supporting Information for details). Only habitat patches that could support at least five females were deemed suitable habitat, corresponding to the smallest known free-ranging herds (Pucek *et al.* 2004). We assumed density-dependent recruitment (Fowler 1981) and adjusted growth rates using a Ricker-type function with a maximum finite rate of increase ($R_{\max}$) of 1.19. Density dependence was based on all (female) individuals (see Appendix S1 Supporting Information).

Variability in environmental conditions (e.g. changes in winter severity or forage availability) can have strong effects on fecundity and survival of European bison (Krasinska & Krasinski 2007; Mysterud *et al.* 2007) and we therefore randomly sampled all vital rates from log-normal distributions with means taken from the Leslie matrix and SD available from the literature (Table 1). Environmental conditions in the Carpathians vary along latitudinal and elevation gradients and we therefore modelled covariation in environmental stochasticity among two populations as a negative exponential function of the distance between these populations (see Appendix S1 Supporting Information).

Dispersal rates (% of source population migrating to a target patch) between patches were based on a negative exponential function (Akçakaya 2005). We parameterized low, medium and high dispersal scenarios. We also included density dependence in dispersal rates and assumed maximum dispersal distances of ~90–100 km (see Appendix S1 Supporting Information).

Our base metapopulation model included the four contemporary Carpathian bison herds with 2009 population numbers (see above), assuming even sex distribution and stable age distributions (inferred from the matrix model). At the time of writing, no exchange was occurring among herds except for the Slovak and western Bieszczady herds that we consequently modelled as a single population. Our base model also included an additional herd of 10 female bison to be reintroduced in northern Romania in 2010 (Fig. 1b). We estimated average poaching rates in the Ukrainian populations at 20% of the population annually (see Appendix S1 Supporting Information). We used 1000 replications and a simulation period of 100 years.

SENSITIVITY ANALYSES

To assess how robust our metapopulation model was to uncertainty in parameter estimates, we compared model runs for the two different HS thresholds (HS = 0.5 and HS = 0.6) and the two spatial resolutions of the habitat map (100 and 500 m, for a 150 × 150 km^2 subset of the study region). We also varied mean demographic rates (by −5%, −2%, −1% and +1%), environmental stochasticity (SD of demographic rates by −20%, −10%, +10% and +20%), carrying capacity (by −25%, −10%, +10% and +25%) and $R_{\max}$ (−10%, 5%, +5% and 10%). We compared metapopulation runs for our low, medium and high dispersal scenarios. Finally, we compared model runs using time horizons of 100 and 200 years, and 1000 and 10 000 model replications.

MANAGEMENT SCENARIOS

We considered three European bison conservation management options: (i) reintroductions; (ii) enhancing dispersal ability via wildlife overpasses; (iii) anti-poaching strategies. We assumed reintroductions of 10 female bison (mixed age group, no calves, distributed among age classes so as to approximate the stable age distribution of our matrix model) and a sufficient number of bulls to ensure reproduction. We selected all patches that had a carrying capacity of at least 50 female bison (Pucek *et al.* 2004) and that included a protected area of at least 50 km^2, and we modelled reintroductions for each patch separately. Wildlife overpasses can substantially enhance habitat connectivity for large mammals (Gloyne & Clevenger 2001; Van Wieren & Worm 2001). Based on the network of permanent barriers and the metapopulation map, we selected 11 locations for potential wildlife overpasses. We then recalculated dispersal rates without these barriers, and ran the metapopulation model separately for each potential overpass. To assess the effect of anti-poaching strategies on metapopulation viability, we reduced poaching levels from 20% in the base model to 10% and 5% in each of the Ukrainian populations separately. Finally, we assessed the effect of combining different conservation management options.

To compare among our scenarios, we extracted the probability that metapopulation size will remain below 1000 female bison during the simulation period of 100 years (*P*1000). We chose this threshold, because a minimum N_e of 50 has been suggested for European bison (Pucek *et al.* 2004) and the ratio of N_e to N is as low as 0.07 for American bison (Frankham 1995), and likely to be even lower for European bison due to high inbreeding (Olech & Perzanowski 2002; Pucek *et al.* 2004; Traill, Bradshaw & Brook 2007). We also extracted total bison population (TBP), metapopulation occupancy (MO) and the number of herds exceeding 100 animals (i.e. 50 females, *N*50) for each scenario. For all these measures, we calculated confidence intervals based on the Kolmogorov–Smirnov test statistics and 1000 replicate runs (Akçakaya 2005).

The cost-effectiveness of all scenarios was compared by first calculating the increases in metapopulation viability for each scenario relative to our base model and second dividing these increases by the cost of a scenario (in 1000€). We assumed a cost of 250 000 € for a reintroduction project, based on the costs of previous European bison reintroduction projects in the Carpathians in which we have been involved (for the herds in Poland, Slovakia and Romania). The average cost for a wildlife overpass was estimated at 2 000 000€ based on a European-wide assessment of wildlife crossing structures (Bank *et al.* 2002; Trocmé *et al.* 2003) as well as cost estimates from Canada (Gloyne & Clevenger 2001; Huijser *et al.* 2009). Safeguarding a herd from poaching was estimated at 20 000€ for one ranger per year (i.e. salary, initial costs for a jeep and equipment and running costs) and we assumed one ranger for herds with a K < 25 female bison, two for herds with K < 50, three for herds with K < 100 bison and four for herds with K > 100. We assumed reducing poaching levels to 5% would be twice as costly as reducing poaching levels to 10% and that anti-poaching measures would be necessary for 20 years.

Results

We identified potential habitat for 151 European bison populations in the Carpathians using a HS threshold of 0.5. If fully utilized, these habitats together could support up to a total carrying capacity of 8038 female bison. Large patches were frequent in the Ukrainian and Romanian Carpathians (Fig. 2), where the three largest potential populations occurred (578 and 510 bison in Ukraine, and 421 in south-western Romania). In contrast, almost all potential populations in the Polish and Slovak Carpathians were small (< 100 individuals), except for the Bieszczady Mountains in south-eastern Poland where four habitat patches could support a combined population of 401 bison (Fig. 2).

Our more realistic base model predicted more modest increases in the Carpathian metapopulation of European bison up to an eventual average final abundance of 1015 female bison (95% CI: 715–1436) after 100 years (Fig. 3). European bison colonized 23 new patches, mainly during the first half of our simulation. With barriers inhibiting dispersal into much of the Carpathian range in our base model, we observed a mean metapopulation occupancy of only 18%. On average, 1568 bison were poached or harvested in Ukraine. Nevertheless, the extinction risk of the European bison metapopulation was relatively low, with a probability

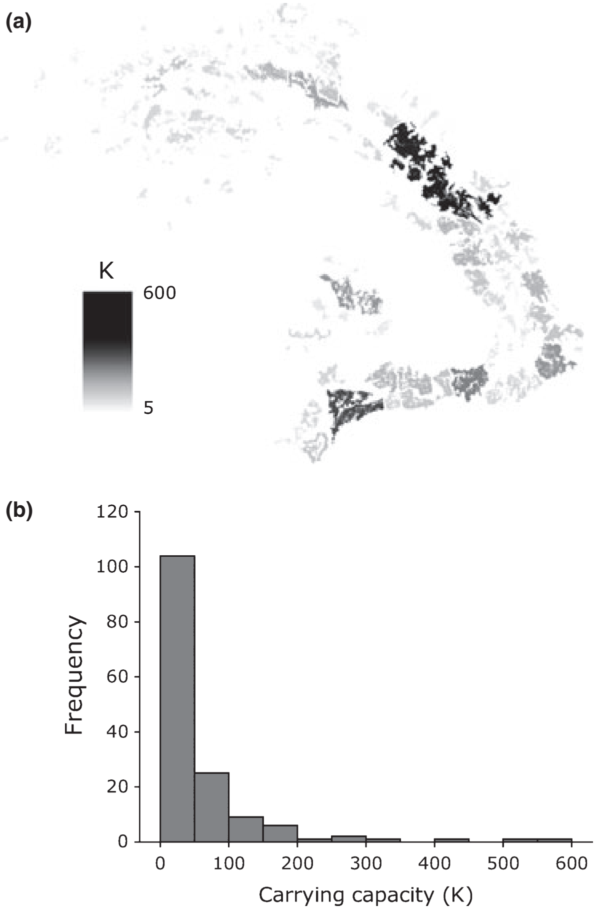

Fig. 2. (a) Potential European bison populations and their carrying capacities (K) and (b) histogram of K.

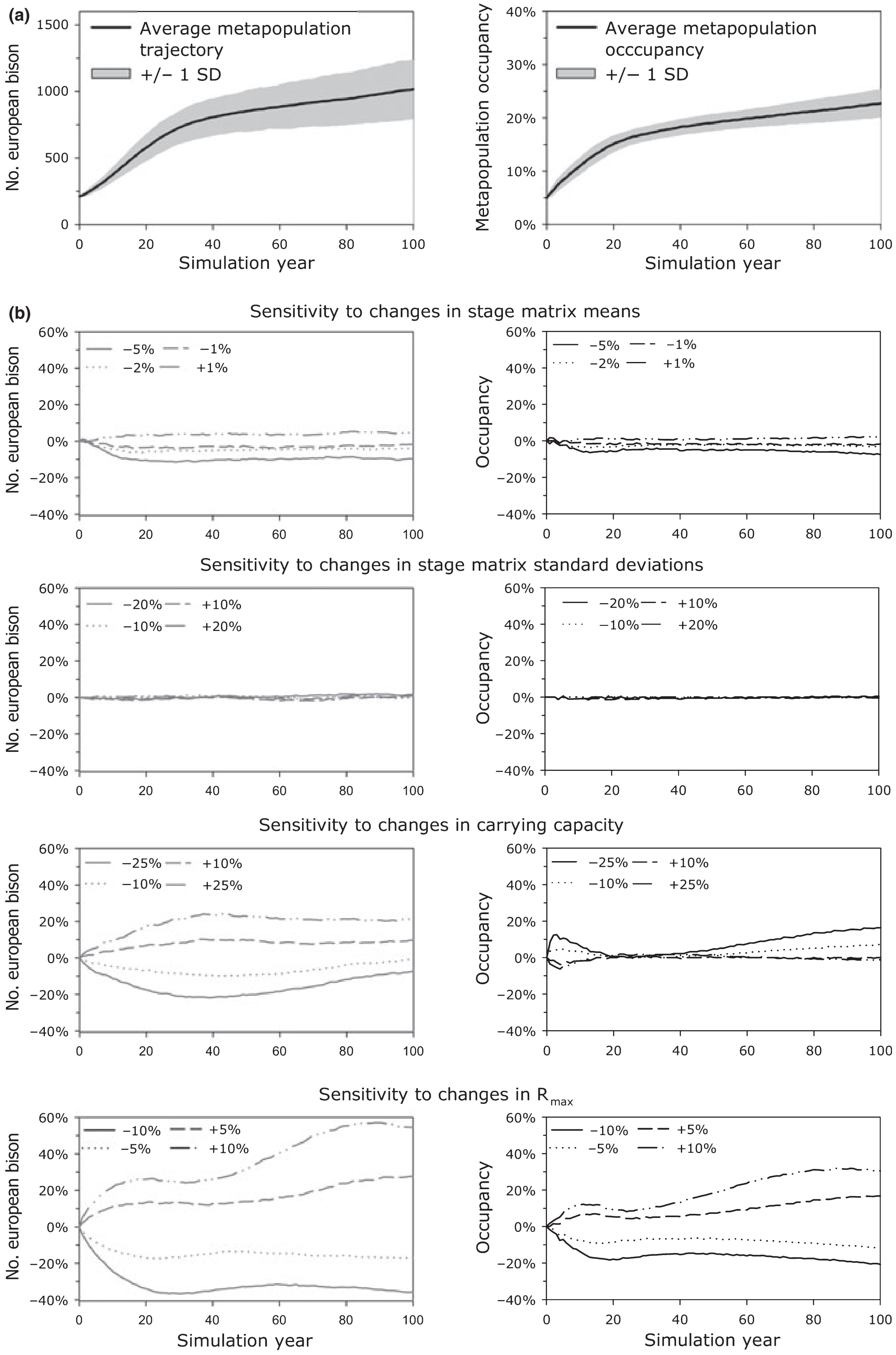

Fig. 3. (a) Metapopulation trajectory and metapopulation occupancy of the base model (i.e. current habitat and herd distribution, HS = 0.5, medium dispersal). (b) Relative changes in metapopulation trajectories and occupancy when varying vital rates (age matrix means), environmental stochasticity (age matrix SD), carrying capacity and the maximum intrinsic growth rate ($R_{\max}$).

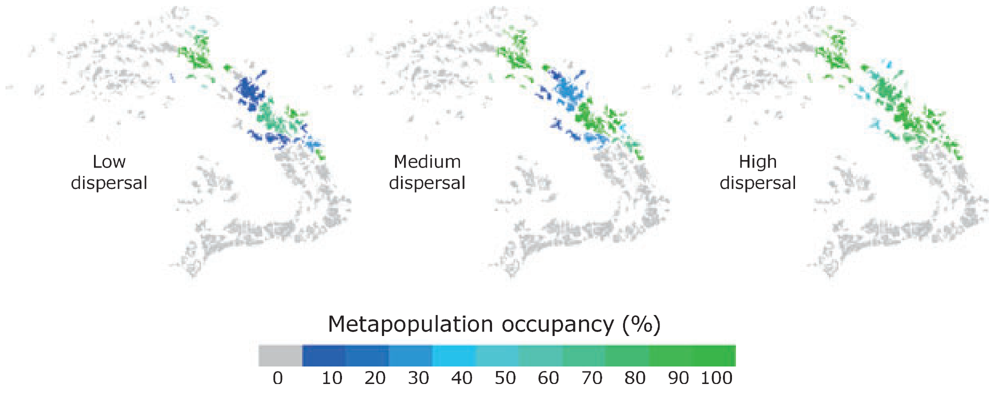

Fig. 4. Metapopulation occupancy for the low, medium and high dispersal scenarios.

of $< 5\%$ that bison numbers will remain below 700 animals (and $< 1\%$ for < 570 bison) during the next 100 years. The probability that the bison metapopulation will not reach 1000 female animals ($P1000$) during the next 100 years was 53%. Six herds exceeded 100 animals (N50) in our base model at the end of our simulation period.

Our metapopulation model was relatively robust to small changes in mean survival and fecundity (Fig. 3b). Decreasing survival and fecundity did not affect patch colonization substantially, but local extinctions became more common, leading to reduced mean patch occupancy. Altering environmental variability also did not affect projections substantially (Fig. 3b). In contrast, varying K had a marked effect, with faster colonization and higher patch occupancy for lower K and *vice versa* (because dispersal is density-dependent, Fig. 3b). Finally, our metapopulation model showed marked sensitivity towards changes in $R_{\max}$, with up to 50% higher abundances when increasing $R_{\max}$ by 10%. Colonization also occurred faster and more patches were occupied for higher $R_{\max}$ values (Fig. 3b). The three dispersal scenarios resulted in markedly different metapopulation occupancy patterns (Fig. 4). All accessible patches (27) were colonized in the high dispersal scenario vs. 13 patches in the low dispersal scenario (19 in the base model) with corresponding differences in the estimated final population sizes (1304 and 773 in the high and low dispersal scenarios respectively). Extending our base metapopulation model to 10 000 replications or 200 years did not affect the average trajectory, but more replications decreased SE.

Increasing, the HS threshold from 0.5 to 0.6 reduced the number of potential populations from 151 to 114 patches and these patches were substantially smaller than in the base model, resulting in a total potential carrying capacity of 4449 bison. Predicted average abundance after 100 years decreased from 1015 to 673 bison although patch occupancy remained similar. Extinction risk rose markedly for an HS threshold of 0.6 (e.g. 98% probability of $P1000$ after 100 years compared with 53% in the base model; only five herds could exceed 100 animals in this scenario). In contrast, changes in the spatial resolution of our habitat map had little effect.

Our base model identified 26 unoccupied habitat patches that satisfied our criteria for reintroductions (i.e. K > 50 and protected area > 50 km^2, Fig. 5). Modelling reintroductions for each patch separately resulted in a median decrease of 47% in $P < 1000$ (probability of female bison population < 1000 after 100 years), an average increase in TBP of 32%, a mean increase in MO (mean occupancy) of 24% and a mean increase in N50 (number of herds larger 100 animals) of 34%. However, these viability estimates varied among the reintroduction scenarios with SD of 18%, 22%, 19% and 29% for P1000, TBP, MO and N50 respectively. Thirteen patches occurred in Ukraine (Fig. 5). Implementing anti-poaching measures for each of these 13 patches separately only improved viability slightly, except for the largest patch and the patch containing the Bukovyna herd (e.g. reducing P1000 by 53% and resulting in higher patch occupancy). Reducing poaching levels to 10% instead of 5% did not affect viability estimates substantially.

Fig. 5. Different European bison conservation scenarios: Patches where reintroductions were modelled (left column). Patches where anti-poaching strategies were assessed (middle column). Locations where wildlife overpasses were assessed (right column).

Constructing wildlife overpasses, however, was predicted to affect metapopulation viability greatly, reducing mean P1000 by 29% and increasing TBP, MO and N50 by 29%, 35% and 17% respectively. The effects of adding overpasses also varied substantially (e.g. 0% to 53% decrease in P1000).

Based on these results, the cost-effectiveness ranking of our scenarios (see below), as well as expert knowledge (i.e. regarding the placement of wildlife overpasses), we modelled nine scenarios that combined different management options: three scenarios each for combining (i) one reintroduction and one anti-poaching measure; (ii) one reintroduction with one overpass and (iii) multiple reintroductions (one scenario each for two, three and four reintroductions). Combining reintroductions and anti-poaching efforts did not increase metapopulation viability substantially compared with reintroductions alone (e.g. < 5% decrease in P1000, < 10% increase in MO). In contrast, combining even a single wildlife overpass with one reintroduction strongly increased metapopulation viability compared with reintroductions alone (e.g. up to P1000 of 0%, 30% increase in TBP, 50% increase in N50). Multiple reintroductions had the strongest effect on metapopulation viability, increasing TBP up to 224%, MO up to 110% and N50 up to 267%.

The potential distribution of bison in the Carpathians varied substantially among the different scenarios (Fig. 6). Wildlife overpasses and reintroductions both allowed European bison

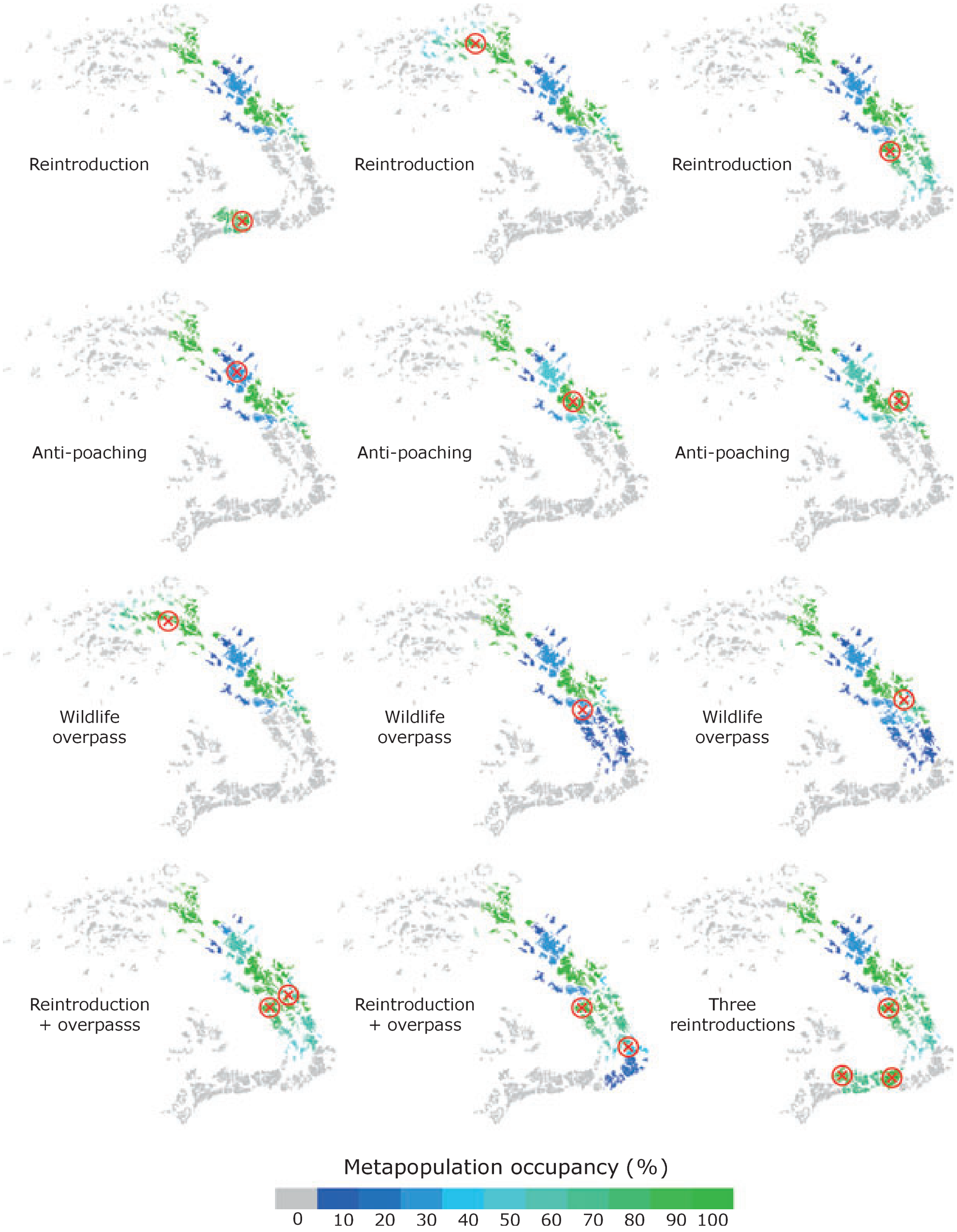

Fig. 6. Metapopulation occupancy for three reintroduction scenarios (first row), three anti-poaching scenarios (second row), three wildlife overpasses (third row) and three combined scenarios (bottom row). Patches where management options were implemented are marked ⊗.

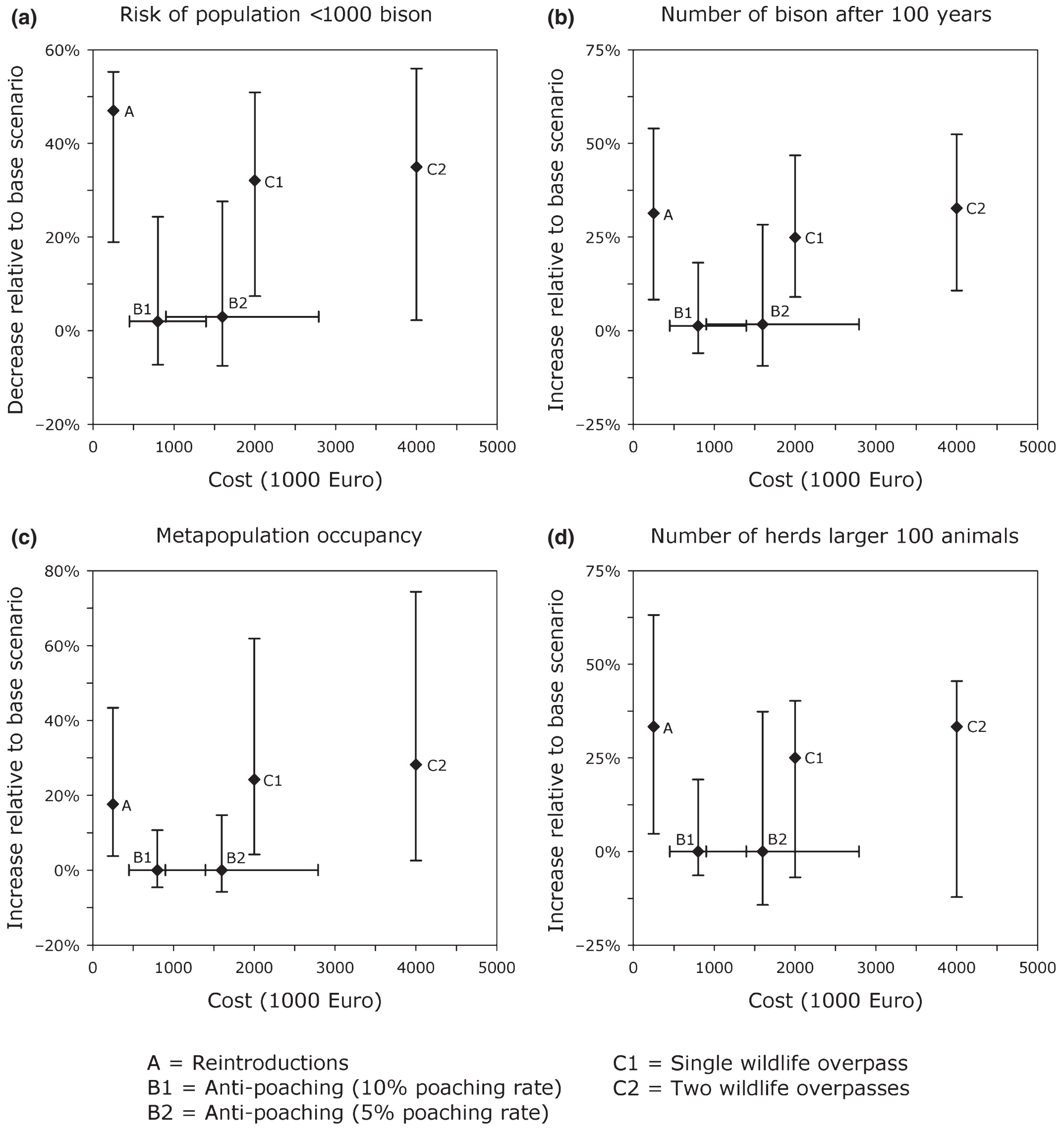

Fig. 7. Cost-effectiveness of different European bison conservation management options regarding four metapopulation viability measures: (a) risk of total population < 1000 female bison after 100 years, (b) total female bison population after 100 years, (c) metapopulation occupancy and (d) number of populations exceeding 100 animals (= 50 female bison) after 100 years (markers = median of viability change compared with the base scenario of all scenarios with the same conservation management strategy; whiskers = ± 1SD; all values measure improvement relative to the base model).

to colonize much habitat, but colonization rates were higher and more patches were colonized following reintroductions. Our results also showed that the southern and north-western Carpathians are dissected strongly by dispersal barriers (i.e. many patches close to source populations remained uncolonized), whereas in northern Romania, introducing a single herd led to the predicted colonization of most habitats. Anti-poaching activities increased the probability of colonization of adjacent patches, but only if large patches were protected (Fig. 6).

Reintroductions emerged as the most cost-effective option to increase population viability in our comparisons of the cost-effectiveness of different bison conservation strategies (Fig. 7), accounting for 20 or more of the 25 most cost-effective scenarios across all viability measures. Reintroductions in Calimani National Park (northern Romania, scenario R19), the Cindrel Mountains in southern Romania (R24) and in Magurski National Park (Poland, R4) were the most cost-effective reintroduction scenarios (see Supporting Information). Wildlife overpasses could also improve viability substantially, especially when combined with reintroduction projects, but tended to be costly. Coupling a reintroduction project in northern Romania with an overpass to connect this region to neighbouring Ukraine emerged as the most cost-effective combined scenario (see Appendix S2 Supporting Information). As the costs of anti-poaching strategies scaled with patch size in our model, protecting herds from poaching emerged as the least cost-effective management option (e.g. anti-poaching strategies for the largest patches in Ukraine increased viability substantially, but the cost-effectiveness of conservation management remained low due to the high costs of anti-poaching strategies).

Discussion

Habitat loss and over-exploitation threaten large mammals worldwide. Preserving their populations in increasingly human-dominated landscapes is thus a grand challenge of conservation biology. European bison, Europe's largest land mammal and last surviving large grazer, today only occur in small and isolated herds. Our results show that conservation management could increase bison numbers and the connectivity among herds substantially. Conservation goals are met in many of our scenarios, suggesting that the Carpathians could support a viable metapopulation provided that the steps are taken to expand and protect existing herds. The collapse of socialism and subsequent EU expansion has reduced human presence and enhanced nature protection in some parts of the Carpathians. Despite increased poaching in the post-socialist period, we may be facing a 'hot moment' for implementing the first comprehensive plan to sustain the European bison metapopulation. Our model suggests that reintroductions, the main conservation strategy during the last decades, is the most cost-effective approach for establishing such a metapopulation, especially when reintroducing several herds or when coupling reintroductions with wildlife overpasses to improve connectivity among herds.

Our metapopulation models suggest that even without management intervention, the Carpathian population of European bison could, if allowed, increase substantially during the 21st century (about fivefold in our base model). Much of this increase depends upon their ability to recolonize more of their former range (Fig 6), which requires local populations to rise markedly (dispersal was density-dependent in our model). Barriers to dispersal exclude bison from much of the Carpathians and inhibit animal movements and thus genetic exchange among herds. Even aside from these difficulties, the probability that bison numbers in our base model reached the conservation goal of 1000 female bison ($N_e \sim 50$) was only 47% and average abundance (1015) was only slightly higher than this goal. This is troublesome in light of the uncertainty we face in the ecological and social carrying capacity (i.e. acceptable population levels in landscapes managed for both, land use and conservation) of European bison (Krasinska & Krasinski 2007). Active conservation management will therefore be necessary to establish and sustain a functioning bison metapopulation in the Carpathians.

Reintroductions emerged as the most cost-effective management option to expand the range of European bison in the Carpathians and boost population numbers. Several large but currently unoccupied habitat patches exist that include protected areas. These are obvious starting points for reintroductions, especially in northern and southern Romania. These areas also contain relatively few dispersal barriers, potentially allowing bison to recolonize larger areas of unoccupied habitat. Our metapopulation model also suggests that because the ongoing reintroduction project in Romania occurs in an isolated patch of habitat, further reintroductions will be necessary if bison are to recolonize other Romanian patches (Fig. 6). Any strategy focused solely on reintroduction though, would confront the disadvantage that barriers (mainly highways) inhibit exchange among herds.

Wildlife overpasses, properly placed to improve connectivity, substantially improved the viability of the European bison metapopulation in our models. Moreover, overpasses would be likely to prove crucial for allowing bulls to disperse among herds, fostering genetic exchange and thus preventing further erosion of genetic diversity. Wildlife crossings now provide movement corridors for many wildlife species while increasing traffic safety, often outweighing the relatively high construction costs (Gloyne & Clevenger 2001; Van Wieren & Worm 2001). Infrastructure is currently being developed in much of the region as most Carpathian countries have joined the EU (UNEP, 2007). Given the importance of this region as a hotspot of large mammal diversity and the fact that wildlife crossings only increase the total cost of a road project by 7–8% (Bank *et al.* 2002), maintaining and improving ecological corridors in the Carpathians should be a priority (UNEP, 2007; Huck *et al.* 2010).

In our models, reactive anti-poaching strategies emerged as less cost-effective than reintroductions and overpasses in improving metapopulation viability. High poaching rates in Ukraine, however, represent real threats that should not be ignored. Poaching reduced patch colonization and dispersal rates substantially in our models. Field evidence also suggests that poaching rates may have increased further since the last census (2009), potentially threatening the existence of the Ukrainian herds. This is particularly worrisome considering that Ukraine emerges as a key area in all our models, connecting the northern and southern Carpathians. The root causes of poaching in Ukraine are corruption, an inadequate legal framework, weak law enforcement and poverty. Ironically, many trophy hunts are carried out under the guise of precautionary culling (e.g. of sick animals, Parnikoza *et al.* 2009). Addressing poaching will therefore not only require adequate law enforcement (which we modelled), but also a combination of legal measures including improved species' protection status, capacity building through education and local participation and long-term conservation programmes. Our analyses demonstrate that relatively large numbers of bison could be harvested without substantially affecting metapopulation viability. As substantial demand for European bison trophies exist, sustainable harvesting could generate conservation funds, mitigate human-wildlife conflict and complement rural incomes.

Our results clearly suggest that the Carpathians could harbour a viable metapopulation of European bison, and that moderate efforts of conservation management could suffice to establish and sustain such a metapopulation. The most promising strategy appears to be reintroducing subpopulations, particularly in the border region of Romania and Ukraine. The addition of a few strategic wildlife overpasses (e.g. bridging north-south running highways in the eastern Carpathians) would further benefit not only the European bison but also large mammals and Carpathian biodiversity generally. Human pressures in many rural areas of the Carpathians have declined following the collapse of socialism and protected area networks and infrastructure expand in the new EU countries. This suggests that we may be facing particularly a favourable time to implement these conservation management options and establish a bison metapopulation.

Our metapopulation model was based on demographic parameters derived from long-term (> 40 years) studies of bison population dynamics and a HS map derived from a comprehensive set of bison locations (Kuemmerle *et al.* 2010a). Sensitivity was high towards changes in $R_{\max}$, yet our $R_{\max}$ estimates were very similar for both herds we assessed and nearly identical to two independent assessments (Mysterud *et al.* 2007; Daleszczyk & Bunevich 2009). Varying carrying capacity and the HS threshold affected our results noticeably and in similar ways. Though we calculated K based on available winter forage and our estimate agreed closely with estimates from the Bialowieza Forest and the K of wood bison *Bison bison* in North America (see Appendix S1 Supporting Information), we cannot fully rule out uncertainty in this parameter. The main goal of our scenario simulation was to compare conservation management options. Changes in K would only affect absolute bison numbers, and not our main conclusions. Varying dispersal rates also affected our results markedly. We carefully parameterize our dispersal functions using available field observations and our base model resulted in realistic occupancy patterns. Dispersal is likely to be density-dependent, yet no Carpathian bison herd is currently at carrying capacity. Dispersal rates and matrix permeability therefore remain weakly understood and further research along these lines is urgent. If dispersal rates were lower than assumed in our base model, we expect the importance of additional reintroductions to increase, whereas the effectiveness of wildlife overpasses would increase if European bison dispersal was higher than assumed in our base model. Finally, we did not model predation explicitly. Predation of European bison by brown bears in the Carpathians has been rare (five reported cases since the 1960s). Romania harbours large populations of bears, and it is possible that predation will increase as bison are released there and more animals approach senescence. How this would affect metapopulation viability is unknown.

While our ecoregion-wide assessments is useful for highlighting key areas for the conservation of European bison in the Carpathians, we recommend our model should be run with a larger number of strategies (e.g. systematically varying the number and timing of reintroductions, and the number and age distribution of the animals reintroduced, and target locations) before conservation strategies are implemented. Likewise, fine-sale assessments of habitat quality (e.g. forage availability) and conflict potentials with land use and people in candidate sites for reintroductions and wildlife overpasses should complement our broad-scale assessment. Finally, the costs of conservation management activities we used represent average estimates and will probably vary among countries. Also, our cost-effectiveness analyses did not include the indirect costs of a large bison population (e.g. damage to crops) nor the benefits from such a population (e.g. *via* trophy hunting). Furthermore, we did not quantify the additional benefits of particular conservation management options such as increased traffic safety and improved ecological corridors in the case of wildlife overpasses. Site-specific cost–benefit assessments that link economic models and metapopulation models should therefore be carried out for the target areas we identified.

Large mammals struggle to survive in human-dominated landscapes around the globe. Our results highlight that incorporating cost-effectiveness analyses into metapopulation models can elucidate the relative value (gain per unit cost) of different conservation management options, allowing the decision-maker to choose cost-effective options to preserve wildlife. While our ecoregion-wide approach does not replace fine-scale habitat assessments and conservation planning, metapopulation models can help us to target conservation actions, and to harmonize conservation planning across large areas and political borders. Our cost-effectiveness analysis of European bison metapopulation viability also shows how careful conservation planning and assessment of different conservation options can enable the establishment of a large metapopulation of this ungulate. Our study thus provides hope for the future of European bison in the Carpathians, one of the last relatively wild areas in Europe, and for restoring the bison's key ecological role.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1: Metapopulation model parameterization.

Appendix S2: Additional results.