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Post-Soviet land-use change effects on large mammals' habitat in European Russia

Anika Sieber [a,*], Nikolai V. Uvarov [b], Leonid M. Baskin [c], Volker C. Radeloff [d], Brooke L. Bateman [d], Alexey B. Pankov [b], Tobias Kuemmerle [a,e]

[a] Geography Department, Humboldt-Universität zu Berlin, Unter den Linden 6, 10099 Berlin, Germany
[b] Oksky State Nature Reserve, Lakash/Brykyn Bor, 391072 Ryazanskaya Oblast, Russia
[c] A. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, 33 Leninsky Prospect, 119071 Moscow, Russia
[d] Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA
[e] Integrative Research Institute on Transformations in Human-Environment Systems (IRI THESys), Humboldt-Universität zu Berlin, Unter den Linden 6, 10099 Berlin, Germany

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ABSTRACT

Land-use change can strongly affect wildlife populations, typically via habitat loss and degradation where land use expands, and also via increasing potentially available habitat where land use ceases. Large mammals are particularly sensitive to land-use change, because they require large tracts of habitat and often depend on habitat outside protected areas unless protected areas are very large. Our research question was thus how land-use change around protected areas affects large mammals' habitat. Russia experienced drastic land-use change after the breakdown of the Soviet Union and – fortunately – wildlife data has been collected continuously throughout this time inside protected areas. We used long-term winter track count data for wild boar (*Sus scrofa*), moose (*Alces alces*), and wolf (*Canis lupus*) to assess habitat change inside and outside of Oksky State Nature Reserve from 1987 to 2007 using a time-calibrated species distribution model. Our results showed a constantly high share (at least 89%) of suitable habitat within the protected area's core zone for each species, yet also substantial habitat increases of up to 23% within the protected buffer zone, and similarly, up to 27% outside the protected area. Of the variables we evaluated, post-Soviet land-use change, particularly farmland abandonment, was the main driver of this expansion of potential habitat for the three species we assessed. Our study highlights that strictly protected areas have been playing an important role in preserving wildlife in European Russia since 1991, and also that their surroundings provide much suitable habitat for large mammals. Post-Soviet land-use change in the surroundings of protected areas may provide opportunities to increase and connect wildlife populations.

1. Introduction

Globally, biodiversity is declining and land-use change is a major reason for this (Foley et al., 2005; Sala et al., 2000). Agricultural expansion is particularly worrisome because it results in habitat loss, degradation, and fragmentation (Fischer and Lindenmayer, 2007). This in turn can result in increased poaching, when new roads provide access into previously remote areas (Coffin, 2007; Laurance et al., 2006), in changing water availability (Power, 2010), and in invasive species spread (Brook et al., 2008). However, while agricultural expansion continues in many tropical regions (Phalan et al., 2013), agricultural abandonment has become a major land-use change trajectory, in tropical (Aide et al., 2013; Grau and Aide, 2008) and temperate (Navarro and Pereira, 2012; Schierhorn et al., 2013) regions. The biodiversity impacts of abandonment, however, are diverse and not well understood (Plieninger et al., 2014; Queiroz et al., 2014; Uchida and Ushimaru, 2014).

Large mammals (i.e., body mass > 20 kg; Vynne et al., 2011) are particularly challenging to maintain in human-dominated landscapes (Dirzo et al., 2014). These species are typically wide-ranging and require large and well-connected habitat networks, and are thus especially prone to land-use change. Furthermore, large mammals often conflict with people, livestock, and cropping (Behdarvand et al., 2014; Hoare, 1999), and are frequently poached for meat or trophies (Hilborn et al., 2006; Stokstad, 2014). Declining populations of large mammals are worrisome because of their importance for ecosystems as their disappearance can result in cascading impacts via altering food webs and triggering ecosystem shifts (Estes et al., 2011; Ripple et al., 2014).

Protected areas are a key conservation tool to safeguard species' populations and their habitats against the direct impacts of land use, and ideally against its indirect effects as well. Yet, many protected areas are too small to harbor viable populations of large mammals (Newmark, 1996) and these species depend on habitat surrounding protected areas. Prime examples include grizzly bears in the Greater Yellowstone Ecosystem (Carroll et al., 2004), giant armadillos and maned wolves in the Brazilian Cerrado (Vynne et al., 2011), Amur

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[*] Corresponding author.
E-mail address: anika.sieber@geo.hu-berlin.de (A. Sieber).

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tiger in the Russian Far East (Carroll and Miquelle, 2006), and Asian and African elephants (Fernando et al., 2008; Galanti et al., 2006). The surroundings of protected areas thus fulfill an important role for biodiversity conservation since they are part of the so-called 'zone of interaction' (DeFries et al., 2010), which represents the landscape comprising the protected area and its surroundings, which is linked to the protected area via multiple ecological processes and often strong interactions between humans and nature. At the same time, protected areas' surroundings are often intensively used which can turn them into population sinks (Woodroffe and Ginsberg, 1998). Therefore, it is important to evaluate how land-use change in the surroundings of protected areas affects wildlife habitat.

Evaluating the effects of land-use change on wildlife often hinges on the availability of habitat use data from before and after land-use change occurred. Long time series of species' presence records are particularly valuable in this context (Boulinier et al., 1998; Bragina et al., 2015; Sauer et al., 2014). If longitudinal wildlife data are available, however, the challenge is how to analyze them given that data have been collected over many decades and while landscapes have changed. Time-calibrated niche models (Kuemmerle et al., 2012; Nogues-Bravo, 2009) offer an approach to maximize the information gain from long-term species occurrence data, since all available data can be used in one model, which can then be used to predict habitat availability in places and times for which no observations exist (Reside et al., 2010; VanDerWal et al., 2013).

Information on habitat availability is important for large mammals' conservation, and in the case of large carnivores, additional information on biotic interaction is required, for example, the occurrence of prey species (Hebblewhite et al., 2014). Identifying suitable prey habitat is thus essential for maintaining and restoring carnivore populations and that may also help to minimize human-wildlife conflicts. So far, only a few studies addressed biotic interaction in species distribution models, such as including food resources (Bateman et al., 2012; Kuemmerle et al., 2012) or prey habitat as predictor for carnivore habitat models (Giannini et al., 2013; Hebblewhite et al., 2014). Generally, including biotic factors improves the predictive power of species distribution models (Wisz et al., 2013), yet applications that incorporate prey habitat distributions for assessing the habitat of predator species remain scarce.

Russia provides unique opportunities to understand the effects of land-use change on wildlife habitats within and outside of protected areas. The collapse of the Soviet Union in 1991 triggered drastic changes in socio-economic and institutional conditions, which in turn resulted in widespread land-use change including agricultural abandonment (Prishchepov et al., 2012) and changes in forest harvesting (Baumann et al., 2012). Agricultural abandonment was especially widespread throughout European Russia and led to the expansion of transitional grassland and early successional forests. These changes in land cover have potentially substantial effects on wildlife by providing new habitats and connecting existing ones, at least in part contributing to the recent rebounding of large mammal populations in European Russia (Bragina et al., 2015). However, the post-Soviet upheaval also caused considerable economic hardships (Klugman and Braithwaite, 1998), lessened support for nature conservation (Wells and Williams, 1998), and resulted in drastic population declines of many large mammal species in Russia, except for wolves during the 1990s (Bragina et al., 2015).

Fortunately, Russia's protected areas were the focus of truly exceptional long-term biodiversity monitoring. Most of the 103 strictly protected state nature reserves ('zapovedniks', IUCN category Ia; IUCN and UNEP, 2014) have permanent scientific staff who collected a broad range of biodiversity and ecosystem variables for decades, using standard survey protocols, and published these in the so-called Chronicles of Nature (Летопись природы) every year (Spetich et al., 2009). An important element of the protected areas' biodiversity monitoring are winter track counts (WTCs, Зимние маршрутные учёты) that provide species' occurrence maps and estimate large mammal population sizes (Bragina et al., 2015; Carroll and Miquelle, 2006; Stephens et al., 2006). In some protected areas, WTCs have been collected since the 1960s (Lomanov, 2007), thus providing a baseline from Soviet times and covering the entire transition period of rapid socio-economic and land-use change after 1991.

Understanding how land-use change affects wildlife habitat and how these land-use changes may affect the zone of interaction surrounding protected areas is important for identifying effective strategies to protect large mammals, which can rarely survive inside protected areas alone. European Russia provides unique opportunities to learn more about these issues in general, because land-use change there has been drastic in response to the socio-economic and institutional shocks of the breakdown of the Soviet Union, and because longitudinal wildlife data have been collected in a standardized manner for decades, including the period of rapid land-use change. Our overarching goal thus was to evaluate how post-Soviet land-use change affected the distribution of potential habitat for large-mammals both inside protected areas and in their surroundings. To explore this question, we analyzed a long-term dataset of annual winter track counts for three large mammals, wild boar (*Sus scrofa*), moose (*Alces alces*), and wolf (*Canis lupus*), from Oksky State Nature Reserve, in the temperate zone of European Russia. The three species represent the largest and most wide-ranging mammals in our study region and have different habitat requirements since they are omnivore, herbivore, and carnivore species, respectively. We related the wildlife data to land-use change information derived from Landsat satellite images in order to map the availability of potential habitat inside and outside the protected area using a time-calibrated species distribution model. We furthermore assessed the impact of including information on prey habitats to model potential habitat of a large carnivore species. Our a priori hypothesis was that land-use change has led to an increasing availability of potential habitat for our target species — both inside and outside the protected area. We also assumed that the inclusion of prey variables will improve the prediction of large-carnivore habitat. Specifically, our objectives were:

1) To model habitat selection of wild boar, moose, and wolf using a time-calibrated species distribution model and to predict habitat distribution for different time periods,
2) To assess changes in habitat availability of the three targeted large mammal species within Oksky State Nature Reserve and its immediate surroundings from 1987 to 2007 due to post-Soviet land-use change, and
3) To explore the relative importance of including prey habitat distributions for analyzing predator habitats.

2. Material and methods

2.1. Study area

Our study area is located in temperate European Russia in Ryazan Oblast and includes Oksky State Nature Reserve and its surroundings (Fig. 1 and Fig. A1 in the Supporting Information). The study area covers about 800,000 ha and falls within the Sarmatic mixed forest ecoregion (Olson et al., 2001) with mainly coniferous and mixed forests, dominated by spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and pedunculate oak (*Quercus robur*) on glacial, sandy soils. Its southern and eastern boundary is the floodplain area of the Oka River with extensive riverine grasslands. The study area is characterized by flat terrain ranging from 76 m to 172 m. The climate is moderate, with the highest mean temperature in July (20 °C) and lowest in February (−12 °C), and an annual precipitation of about 534 mm (Priklonsky and Tichomirov, 1989).

About 10% of the study area is managed by the Oksky State Nature Reserve. This federal strictly protected area was established in 1935, originally to protect the Russian desman (*Desmana moschata*) and the wetland around the Pra River, a tributary of the Oka River. In 1978, Oksky State Nature Reserve became a biosphere reserve and in 1989, a

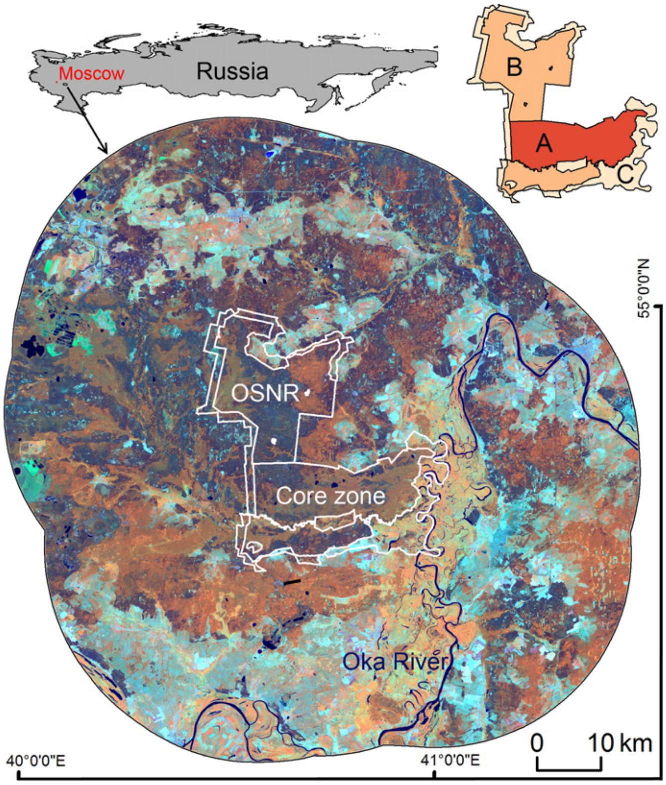

Fig. 1. Study area with Oksky State Nature Reserve in Russia and related biosphere reserve zoning (A = core zone, B = transition zones, and C = buffer zone) and the protected area's surroundings (Landsat TM 5 image in 4–5–3 false colors from 31st May, 2007).

transition zone of 33,000 ha and a buffer zone of 22,000 ha were added to the 23,000 ha core zone (Fig. 1). The core zone is strictly protected, all land uses are prohibited, and access is limited to scientists and protected area staff only. In the transition zone, non-timber forest products (e.g., mushrooms and berries) can be collected. In the buffer zone, sustainable land management is the overarching goal (Ivanchev 2009, 2011, personal communication; MAB — Man and Biosphere Programme, 2010). Three large mammals are emblematic of the protected area today: wild boar, moose, and wolf.

After the collapse of the Soviet Union in 1991 widespread land-use changes occurred across Russia (Achard et al., 2006; Alcantara et al., 2013), mainly due to a combination of declining rural populations and the diminishing profitability of agriculture due to the reduction of state-support, price liberalization, and disappearing markets within the former Soviet sphere of influence (Prishchepov et al., 2013). For example, the rural population in Ryazan Oblast declined from 1987 to 2007 by 24% (ROSSTAT, 2013) and in our study area, about 40% of the farmland in use in 1988 was abandoned by 2010 (Sieber et al., 2013). Most importantly, vast areas of former pastures were abandoned when the region's livestock sector collapsed (cattle, pig, and sheep numbers decreased by more than 75% from 1987 to 2007 in Ryazan Oblast; ROSSTAT, 2008). As of 2010, many abandoned areas were encroached by shrubs or young forests. In terms of forest management, logging rates decreased by 50% in 2000 compared to the mid-1980s (Sieber et al., 2013). Thus, human pressure in terms of land use appears to having decreased in the post-Soviet period in our study area.

2.2. Species occurrence data

Long-term winter track counts (WTCs) of all three large mammals were collected by co-author Nikolai V. Uvarov along transects within the core zone of Oksky State Nature Reserve. Data for wild boar were collected consistently from the winter of 1978/9 to 2007/8, for moose from 1992/3 to 2008/9, and for wolf from 1994/5 to 2008/9. Each year from October until March, transect locations and species tracks crossing these transects were noted based on fresh snow. We scanned the WTC maps, georeferenced them, and digitized the occurrence points for each species and year (Fig. A2 in the Supporting Information). To avoid pseudo-replication, we overlaid the occurrence points for each species and year with a 100-m grid and randomly selected one point in cells with multiple points (Elith et al., 2011).

2.3. Environmental and human-impact variables

To analyze habitat selection and to map suitable habitat, we compiled a set of environmental and human-impact variables that were assumed to affect wildlife habitat suitability in our study area. Variable selection is a crucial step for modelling wildlife habitats (Velez-Liendo et al., 2013). Candidate variables were identified based on the literature and expert knowledge (Table 1), and we used variables on land cover and land use, topography, human disturbance, and biotic interactions in our analyses. In terms of land cover and land use, we included information on, for example, different forest types, neighborhood information on the percentage of farmland and unmanaged grassland, and the Euclidean distances to core and edge forests. All of these variables were available for the years 1987, 1994, 1997, 2002, and 2007. In addition, we included the time-invariant variables for topography (e.g., elevation and slope) and human disturbance (e.g., Euclidean distance to roads) as control factors (Table 1 and Table A1 in the Supporting Information).

To model the habitat of wild boar and moose, we used all of these variables. To model the habitat for wolf, we used these variables plus potential wild boar and moose habitat (i.e., the respective relative habitat suitability index outcome scaled between 0 and 1, see Section 2.4 and Table 1), since wolves prey on both ungulates. We additionally parameterized a second wolf model without any prey habitat variables and a third wolf model with only wild boar habitat as a prey variable to explore the relative importance of including the prey variables (Table B1 in the Supporting Information). We selected wild boar habitat as the only prey-related variable in the third model because the wild boar variable performed slightly better than an alternative model including only the moose habitat variable (Table B1).

2.4. Time-calibrated habitat modeling

Species distribution models (SDMs) are powerful tools to explore spatial patterns of wildlife habitat (Elith et al., 2006; Hegel et al., 2010). SDMs describe a species' potential distribution by estimating the relationship between species occurrences and the environmental characteristics at these sites (Elith and Leathwick, 2009). Typically, SDMs are either based on data for a single snapshot in time (e.g., a recent land-cover classification) or on mean values (e.g., average temperature). Snapshots in time do not capture habitat changes, and mean values can easily obfuscate crucial environmental conditions that occurred during the time that the occurrence record was collected. One approach to account for changing environmental conditions would be to derive unique habitat models for each time step. However, this is rarely feasible because this requires large numbers of occurrence records and would still bear the risk of underestimating true habitat suitability if species do not occupy all potentially suitable habitats in a given time step (Franklin, 2010; Nogues-Bravo, 2009).

The alternative is to apply a time-calibrated species distribution model (Kuemmerle et al., 2011; Nogues-Bravo, 2009). A time-calibrated SDM is a single model parameterized for the entire time period of interest, trained with data from all time periods represented in the occurrence points (i.e., multiple years in our case). To parameterize the time-calibrated model, occurrence records are matched with the environmental conditions from the time when the occurrence point

Table 1
Variable selection for modelling suitable wildlife habitats in the study area. The terrain and human disturbance variables are time-invariant, whereas all other variables were available for the years 1987, 1994, 1997, 2002, and 2007. The detection of farmland abandonment, i.e., the conversion from farmland to unmanaged grassland, was based on two Landsat TM/ETM+ satellite image classifications and resulted in separate farmland abandonment maps for the years 1994/97 and 2002/07.

Variable	Comments	Source	Data type and range
Land cover/land use			
Land cover	9 classes: background, farmland, unmanaged grasslands & riparian trees, forest, forest disturbances, coniferous forest, oak (*Quercus*) and linden (*Tilia*) forest, deciduous forest, and mixed forest	Landsat TM/ETM+ images (Sieber et al., 2013); forest-type map of Oksky State Nature Reserve	Categorical; classes 1–9
Fraction of farmland	Percent of farmland in a 2-km neighborhood	Landsat TM/ETM+ images	Continuous; 0–100%
Fraction of grassland	Percent of unmanaged grassland (and riparian trees) in a 2-km neighborhood	Landsat TM/ETM+ images	Continuous; 0–100%
Distance to core forest	Euclidean Distance in m; calculated with Morphological Spatial Pattern Analysis (MSPA) using GUIDOS software (Vogt et al. 2007), edge width: 30 m	Landsat TM/ETM+ images	Continuous; 0–3700 m
Distance to forest edge	Euclidean Distance in m; calculated with MSPA (Vogt et al. 2007), edge width: 30 m	Landsat TM/ETM+ images	Continuous; 0–3000 m
Terrain			
Elevation	In m	Shuttle Radar Topography Mission (SRTM) of the United States Geological Survey (USGS)	Continuous; 76–172 m
Slope	In degrees, calculated from the elevation variable	SRTM USGS	Continuous; 0–11.1°
Human disturbance			
Distance to roads	Euclidean distance in m	Soviet 1:100,000 topographic maps	Continuous; 0–8000 m
Biotic interactions			
Wild boar and moose as prey for wolf	Predictions of potential habitat for wild boar and moose (Maxent outcomes)	Winter track counts of Nikolai V. Uvarov from Oksky State Nature Reserve, Russia	Continuous; 0–1

was recorded. The resulting single SDM is thus independent from a particular time period and can be projected to each time period for which a set of predictors is available. Thus, a time-calibrated SDM allows to predict changes in habitat availability over time as well as to assess habitat distribution for time periods in which occurrence data may be unavailable. Moreover, model outcomes for each time step are comparable, because they rely on the same time-calibrated model. We calibrated our SDM with the occurrence data available for the winter periods of 1994/5, 1997/8, 2002/3, and 2007/8 for each of the three species, respectively.

We used maximum entropy modeling (Maxent, Phillips et al., 2006), a machine-learning approach, widely applied for species distribution modeling (Elith et al., 2011). As an SDM algorithm, Maxent frequently outperforms other presence-only modeling techniques (Elith et al., 2006; Hernandez et al., 2006; van Gils et al., 2014). We used the Maxent version 3.3.3 k available at www.cs.princeton.edu/~schapire/maxent/. We tested all predictor variables for collinearity by calculating pairwise Pearson's correlation coefficients based on 5000 random points to facilitate interpreting the variable importance. We found strong correlation ($r > 0.8$) between the two prey habitat variables ($r = 0.93$). Even though model performance in Maxent is generally not sensitive to collinearity (Elith et al., 2011), collinearity can hinder model interpretation (Dormann et al., 2012). We therefore evaluated the relative variable importance based on single-variable models and based on comparing wolf models with none, only one, or both prey habitat variables, and selected the model with the best performance (in our case the wolf model using both prey variables) for predicting wolf habitat. Furthermore, we also did not allow for extrapolation into environmental conditions not covered by our input data using the 'clamping' function in Maxent as a precautionary measure (Phillips et al., 2006).

We ran our time-calibrated models for each of the three wildlife species using a sample of the WTC occurrence points. We used the same number of points per time step to avoid bias due to potentially changing species abundance over time. Sample size was determined by the smallest amount of occurrence points for a given year (i.e., 80 random points per year for wild boar and 250 points for moose and wolf, respectively). Maxent then contrasts the environmental characteristics at the occurrence locations with those at a random set of background points. As the WTCs were mainly collected inside Oksky State Nature Reserve, our occurrence dataset was based on an uneven sampling effort. To account for this, we used a bias file for background point selection, i.e., a mask restricting the random sampling of background points to those areas where occurrence points were sampled. To do so we used a maximum convex polygon around the sampling transects and occurrence points plus a 100-m buffer (Elith et al., 2011; Phillips et al., 2009). We randomly selected 5000 background points (Elith et al., 2011; Phillips and Dudik, 2008; Renner and Warton, 2013), and assigned 1250 points to the environmental conditions of each of the four time steps, respectively (Table A1).

We evaluated our models based on 10-fold cross-validation in two ways. First, we used the area under the curve (AUC) value of the receiver operating characteristics (ROC) curve to evaluate model performance (Phillips et al., 2006). Second, we evaluated the relative importance of variables to identify the variables with highest impact using a) jackknife estimates of the AUC and relative gain changes by either using a single-variable model or dropping single variables compared to the full model, and b) response curves of single-variable models (Elith et al., 2011; Kuemmerle et al., 2010). Based on the best-performing (highest AUC) models for each species, we made predictions for Oksky State Nature Reserve and a 30-km buffer around it, and for each time step for which environmental variables were available (1987, 1994, 1997, 2002, and 2007). Suitable habitat was defined as areas with suitability index values above the minimum predicted value (i.e., minimum training presence logistic threshold; Anderson and Raza, 2010; Phillips et al., 2006), meaning that all values predicted at actual occurrence points were assumed to represent suitable habitat. Finally, we evaluated whether changes in the predicted habitat over time were significant at the 0.05 level by applying the SigDiff function (available in the R package SDMTools; Bateman et al., 2012; Januchowski et al., 2010), which quantifies the significance of pairwise differences relative to the mean and variance of all differences between two habitat maps, and provides a map highlighting areas where significant differences occur.

3. Results

3.1. Habitat selection

We parameterized models that were generally robust and resulted in reasonable maps of habitat suitability for all three large mammals we studied (Fig. B1 in the Supporting Information). The best-performing models had an AUC of 0.77 for wild boar, 0.73 for moose, and 0.68 for all three wolf models, and standard errors of 0.01 for all species. Of the eight variables included to the SDM for ungulates, those with the highest relative importance were elevation, land cover, and distance to core forest for wild boar, as well as elevation, distance to roads, and land cover for moose (Table B1). The predicted suitable winter habitat for wild boar in our study was at elevations around 100 m, more than 3 km away from roads, within deciduous forest including oak and linden (*Tilia*) and coniferous forest, with only little farmland in the neighborhood, but up to 25% grassland, and preferable close to the forest edge. Preferred habitat for moose was similar to that of wild boar, except for grasslands being of greater importance, both in the land-cover variable and in the neighborhood variable.

Of the ten variables available to model potential wolf habitat, the prey-related variables (i.e., wild boar habitat and moose habitat) as well as elevation, fraction of grassland, and distance to forest edge were the most important based on the single-variable models (Table B1). To further explore the relative variable importance, we compared the wolf model with both prey variables to a wolf model without prey variables, and a model including only wild boar habitat. We found that land cover, elevation, and the fraction of farmland provided the most unique information based on AUC decrease when one of these variables was dropped (Table B1). In general, the predicted habitat characteristics for wolf were similar to those of the prey species, besides a smaller distance to roads (2–5 km).

3.2. Habitat availability

We defined suitable habitat as the area with habitat suitability values greater than the minimum predicted value, which was 0.10 for wild boar, 0.03 for moose, and 0.12 for wolf. Our results showed that the area of suitable habitat for all three wildlife species changed substantially over time. In Soviet times, wild boar habitat covered ca. 110,980 ha, a total share of 15% of the study region (Fig. 2, Table B2 in the Supporting Information). Over the next 20 years, wild boar habitat increased to a total share of 17% in 2007 (ca. 124,010 ha). Habitat gain was higher in the first period until 1997 (9% increase in habitat area from 1987 to 1997) than until 2007 (3%). The increase in suitable habitat was significant at the 0.05 level (Fig. B2 in the Supporting Information) and occurred mainly in areas adjacent to forest that were already predicted as suitable in the preceding time periods and in areas outside of Oksky State Nature Reserve where regrowing forests occurred on abandoned farmland. The share of suitable habitat within the protected area was generally higher than in the unprotected surroundings. Wild boar habitat always occupied most of the core zone of Oksky State Nature Reserve (>89%; Fig. 3). In contrast, only 21% of Oksky's transition zones were suitable habitat in 1987 (ca. 7100 ha, slightly increasing by 180 ha until 2007). In the buffer zone, the share of wild boar habitat was equally low in 1987, however, suitable habitat increased by 10% (ca. 450 ha) until 2007. The surroundings of Oksky State Nature Reserve had the smallest share of wild boar habitat (79,350 ha or 12% in 1987), even though the increase was largest (12,320 ha, or 16% growth by 2007).

Moose habitat increased to an even greater extent in our case. In 1987, 42% of our study area was predicted suitable (314,990 ha; Fig. 2, Table B2). Until 2007, moose habitat increased by 23%, which equals a gain of ca. 72,210 ha, leading to a share of 52% suitable habitat in our study region (ca. 387,200 ha). Most of this increase occurred in the 1990s, right after the breakdown of the Soviet Union. Moose habitat expanded especially into areas that were agriculturally used (cropland or pastures) during Soviet times, but were abandoned after 1991. Furthermore, habitat gain was significant at the 0.05 level (Fig. B2) and mainly occurred conterminous to areas predicted as suitable habitat in earlier time slots investigated. Similar to wild boar, new habitat occurred mainly outside of Oksky State Nature Reserve, whereas there was always a higher share of suitable habitat within the protected area. The core area of Oksky State Nature Reserve was effectively suitable moose habitat throughout the entire time we investigated (>98%; Fig. 3). Within the transition zones, 70% of the area was predicted suitable for moose in 1987 (ca. 23,290 ha), increasing to 72% in 2007 (ca. 23,830 ha). The buffer zone had a share of 45% of moose habitat in 1987 (ca. 9820 ha) that increased substantially to 55% in 2007 (ca. 12,120 ha), resulting in a gain of 23% of the 1987's area. Nevertheless, this growth of suitable potential habitat for moose was even exceeded in the surroundings of Oksky State Nature Reserve, where 259,580 ha in 1987 increased to 328,910 ha in 2007, equaling an increase of 27% of the 1987's area.

Suitable wolf habitat covered the largest portion of our study area of any of the three wildlife species we investigated, for the first wolf model a total of 494,370 ha in Soviet times, or 66% of the study area (Fig. 2, Table B2). Until 2007, wolf habitat increased by 20%, ca. 98,380 ha, for a total of 592,740 ha (79%). Again, most of the increase occurred until 1997, when wolf habitat gained twice as much area as in the second period from 1997 to 2007. Habitat expanded significantly (0.05 level; Fig. B2) and mainly onto abandoned fields close to settlements and in the floodplain areas of Oka River and its tributaries. The wolf model omitting the prey habitat variables showed different results, with less predicted suitable habitat across time (26% unpredicted habitat versus 17% for the first wolf model; Fig. 4) and an always smaller share. In 1987, the share of predicted suitable wolf habitat was slightly smaller (65%; 488,090 ha) than for the wolf model with both prey variables, but substantially decreased from 1997 (71%) to 2007 (58%; Fig. 4; Table B2). Compared to the ungulates, wolf habitat also had the highest shares of potential habitat inside and outside of Oksky State Nature

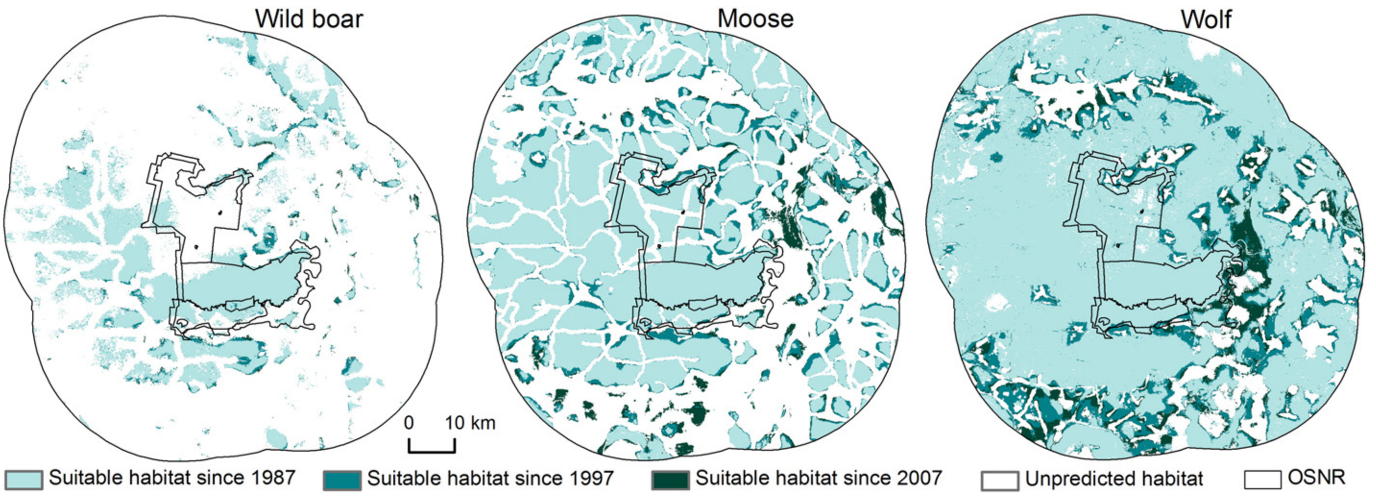

Fig. 2. Changes in predicted suitable habitat for wild boar, moose, and wolf within and outside Oksky State Nature Reserve (OSNR) from 1987 to 2007 (based on the minimum training presence logistic threshold).

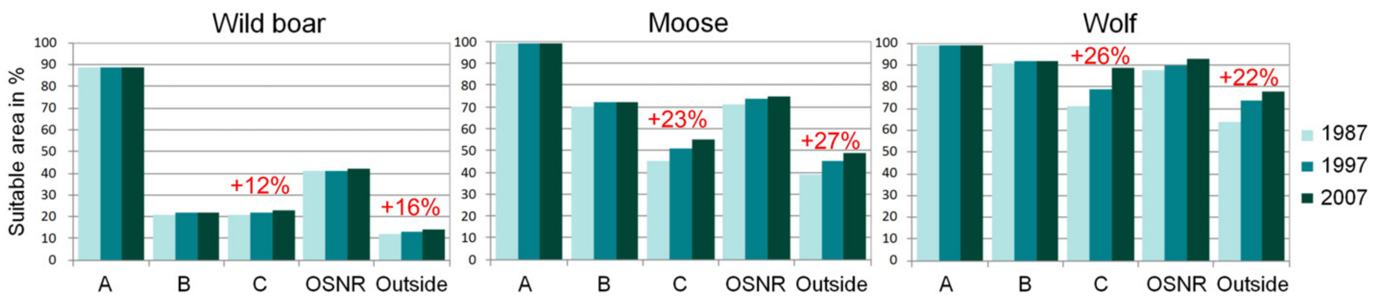

Fig. 3. Percentage of area with predicted suitable habitat for wild boar, moose, and wolf within the entire Oksky State Nature Reserve (OSNR), the three zones of the biosphere reserve (A = core zone, B = transition zones, and C = buffer zone), and the 30-km surrounding of the protected area (outside) for three time steps. The percentages of relative area changes from 1987 to 2007 are highlighted in red for the protected area's buffer zone and the surroundings.

Reserve. Wolf habitat almost completely covered the core zone with >99% of the area ranked as suitable habitat across all years, and occurred in >91% of the transition zones' area (Fig. 3). Habitat gain in our study period was largest for the buffer zone. Here, a share of 71% in 1987 (ca. 15,570 ha) increased to 89% in 2007 (ca. 19,600 ha), resulting in a gain of 26% of the 1987's area. Within the surroundings of the protected area, wolf habitat covered 64% of the area in 1987 (ca. 426,250 ha), expanding to 78% in 2007 (ca. 520,320 ha), which corresponded to an increase of 22% of the 1987's area.

4. Discussion

4.1. Habitat selection and availability

The collapse of the Soviet Union in 1991 triggered widespread land-use change and we found an increase in potentially suitable habitat of large mammals in response. The factors we identified as influential for determining the habitat selection of the three large mammals we investigated were well in line with prior studies. For example, the presence of deciduous forests with oak mast and coniferous forest stands were important in determining wild boar habitat in Poland (Fonseca, 2008), Sweden (Thurfjell et al., 2009), and Europe in general (Melis et al., 2006), and the availability of deciduous forests and grassland as well as large distances to roads affected moose habitat selection in Sweden (Neumann et al., 2012) and Russia (Baskin and Danell, 2003; Heptner et al., 1988). Interestingly, and in contrast to other studies, we found that elevation was important in determining ungulates' habitat selection, which may be due to the digital elevation model of the Shuttle Radar Topography Mission (SRTM) that also captures land cover since the radar waves may not penetrate the vegetation canopy, and the data thus do not represent the ground surface (Farr et al., 2007). In terms of wolf habitat, our study confirmed the generalist nature of

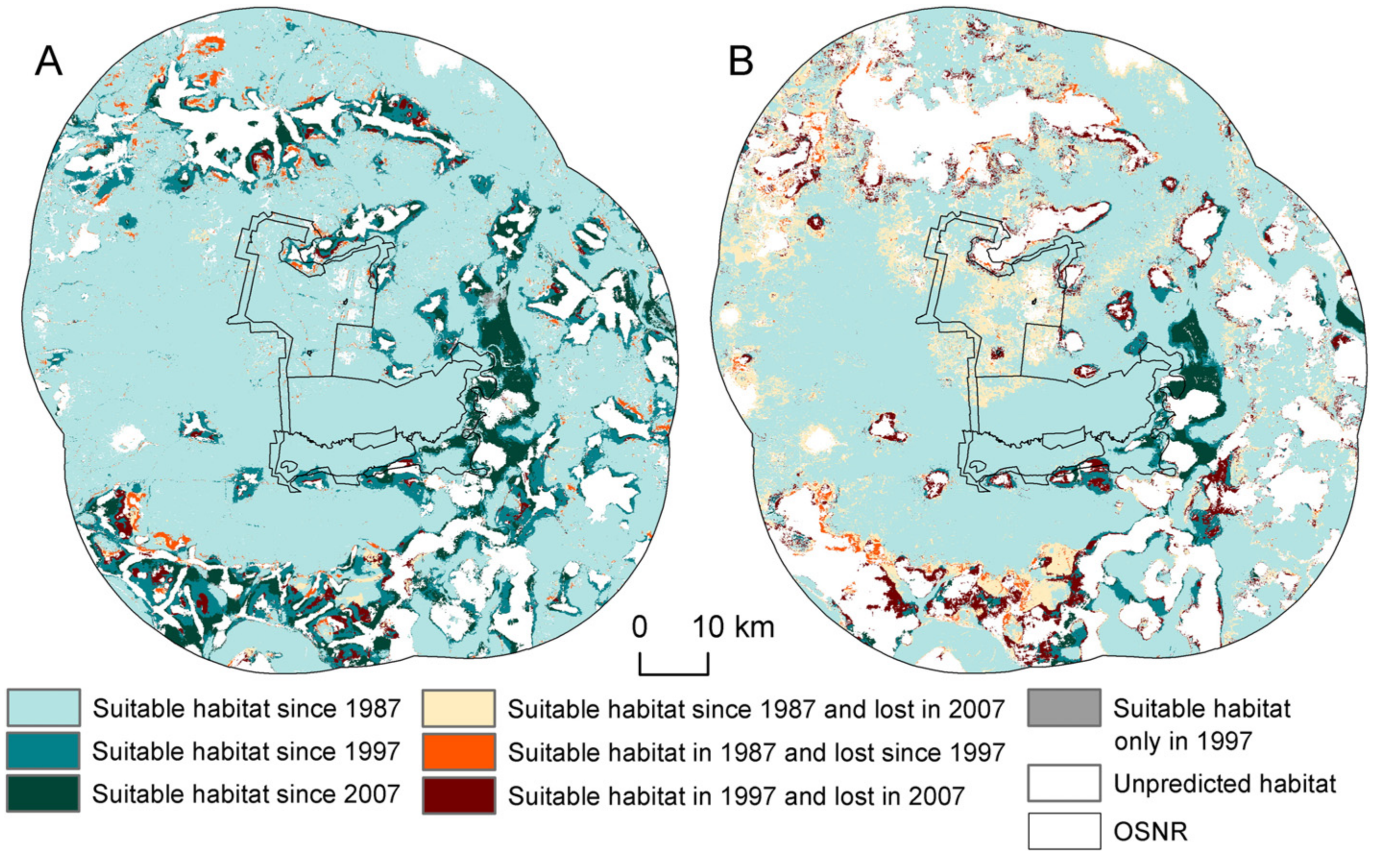

Fig. 4. Predicted suitable wolf habitat within and outside Oksky State Nature Reserve (OSNR) for the model including prey-related habitat variables (A) and the model without prey habitat variables (B) for three time steps.

wolves, and the importance of human disturbance as a driver of habitat selection as in Poland (Jedrzejewski et al., 2004) and Canada (Lesmerises et al., 2012). Wolves are a special case in Russia for the post-Soviet period (Bragina et al., 2015) because they were the only large mammal with increasing populations during the 1990s, as a result of decreasing wolf persecution then. In our case, wolf habitat increased since 1991, possibly at least in part due to more widespread ungulate habitat, given that wild ungulates are the main prey of wolf in Eastern Europe (Okarma, 1995), and the collapse of livestock farms substantially reduced feeding opportunities on carcasses after 1991 (Gubar, 2000), yet wolf populations still increased (Bragina et al., 2015).

From 1987 to 2007, the area of suitable habitat for the three wildlife species we investigated increased up to 23%. Several reasons explain this increase. First, post-Soviet land-use change, particularly farmland abandonment, was widespread in Eastern Europe (Alcantara et al., 2013; Estel et al., 2015). In our study area, mainly marginal farmland in the vicinity of forests was abandoned, and most abandonment happened in the early 1990s (Prishchepov et al., 2012; Sieber et al., 2013), whereas the succession of shrubland and forests on farmland far away of the forest edge happened delayed. Yet, as in other regions characterized by large-scale farmland abandonment, regrowing natural vegetation likely provided forage and shelter important to wildlife in our case as well (Bowen et al., 2007; Plieninger et al., 2014), and may have increased habitat connectivity among existing habitat patches (Hernandez et al., 2015; Sitzia et al., 2010). As a result, post-Soviet land-use change and the recovery of large mammal populations in the 2000s (Bragina et al., 2015) may be interpreted as signs of large-scale rewilding, similar to trends in some parts of Western Europe (Ceauşu et al., 2015; Navarro and Pereira, 2012).

A second reason contributing to the increasing availability of potential habitat for our species was the expansion of protected areas in our study area. The current core zone of Oksky State Nature Reserve represented the entire protected area from 1935 to 1988 and was strictly protected throughout, resulting in a high share of suitable wildlife habitat there. In contrast, forestry and agriculture in the transition zone were restricted only after 1989, when the biosphere reserve regulations were implemented (MAB 2010), and these restrictions contributed to the increasing availability of wildlife habitat in this zones (Fig. 3). Land use in the buffer zone is not restricted, however, yet we still found declining land-use pressure and farmland abandonment in this area. Increasing habitat quality in this zone was therefore mostly due to the socio-economic and institutional changes in the aftermath of the breakdown of the Soviet Union. Similarly, the landscape surrounding the biosphere reserve changed much in post-Soviet times, creating new suitable habitat over time, and potentially connecting suitable habitat within the protected area and in its surroundings. Post-Soviet land-use change and the expansion of buffer zones thus improved large mammal habitat quality and availability in the protected area's zone of interaction (Hansen and DeFries, 2007), a trend opposite to most other world regions where protected areas are becoming increasingly isolated (DeFries et al., 2005; Newmark, 1996). How increasing habitat availability and connectivity in post-Soviet Russia affected mammals' populations would be worthwhile to explore in future research.

Including biotic information into models evaluating the habitat selection of large mammal species has been shown to improve model performance and outcomes (Hebblewhite et al., 2014) and our study provides further evidence for this. We assessed the habitat suitability for wolf and compared models with and without prey habitat variables. Although both model types resulted in overall relatively similar wolf habitat maps, and similar conclusions about wolf habitat selection (Figs. 2 and 4), including prey habitat improved model performance and highlighted more potentially suitable habitat patches than models without these variables. This suggests potentially suitable habitat for large carnivores may be underestimated if prey habitat is not taken into account, and there is a benefit of including multiple prey species in cases where the habitat selection of these species differs such as in the case of wild boar (generalist) and moose (forest specialist). However, as the prey habitat variables are the result of an SDM application, we caution that uncertainty in this modelling exercise may propagate into the results of the wolf habitat model. In our case, including the prey variables improved model performance, similar to prior studies (Giannini et al., 2013; Hebblewhite et al., 2014).

4.2. Limitations

We evaluated potential wildlife habitats by applying time-calibrated species distribution models, yielding generally good model fits and plausible habitat maps. Still, several sources of uncertainty need mentioning. First, we analyzed winter track count data, and thus modeled winter habitat. However, we did not have fine-scale, spatially explicit data on winter severity or snow cover, which can be crucial for the survival of large ungulates and large carnivores (Baskin and Danell, 2003; Nasimovich, 1955). Some of our predictors may thus act as proxies for weather variability across the study region (e.g., elevation as a proxy for snow depth). Second, we mapped only winter habitat, the most critical time period for all species we investigated, and summer habitat may be more widespread. While this would not impair comparisons over time, focusing on winter habitat means that our estimates of potentially available habitat are conservative. Third, our species occurrence points were collected along transects and did not represent a fully random sample of points. Yet, the risk of potential bias induced by non-random transect placements seems small, because transects cover the entire core zone of Oksky State Nature Reserve, and we randomly sampled from all occurrence data using a minimum distance between points. Further, we addressed the issue of a potential sampling bias by limiting the random background point selection (Phillips et al., 2009). Although we cannot fully rule out remaining bias, our models did not suggest that we extrapolated in environmental space when projecting to the entire study region.

Fourth, our species occurrence data did not account for potentially varying hunting pressure. Human pressure, and especially hunting, is crucial in determining the habitat selection (Keuling et al., 2008; Thurfjell et al., 2009). Although we addressed this in our modeling approach, we could only use relatively indirect proxies for hunting and human pressure (e.g., distance to roads as a proxy for accessibility of a location to hunters). Wild boar and moose are important game species (Fonseca, 2008), and all areas outside the Oksky State Nature Reserve are subject to hunting. More direct spatial measures of hunting, both legal hunting and poaching, would have been desirable, but do not exist to the best of our knowledge. Fifth, our species occurrences did not cover the full gradient of land-use intensity in our study area, as the most intensive land uses are not found inside the protected areas. Our model outcomes may thus underestimate wildlife habitat availability for species that are tolerant to land use, which may especially be the case for more generalist species (e.g., wild boar). At the same time, the availability of suitable habitat might be overestimated for wildlife species sensitive to land management. Sixth, as with any SDM, our model only predicts potentially suitable habitat, but cannot attest to whether or not habitat is actually used. This would be particularly relevant if hunting pressure was high, for example, due to high poaching during the 1990s (Bragina et al., 2015), meaning that not all habitat that we identify may have been occupied during that period. Likewise, changing legal hunting pressure may also lead to some of the potential habitats not being occupied.

Seventh, our models achieved moderate AUC values (Franklin, 2009), ranging between 0.7 and 0.8. Lower AUC values are to be expected for generalist species such as wild boar and wolf, because the contrast between occurrence and background points can be low if a species is using a wide range of habitat (Lobo et al., 2008). Finally, to discriminate suitable from unsuitable habitat, we decided to use the minimum predicted value (i.e., minimum training presence logistic threshold; Pearson, 2007; Phillips et al., 2006) as our threshold, because our occurrence data were of high spatial precision and because our species are all generalists. Thus, our focus here was on avoiding omission errors, and on identifying all habitat suitable for these species rather than to only identify best, or only high quality habitat. More conservative thresholds would result in a proportional decline of predicted increase of suitable habitat, yet would not affect our conclusions about relative habitat change inside and outside the protected area (Fig. B1).

4.3. Conservation implications

In summary, we analyzed a long-term dataset on large mammal occurrence, spanning 20 years from 1987 to 2007, to assess the effects of widespread land-use change after the collapse of the Soviet Union on wildlife habitat and how these land-use changes affected the zone of interaction surrounding protected areas. While the land changes that happened in the wake of the collapse of the Soviet Union were unusual in magnitude, our time-calibrated species distribution models are broadly applicable and could be used for any protected area and for any land-use change as long as longitudinal wildlife data and land-change maps are available.

Finally, our study highlights that strictly protected areas provided suitable habitat for emblematic species throughout the post-Soviet transition period. Many wildlife populations were declining in the 1990s, likely due to overharvesting (i.e., poaching as a result of lower levels of control and a period of economic hardship; Bragina et al., 2015) and rebounded after 2000 as socio-economic conditions became more stable (Hanson, 2009) and poaching decreased. Given that protected areas in European Russia remained relatively effective after the breakdown of the Soviet Union (Sieber et al., 2013; Wendland et al., 2015), it appears that these areas played an important role as havens for large mammals during times of instability and raising pressure on wildlife from poaching (Bragina et al., 2015), which might not be the case in other regions (Craigie et al., 2010). Given that globally many regions of conservation are unfortunately experiencing turbulent institutional and socio-economic times, our study thus highlights the potential gains of supporting conservation action even during such times. However, our study also shows that habitat effects occur lagged, as vegetation succession took time, and can only translate into a benefit for wildlife populations once more direct threats to species' survival (poaching in our case) are curbed.

Our results indicated that the pulse of farmland abandonment that occurred after 1991 initiated in a phase of rewilding, with decreasing human impact and expanding potential wildlife habitat. Across Europe, such rewilding trends are increasingly observed, with recovering large mammal populations (Chapron et al., 2014). Continued abandonment in some European regions is likely (Verburg et al., 2010) and other world regions may see declining agricultural areas in the future, too (Meyfroidt and Lambin, 2011). Conversely, rising demand for agricultural commodities may lead to a reversal of recent abandonment trends, as already seen across some parts of the former Soviet Union (Estel et al., 2015; Kamp et al., 2011). This suggests we may be in a critical moment for implementing conservation action that can benefit large-bodied and wide-ranging species, and thus biodiversity in general. Future analyses highlighting which currently abandoned areas are most important in terms of providing connectivity in the habitat network of large mammals would be particularly important for conservation planning – in European Russia and elsewhere.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2015.07.041.

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