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Future Range Dynamics Suggest Increasing Threats of Grey Squirrels (*Sciurus carolinensis*) against Red Squirrels (*Sciurus vulgaris*) in Europe: A Perspective on Climatic Suitability

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Abstract: Interactions between the introduced gray squirrel (*Sciurus carolinensis*) and the native red squirrel (*S. vulgaris*) play an important role in the ecological equilibrium of European forest ecosystems. However, the range dynamics of the grey squirrel and red squirrel under future climate change scenarios remain unknown. The present study examined the range dynamics of grey squirrels and red squirrels in Europe and their range overlap now and in the future based on climate change. Under the most optimistic climate change scenario (SSP126), expansion of the grey squirrel's range was mainly predicted in Germany, France, Croatia, Serbia, and Bulgaria. Under the most pessimistic climate change scenario (SSP585), expansion of the grey squirrel's range was predicted in vast and scattered regions. Additionally, France, Italy, and Germany were overlapping ranges for the grey squirrel and red squirrel in the future under the SSP126 scenario but not under the current conditions, suggesting that there will be new regions where grey squirrels may threaten red squirrels in the future under SSP126. The range overlaps under the SSP585 scenario but not under the current conditions were vast and scattered, suggesting that there will be new regions in the future where grey squirrel may displace red squirrels under SSP585. Despite considerable variation, we detected expansions in the grey squirrel and red squirrel ranges and an increase in overlapping ranges between grey squirrels and red squirrels in the future. Therefore, our prediction suggests increasing threats of grey squirrels toward red squirrels in Europe in the future under climate change, which may impact the ecological equilibrium of European forest ecosystems.

Keywords: climatic suitability; Europe; grey squirrels; range dynamics; red squirrels; threats

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Citation: Nie, P.; Yang, R.; Feng, J. Future Range Dynamics Suggest Increasing Threats of Grey Squirrels (*Sciurus carolinensis*) against Red Squirrels (*Sciurus vulgaris*) in Europe: A Perspective on Climatic Suitability. *Forests* **2023**, *14*, 1150. https://doi.org/10.3390/f14061150

Academic Editor: Mike McKinney

Received: 26 April 2023
Revised: 26 May 2023
Accepted: 28 May 2023
Published: 2 June 2023

1. Introduction

Biological invasion causes adverse effects on ecosystems [1,2], the economy, and human health [3,4], particularly loss of global biodiversity [5,6]. Although human activities, such as international trade and transport, promote worldwide biological invasions [7], global climate change is also playing a role, and recent studies have shown that global climate change is a primary factor responsible for the global distribution of invasive species and their shifts in the future [8–13]. Therefore, understanding the impacts of climate change on biological invasions and the underlying mechanisms are key challenges for ecological research and conservation biology [9,14].

Investigating the range dynamics of alien invasive species (AIS) and the underlying mechanisms is of great significance since efficient strategies against biological invasions can be developed [15–18]. Therefore, an essential need is to project the range dynamics of AIS under future climate change scenarios [19–21]. Previous studies have shown that the ranges of AIS may be modified by future climate change, probably because AIS will track their once-occupied climatic-suitable habitats, and climate change could reallocate suitable habitats [12,22,23]. Most studies have shown that climate change will promote biological invasions [8,12,22–24]. However, de Albuquerque et al. (2019) reported that climate change may cause a contraction of the potential range of highly invasive buffelgrass (*Cenchrus ciliaris* L.) [25]. Additionally, Gong et al. (2020) showed that climate change could have two-sided effects on the potential ranges of AIS, possibly because the impacts of climate change on the potential ranges of AIS will be species-specific [20]. Therefore, the dynamics of the potential ranges of AIS under climate change remain controversial, so further investigations are needed [8].

Range overlap between AIS and native species is important since overlaps are generally closely associated with inter-specific competition [26], food web dynamics [27], the persistence of less competitive species [27,28], and conservation initiatives [29]. Therefore, it is essential to understand range overlaps between AIS and native species and the underlying mechanisms. As discussed above, climate change may change the range dynamics of AIS; hence, it is reasonable to infer that climate change could modify the range overlap of native species and AIS.

The introduced grey squirrel (*Sciurus carolinensis*) is impacting the equilibrium of European forest ecosystems by breaking trophic cascades of European forest ecosystems between herbivores and plants [30]. As an invader from North America, the grey squirrel was first introduced into Europe in 1892 [31], and it has reportedly posed a huge threat to the red squirrel (*Sciurus vulgaris*), a sympatric rodent native to Europe. In addition to competition against red squirrels [32–34], grey squirrels have considerably displaced red squirrels by passing helminth [35,36] and pathogenic squirrelpox virus (SQPV) infections [37–39]. Many studies have investigated the invasions of grey squirrels and their threats to the survival of red squirrel populations in Europe [34,37,40–42]. Additionally, a variety of studies have focused their attention on the interactions between red squirrels and grey squirrels [43], including the effects of habitat fragmentation on interspecific competition [42], the differentiation of niche use between grey squirrels and red squirrels [28], resource partitioning between grey squirrels and red squirrels [34], and the ranges of grey squirrels in Europe [44,45]. These studies have provided essential information for countering the competition between grey squirrels and red squirrels and developing conservation strategies for red squirrels in Europe.

Notably, many studies have explored the range dynamics or distribution patterns of grey squirrels [41,44–51]. These studies have promoted our understanding of the spatial patterns of grey squirrels and threats against red squirrels. Nevertheless, most of these studies investigated the roles of non-climatic factors, such as population dynamic metrics, vegetation, and land cover, in the range dynamics or distribution patterns of grey squirrels, whereas the effects of climate have received little attention, despite vegetation patterns and land cover being closely associated with climate change [52–54], which in turn has shuffled the distribution or range dynamics of grey squirrels [55,56].

Di Febbraro et al. (2016, 2019) used species distribution models (SDMs) to investigate range dynamics of the grey squirrel and provided important information for developing strategies against grey squirrel invasions [44,45]. However, they did not investigate the potential range overlap between red squirrels and grey squirrels or shifts in the ranges under climate change. In the present study, we assumed that climate change will induce changes in the grey squirrel and red squirrel ranges, resulting in considerable shifts in range overlap between them.

In summary, climate change may induce changes in the ranges of grey squirrels and red squirrels, resulting in shifts in the range overlaps between them, which could modify their interactions and the survival of red squirrels in Europe. Here, from a perspective on climatic suitability, we developed range-dynamic models to examine the range dynamics of grey squirrels and red squirrels, and we determined the degree of range overlap between them under a climate change scenario. The results provide novel information for developing strategies to counter the invasion of grey squirrels and to conserve red squirrels in Europe in the future.

2. Materials and Methods

2.1. Species Occurrence Records

We downloaded 674,269 occurrence records for grey squirrels (176,095) and 497,874 records for red squirrels from the Global Biodiversity Information Facility (accessed on 1 May 2021). Then, we refined the dataset by removing the occurrence records with uncertainty in the geographical coordinates >10 km. To account for the effects of spatial autocorrelation, we applied SDMtoolbox software, version 2.0, to spatially rarefy the occurrence records with a radius of 10 km [57,58]. We obtained 13,477 occurrence records, including the occurrence records for grey squirrels (1352) and red squirrels (12,125) in Europe (Figure 1, Online dataset 1).

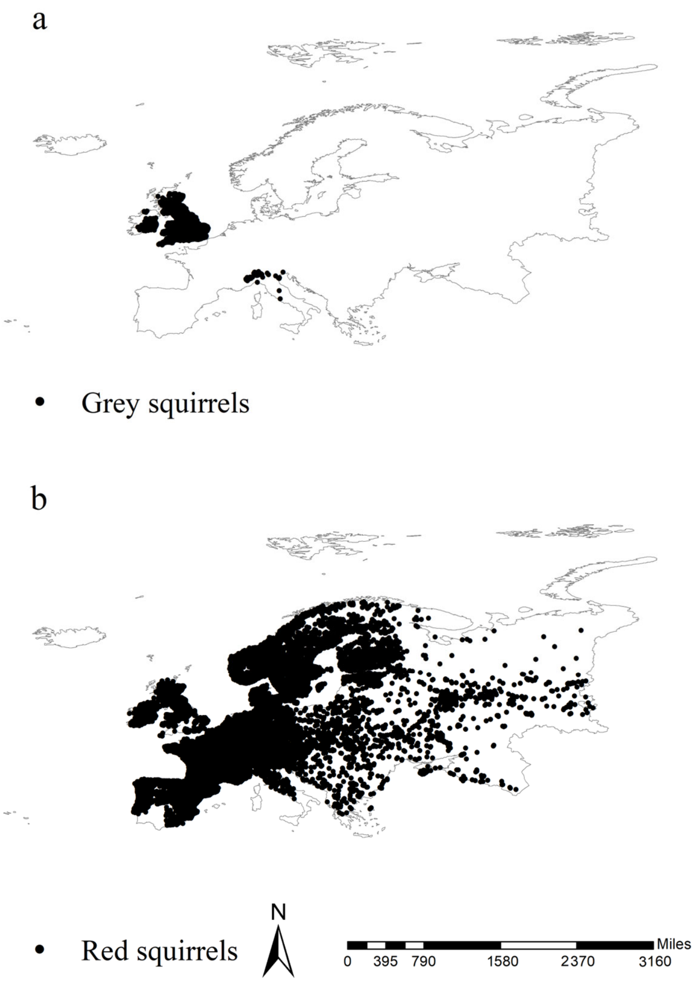

Figure 1. Occurrence records of the grey and red squirrels. Black points in (**a**,**b**) indicate the occurrence records of grey and red squirrels in Europe, respectively. After spatial rarefication and time stamp filtering, we retrieved totals of 1354 and 12,125 records of grey and red squirrels, respectively.

2.2. Climatic Predictors

We downloaded the spatial layers of 19 bioclimatic predictors for the current conditions (an average of the 1970–2000 values) with a spatial resolution of 5 arc min from WorldClim 2.1 [59]. Then, we retrieved the spatial layers of 19 bioclimatic predictors for the future climate change scenarios (2100) at a spatial resolution of 5 arc min, in which we adopted two General Circulation Models (GCMs), FIO-ESM-2-0 and MPI-ESM1-2-HR, which are robust and complementary [60]. Additionally, due to strong influences of climatic change (scenarios) on the range shifts of grey squirrels and red squirrels (and other small mammals of forests) [45,61], we selected SSP126 and SSP585 to represent the most optimistic and pessimistic climatic change scenarios, respectively. In summary, we obtained four climatic change scenarios, including SSP126 derived from FIO-ESM-2-0 (F126) and MPI-ESM1-2-HR (M126) and SSP585 derived from FIO-ESM-2-0 (F585) and MPI-ESM1-2-HR (M585).

2.3. Climatic Predictors in the Ecological Niche Models (ENMs)

With reference to Liu et al. (2020), we used the following methodologies to reduce the effects of multi-collinearity among the climatic predictors in the ecological niche models for projecting the potential grey squirrel and red squirrel ranges [17]. First, biomod2, an assembled ecological niche model platform [62], was used to build the preliminary ecological niche models to estimate the relative importance values of the 19 predictors (Table S1). Second, Pearson's pairwise correlation analyses were conducted to identify the collinearity among the 19 predictors, in which the threshold of collinearity was a correlation coefficient $\geq$0.7 [63] (Table S2). Then, we removed the predictor with smaller relative importance in each pair of predictors that showed collinearity. We ended these processes when strong collinearity was not observed. The retained climatic predictors were found in Table S3.

2.4. Potential Ranges of Grey Squirrels and Red Squirrels

Using the occurrence records of grey squirrels and the current spatial layers of the retained climatic predictors for grey squirrels (Table S3), we applied Biomod2, an ensemble platform for ecological niche models [62], to develop ecological niche models to project the potential ranges of grey squirrels in Europe. Seven algorithms were applied: classification tree analysis, artificial neural networks, flexible discriminant analysis, a maximum entropy model, a generalized additive model, a generalized boosting model, and the random forest classifier [63]. We followed the method recommended by Barbet-Massin et al. (2012) to retrieve pseudo-existence records (PAs) [64]; i.e., if the number of occurrence records was <1000, we randomly selected 1000 PAs, or we randomly selected an equal number of PAs. We obtained the importance values for each predictor using these ecological niche models. A similar method was applied to project the potential ranges of grey squirrels in future scenarios, in which we used the occurrence records of grey squirrels and the retained climatic predictor spatial layers in future scenarios. This method was applicable for projecting the potential ranges of reds squirrel under the current conditions and in future scenarios.

We used a five-time cross-validation procedure to evaluate the reliability of the ecological niche models. In this procedure, we used 70% of the occurrence records to develop the ecological niche models and the remaining 30% to assess the reliability of the ecological niche models. To guarantee the reliability of the ensemble ecological niche models, we only retained the ecological niche models with areas under the receiver operating characteristic curve (AUC) >0.8 or true skill statistics (TSS) >0.7 [65]. The maximization sensitivity-specificity sum threshold (MSS threshold) was applied to calibrate the potential ranges of each species. This MSS threshold approach considers both the sensitivity and specificity of models, as well their sum, and the threshold is determined by maximizing the sum of sensitivity and specificity [66]. This threshold approach has shown good performance in a comparative study of the thresholds [67].

2.5. Range Shifts and Overlap of Grey Squirrels and Red Squirrels

We developed a dynamic range model to investigate the range shifts in grey squirrels and red squirrels. In this model, we divided all ranges of a species into three elements: range unfilling (*RU*), range stability (*RS*), and range expansion (*RE*). *RU* was defined as the range potentially occupied only by a species under the current conditions. RS was defined as the range potentially occupied by a species under the current conditions and in future scenarios. *RE* was defined as the range potentially occupied by a species only in future scenarios. The range of a species in a future scenario (*RF*) was defined as the sum of *RE* and *RS*, and the range of a species under the current conditions (*RC*) was defined as the sum of *RS* and *RU*.

Range ratio (*RR*) [68] is an index reflecting the changes in range sizes of a species from current conditions to future scenarios, and it could be calculated as follows:

$$RR = \frac{RF}{RC}$$

Range similarity index (*RSI*) [68] is an index representing the changes in range centroids of a species from current conditions to future scenarios, and it could be calculated as follows:

$$RSI = \frac{2RS}{RC + RF}$$

Additionally, we overlapped the potential ranges of grey squirrels and red squirrels under the current conditions and in the future climate change scenarios to identify the regions requiring attention to strategize against grey squirrels under the current conditions and in future scenarios.

3. Results

3.1. Performance of Ecological Niche Models and the Maximization Sensitivity-Specificity Sum Threshold

All ecological niche models showed excellent performance: areas under the receiver operating characteristic curve and true skill statistics for grey squirrels (red squirrels) were 0.99 (0.92) and 0.97 (0.69), respectively, exceeding their respective thresholds. The maximization sensitivity–specificity sum thresholds for determining the potential ranges of grey squirrels and red squirrels under the current conditions were 0.49 and 0.50, respectively. Under the scenarios of F126, F585, M126, and M585, the maximization sensitivity-specificity sum thresholds for calibrating the potential ranges of grey squirrels were 0.32, 0.03, 0.43, and 0.01, respectively, and those under the scenarios of F126, F585, M126, and M585 were 0.40, 0.22, 0.43, and 0.34, respectively.

3.2. Predictors Responsible for the Potential Ranges of Grey Squirrels and Red Squirrels

Our ecological niche models showed that, for the potential ranges of grey squirrels, the mean temperature of the coldest quarter had the highest importance value (0.474), followed by temperature seasonality (0.328), while precipitation of the wettest quarter showed the lowest importance value (0.011), followed by the mean temperature of the wettest quarter (0.016) (Table S3). The species response curve indicated that grey squirrel habitat suitability increased with the increase in the mean temperature of the coldest quarter (Figure 2a). The most important predictors of the potential ranges of red squirrels were temperature seasonality (0.638), followed by mean temperature of the warmest quarter (0.109), whereas the mean diurnal range (0.032) and precipitation seasonality (0.031) were the least important predictors (Table S3). The species response curve showed that habitat suitability for red squirrels roughly decreased with the increase in temperature seasonality (Figure 2b). In summary, the most important predictors for the potential climatic change ranges of both species were temperature-related variables.

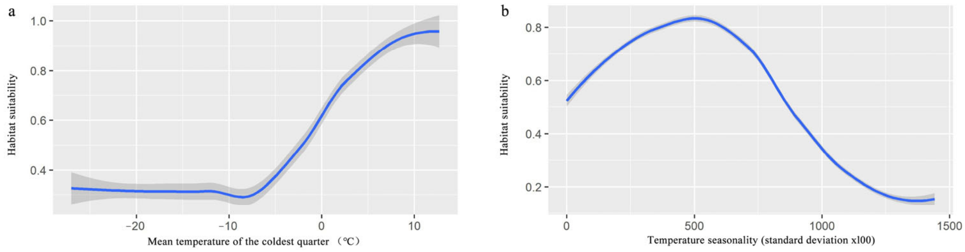

Figure 2. Responses curves of squirrels to the most important predictors. (**a**,**b**) indicate grey squirrels to mean temperature of the coldest quarter and red squirrels to temperature seasonality, respectively. With the increase in mean temperature of the coldest quarter, habitat suitability for grey squirrels increased. With the increase in temperature seasonality, habitat suitability for red squirrels roughly decreased.

3.3. Potential Ranges of Grey Squirrels and Red Squirrels

Under the current conditions, the potential ranges of grey squirrels were mainly observed in the entire territory of the UK, Ireland, and scattered regions of northern Italy, covering 33.45 × 10^4 km^2 (Figure 3a). The potential ranges of red squirrels under the current conditions were predicted to be western Europe, Estonia, and some scattered regions in eastern Europe, covering 262.41 × 10^4 km^2 (Figure 3b).

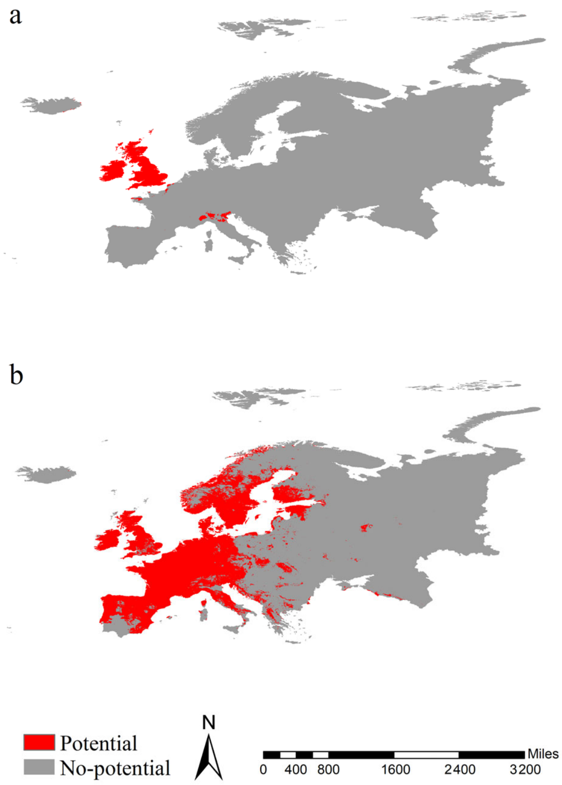

Figure 3. Potential ranges of grey and red squirrels under the current conditions. (**a**,**b**) indicate the potential ranges of grey and red squirrels under the current conditions, respectively. Red and grey indicate the potential ranges and no potential, respectively.

The potential ranges of grey squirrels under the F126 scenario were identified in Iceland, Ireland, the UK, France, Italy, the Netherlands, Croatia, Serbia, and Bulgaria, covering 65.00 × 10^4 km^2 (Figure 4a). Under the M126 scenario, the potential ranges of grey squirrels were observed in the UK, Ireland, Serbia, Italy, Croatia, and Bulgaria, covering 44.86 × 10^4 km^2 (Figure 4b). Under the F585 scenario, the potential ranges of grey squirrels were in Iceland, Ireland, the UK, Spain, Portugal, France, Norway, Sweden, most of southern Europe, and the southwest part of Russia, covering 424.88 × 10^4 km^2

(Figure 4c). The potential ranges of grey squirrels under the M585 scenario were similar to those under F585, covering 519.77 × 10^4 km^2 (Figure 4d).

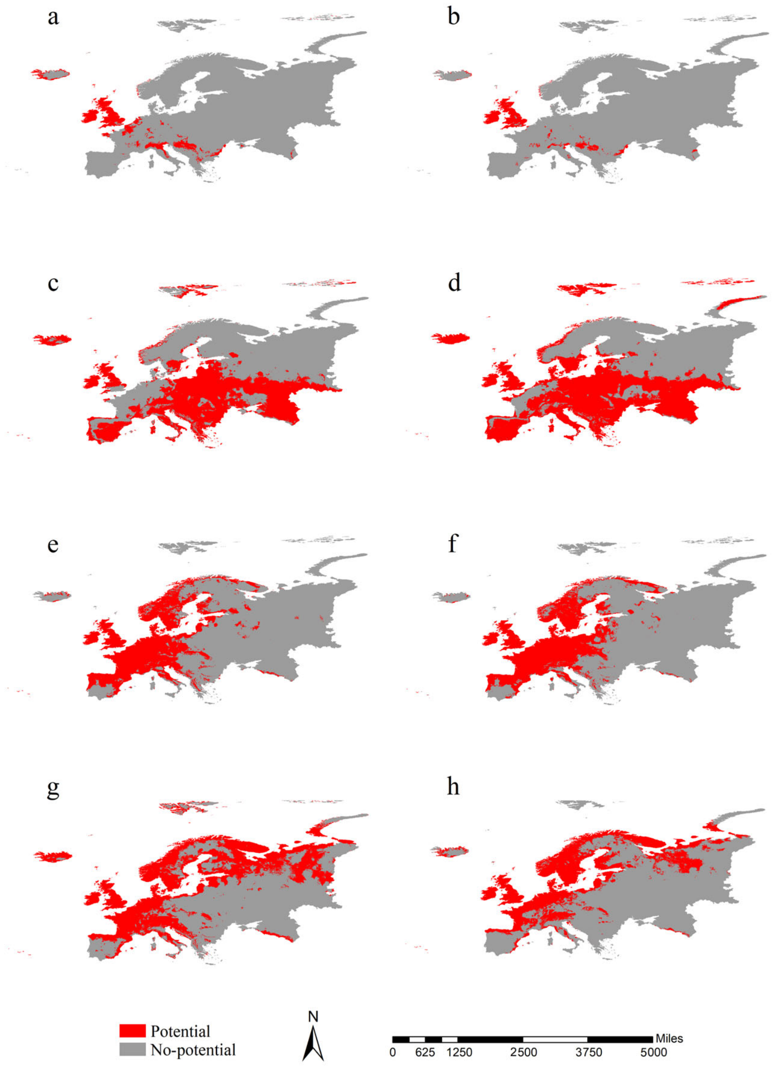

Figure 4. Potential ranges of grey squirrels under the future climate change scenarios. (**a**,**b**) indicate the potential ranges of grey squirrels under the scenarios of SSP126 derived from two General Circulation Models (GCMs), i.e., FIO-ESM-2-0 and MPI-ESM1-2-HR, respectively. (**c**,**d**) indicate the potential ranges of grey squirrels under the scenarios of SSP585 derived from two General Circulation Models (GCMs), i.e., FIO-ESM-2-0 and MPI-ESM1-2-HR, respectively. (**e**,**f**) indicate the potential ranges of red squirrels under the scenarios of SSP126 derived from two General Circulation Models (GCMs), i.e., FIO-ESM-2-0 and MPI-ESM1-2-HR, respectively. (**g**,**h**) indicate the potential ranges of red squirrels under the scenarios of SSP585 derived from two General Circulation Models (GCMs), i.e., FIO-ESM-2-0 and MPI-ESM1-2-HR, respectively. Red and grey indicate the potential ranges and no potential, respectively.

Under the F126 scenario, the potential ranges of red squirrels were mainly predicted to be in western Europe, Norway, Sweden, Finland, and Estonia, covering 297.25 × 10^4 km^2 (Figure 4e). The potential ranges of red squirrels under the M126 scenario were similar to those under the F126 scenario, covering 304.60 × 10^4 km^2 (Figure 4f). Under the F585 scenario, the potential ranges of red squirrels were in western Europe, northern Europe, and northwest Russia, covering 449.87 × 10^4 km^2 (Figure 4g). The potential ranges of red squirrels under the M585 scenario were similar to those under the F585 scenario, covering 328.21 × 10^4 km^2(Figure 4h).

3.4. Range Dynamics of Grey Squirrels and Red Squirrels

Our range models showed that, under the F126 scenario, expansion of the grey squirrel ranges mainly occurred in Iceland, the Netherlands, Germany, France, Italy, Croatia, Serbia, and Bulgaria, covering 32.41×10^4 km^2 (Figure 5a), and stable ranges were observed in Ireland and the UK, covering 32.59×10^4 km^2 (Figure 5a). Range unfilling was mainly projected in a small part of the eastern UK, covering 0.85×10^4 km^2 (Figure 5a). Additionally, the range ratio and range similarity index were 1.94 and 0.66, respectively. Expansion of the grey squirrel ranges was observed under the M126 scenario in Germany, France, Croatia, Serbia, and Bulgaria, covering 14.16×10^4 km^2 (Figure 5b), and stable ranges were detected in Ireland and the UK, covering 30.69×10^4 km^2 (Figure 5b). Range unfilling was projected in the UK and a small part of western France, and Italy, covering 2.75×10^4 km^2 (Figure 5b). Additionally, the range ratio and range similarity index were 1.34 and 0.78, respectively. Under the F585 scenario, expansion of the grey squirrel range was observed in Iceland, southwest Russia, eastern Europe, Austria, Italy, eastern France, Spain, Portugal, eastern Germany, southern Sweden, and the coastal regions of Norway, covering 396.41×10^4 km^2 (Figure 5c), and stable ranges were identified in Ireland and the UK, covering 28.40×10^4 km^2 (Figure 5c). Range unfilling was mainly projected in the eastern part of the UK, covering 5.04×10^4 km^2 (Figure 5c). Additionally, the range ratio and range similarity index were 12.70 and 0.12, respectively. The range dynamics of grey squirrels under the M585 scenario were similar to those under the F585 scenario, covering 486.39×10^4, 33.29×10^4, and 0.15×10^4 km^2, respectively, and the range ratio and range similarity index were 15.54 and 0.12, respectively, (Figure 5d).

Under the F126 scenario, the red squirrel ranges expanded in a scattered pattern but were observed in Iceland, the UK, Norway, Sweden, Finland, Poland, the Czech Republic, Slovakia, Romania, Croatia, Latvia, Lithuania, and the northwest coast of Russia, covering 65.69×10^4 km^2 (Figure 5e), and range unfilling was also detected in a scattered pattern, and was mainly observed in Sweden, Finland, Estonia, Poland, the Czech Republic and Slovakia, and Spain, covering 30.86×10^4 km^2 (Figure 5e). The ranges were stable in most of western Europe, covering 231.50×10^4 km^2 (Figure 5e). Additionally, the range ratio and range similarity index were 1.13 and 0.83, respectively. Under the M126 scenario, the red squirrel ranges expanded in eastern Europe, Finland, Sweden, and western Russia, covering 70.86×10^4 km^2 (Figure 5f), and the pattern of the stable ranges was similar to those under the F126 scenario, covering 233.69×10^4 km^2 (Figure 5f). Range unfilling was primarily observed in Spain, Finland, and Estonia, covering 28.68×10^4 km^2 (Figure 5f). Additionally, the range ratio and range similarity index were 1.16 and 0.82, respectively. The red squirrel ranges expanded under the F585 scenario in Iceland, Latvia, Lithuania, Poland, Norway, Sweden, and northwest Russia, covering 242.54×10^4 km^2 (Figure 5g), and the ranges were stable in western Europe, covering 207.25×10^4 km^2 (Figure 5g). Range unfilling was detected in a scattered pattern and was mainly predicted in Portugal, Spain, southwest Finland, Sweden, East Germany, Romania, and Italy, covering 55.11×10^4 km^2 (Figure 5g). Additionally, the range ratio and range similarity index were 1.71 and 0.58, respectively. Under the M585 scenario, the expansion, stability, and unfilling of the red squirrel ranges were similar to those under the F585 scenario, covering 142.58×10^4, 185.57×10^4, and 76.80×10^4 km^2 (Figure 5h), respectively, with range ratio and range similarity index values of 1.25 and 0.63, respectively.

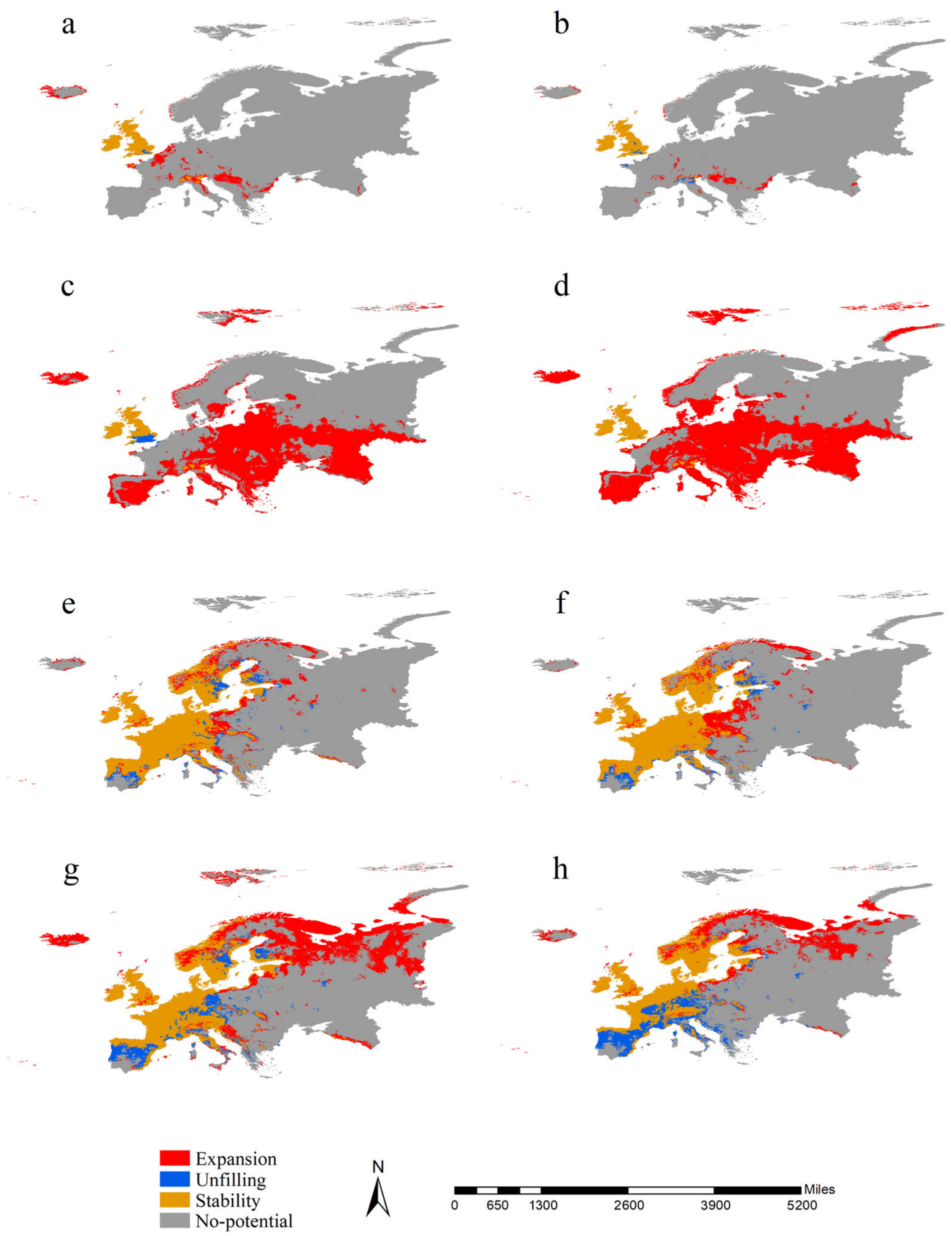

Figure 5. Range dynamics of grey squirrels under the future climate change scenarios. (**a**,**b**) indicate range dynamics of grey squirrels under the scenarios of SSP126 derived from two General Circulation Models (GCMs), i.e., FIO-ESM-2-0 and MPI-ESM1-2-HR, respectively. (**c**,**d**) indicate range dynamics of grey squirrels under the scenarios of SSP585 derived from two General Circulation Models (GCMs), i.e., FIO-ESM-2-0 and MPI-ESM1-2-HR, respectively. (**e**,**f**) indicate range dynamics of red squirrels under the scenarios of SSP126 derived from two General Circulation Models (GCMs), i.e., FIO-ESM-2-0 and MPI-ESM1-2-HR, respectively. (**g**,**h**) indicate range dynamics of red squirrels under the scenarios of SSP585 derived from two General Circulation Models (GCMs), i.e., FIO-ESM-2-0 and MPI-ESM1-2-HR, respectively. Red, orange, and blue indicated range expansion, range stability, and range unfilling, respectively.

3.5. Range Overlap between Grey Squirrel and Red Squirrel

The ranges of grey squirrels and red squirrels overlapped under the current conditions in Ireland and the UK, covering 30.40×10^4 km^2 (Figure 6a). Under the F126 scenario, the ranges of grey squirrels and red squirrels overlapped in Ireland, the UK, France, Belgium, the Netherlands, Germany, Italy, Croatia, and peripheral regions of Iceland, covering 48.90×10^4 km^2 (Figure 6b). Under the M126 scenario, the ranges of grey squirrels and red squirrels overlapped in Ireland, the UK, Italy, and Croatia, covering 35.64 $\times$ 10^4 km^2 (Figure 6c). Under the F585 scenario, the ranges of grey squirrels and red squirrels ranges overlapped in a scattered pattern in Iceland, Ireland, the UK, France, Spain, Norway, Sweden, Switzerland, Italy, Austria, Poland, Lithuania, Latvia, Estonia, Russia, and Slovenia, covering 128.86 $\times$ 10^4 km^2 (Figure 6d). The overlap between the ranges of grey squirrels and red squirrels under the M585 scenario was also scattered and was similar to that under the F585 scenario with a larger area, covering 141.88 $\times$ 10^4 km^2 (Figure 6e). In summary, compared with those between grey squirrels and red squirrels, overlapped ranges between them in the future showed larger range sizes, although considerable variation remained.

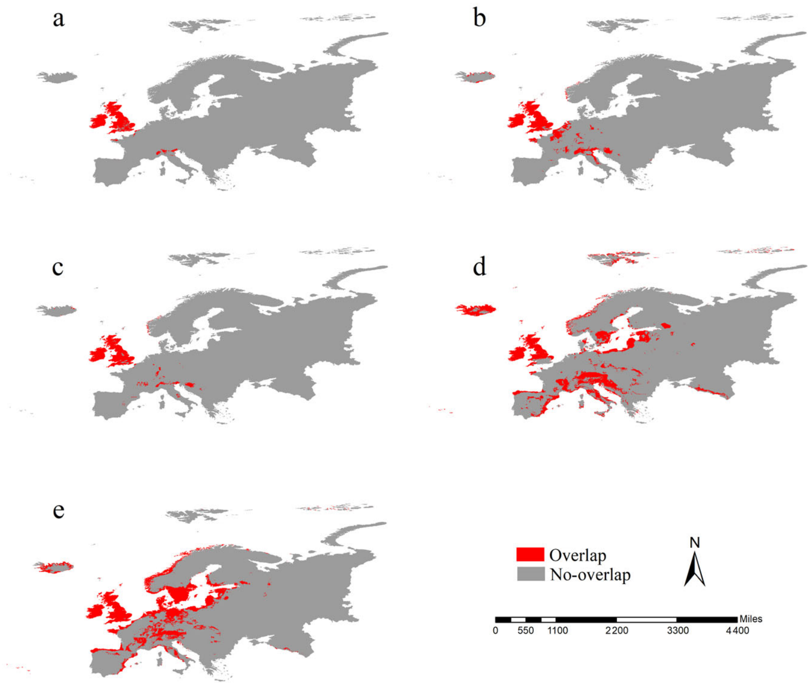

Figure 6. Range overlap between grey and red squirrels. (**a**) indicates range overlap between grey and red squirrels under the current conditions. (**b**,**c**) indicate range overlap under the scenarios of SSP126 derived from two General Circulation Models (GCMs), i.e., FIO-ESM-2-0 and MPI-ESM1-2-HR, respectively. (**d**,**e**) indicate range overlap under the scenarios of SSP585 derived from two General Circulation Models (GCMs), i.e., FIO-ESM-2-0 and MPI-ESM1-2-HR, respectively. Red and grey indicate the range overlap and no overlap, respectively.

Under the F126 scenario, the future range overlap of the grey squirrel and red squirrel, but in the current conditions (expanded range overlap), was observed in France, Switzerland, Austria, Germany, Italy, Belgium, and the Netherlands, covering 19.34 $\times$ 10^4 km^2 (Figure 7a). Under the M126 scenario, an expanded range overlap was observed in France, the UK, Italy, Croatia, Norway, and Germany, covering 7.47 $\times$ 10^4 km^2 (Figure 7b). Under the F585 scenario, the expanded range overlap was scattered in Iceland, Spain, Norway, Sweden, Switzerland, Italy, Austria, Poland, Lithuania, Latvia, Estonia, Russia, and Slovenia, covering 103.46 $\times$ 10^4 km^2 (Figure 7c). Under the M585 scenario, the expanded range overlap was also scattered, and the spatial patterns were similar to those under the F585 scenario with a larger area, covering 113.27 $\times$ 10^4 km^2 (Figure 7d).

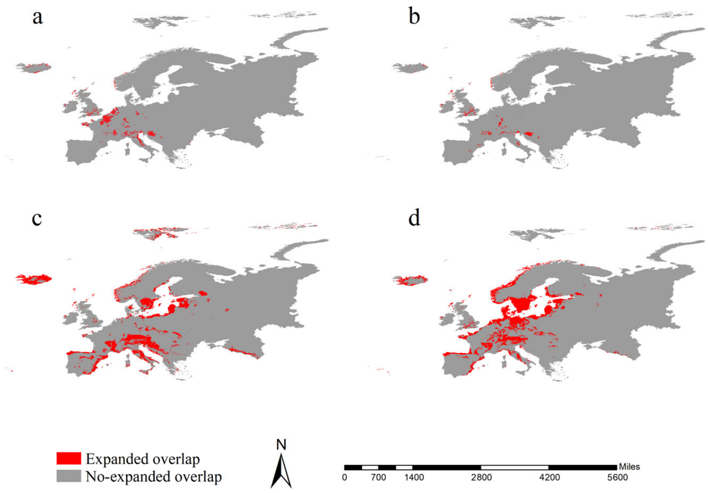

Figure 7. Expanded range overlap in future, but not current, conditions. (**a**–**d**) indicate the range overlap in future, but not in current, conditions under SSP126 derived from FIO-ESM-2-0, SSP126 derived from MPI-ESM1-2-HR, SSP585 derived from FIO-ESM-2-0, and SSP585 derived from MPI-ESM1-2-HR, respectively.

4. Discussion

Using two robust and complementary GCMs, we developed range dynamic models to estimate the shifts in the potential ranges of grey squirrels and red squirrels under future climate change scenarios, and we identified the regions to which grey squirrels may expand in the future. Additionally, we predicted the regions in which the ranges of the two species would overlap in the future. Therefore, from the perspective of climatic suitability, our study provides important information for developing strategies to counter the invasion of grey squirrels and conserve red squirrels in Europe under future climate change.

Our ecological niche models showed that the mean temperature of the coldest quarter was the most important value predicting the potential ranges of grey squirrels, and a positive relationship was detected between the mean temperature of the coldest quarter and the habitat suitability of grey squirrels. This finding suggests that changes in the mean temperature during the coldest quarter in the future may play an essential role in the range dynamics of grey squirrels and that the grey squirrel range may expand by the increase in the mean temperature of the coldest quarter, which is similar also for some other Sciuridae species. For example, Stapp et al. (1991) found that winter energy was closely associated with the distribution of southern flying squirrels (*Glaucomys volans*) [69]. In addition, Jokinen et al. (2019) reported that winter temperatures had relatively large predictive power for the distribution patterns of the Siberian flying squirrel (*Pteromys volans*) [70].

The most important predictor of the potential ranges of red squirrels was temperature seasonality, and a negative relationship was observed between temperature seasonality and red squirrel habitat suitability. This result suggests that changes in temperature seasonality in the future will largely determine the range dynamics of red squirrels and that the future expansion of the red squirrel ranges observed in our study may be induced by a decrease in temperature seasonality, consistent with Aidoo et al. (2022) and Johovic et al. (2020), who found that decreasing temperature seasonality is closely associated with the range expansion of their target AIS [71,72]. In summary, climate change may play an important role in the range dynamics of AIS, and climatic predictors responsible for the dynamics may vary among AIS [20].

Our results showed that the range of grey squirrels expanded under the F126 scenario in Iceland, the Netherlands, Germany, France, Italy, Croatia, Serbia, and Bulgaria, covering 32.41×10^4 km^2. Under the M126 scenario, expansion of the range of grey squirrels was observed in Germany, France, Croatia, Serbia, and Bulgaria, covering 14.16×10^4 km^2. Although the sizes of the expanded ranges under the SSP126 scenario varied considerably with the GCM, the Netherlands, France, Germany, Croatia, Serbia, and Bulgaria consistently remained parts of the expanded grey squirrel ranges. Therefore, if we could efficiently control future climate change, these two regions would be focal regions for controlling the invasion of grey squirrels in the future. Under the F585 and M585 scenarios, expansion of the grey squirrel ranges included vast regions (396.41×10^4 and 486.39×10^4 km^2, respectively), including Iceland, southwest Russia, eastern Europe, Austria, Italy, eastern France, Spain, Portugal, eastern Germany, southern Sweden, the Netherlands, Iceland, and the coastal regions of Norway, suggesting that we should efficiently control future climate change, or these vast regions will be invaded by grey squirrels in the future.

Under the current conditions and all of the climate change scenarios, Ireland and the UK were consistently in overlapping regions of the grey squirrel and red squirrel ranges in the future. Therefore, these two areas are the focal regions for controlling the grey squirrel threats against red squirrel conservation, and strict control management strategies are already ongoing in the UK and Ireland [43]. Additionally, under the SSP126 scenario, France, Italy, and Germany were in the overlap ranges of grey squirrels and red squirrels but not under the current conditions. This finding suggests that, under the most optimistic climate change scenario, grey squirrels may displace red squirrels in these three regions in the future. Therefore, these regions were the new regions where grey squirrels may displace red squirrels in the future. Under the SSP585 scenario, but not under the current conditions, range overlap was in scattered patterns in Iceland, France, Spain, Norway, Sweden, Switzerland, Italy, Austria, Poland, Lithuania, Latvia, Estonia, Russia, and Slovenia, suggesting that, under the most pessimistic climate change scenario, these regions are the new regions where grey squirrels may displace red squirrels in the future, and the cost of controlling the threats of grey squirrels against red squirrels would be huge. Our future strategy for controlling the invasion of grey squirrels and conserving red squirrels should be modified for these regions.

A variety of studies have projected the range of grey squirrels at the local or country scale using spatially explicit population dynamics models and the vegetation distribution or land cover [41,48–51], with climatic change receiving little attention, although vegetation distribution or land cover used in spatially explicit population dynamics models may be affected by climate changes [52–54]. As a result, the grey squirrel and red squirrel distribution patterns were closely associated with vegetation distribution or land cover [55,56]. Nevertheless, our study projected the range dynamics of grey squirrels and red squirrels from a climatic suitability perspective and their potential range overlap on the European scale. Therefore, our European scale study provides novel information on controlling grey squirrel and red squirrel conservation in the future.

Using similar methods (i.e., ecological niche models), Febbraro et al. (2016) predicted the future patterns of alien squirrels under climate change scenarios and invasion hotspots at the global scale [44]. However, they did not investigate grey squirrel range dynamics under climate change scenarios. In contrast, our study developed range dynamic models to explore the potential expansion of the ranges, the stability of the ranges, and range unfilling by grey squirrels, as well as the range overlap between red squirrels at the European scale, which from a climatic suitability perspective may provide information for efficiently controlling the invasion of grey squirrels and conserving red squirrels in Europe.

The grey squirrel range ratio from current conditions to the future ranged from 1.34 to 15.54, suggesting an increase in the potential ranges of grey squirrels, suggesting that climate change will promote the invasion of grey squirrels in Europe, although great uncertainty remains. Additionally, the similarity index values for the current conditions and the future ranges were 0.12 to 0.66, suggesting that grey squirrels under future climate change scenarios may occupy different range positions across space from those under the current conditions, although great uncertainty remains. Therefore, future strategies against grey squirrel invasions may need to be modified to meet the shifts in the range positions of grey squirrels in the future.

Grey squirrels are impacting trophic cascades of European forest ecosystems, especially those between herbivores and plants, suggesting huge impacts on the ecological equilibrium of European forest ecosystems [30]. We observed amplification of the grey squirrel range under future climate scenarios, i.e., larger potential ranges compared with those under the current conditions, as well as larger range overlap between grey squirrels and red squirrels, suggesting a greater threat against the red squirrel in the future. However, our observations varied considerably with the two different GCMs used, i.e., FIO-ESM-2-0 and MPI-ESM1-2-HR. For example, under the F126 and M126 scenarios, the expanded areas of the grey squirrel range were 32.41×10^4 km^2 and 14.16×10^4 km^2, respectively, and the range overlaps were 48.90×10^4 km^2 and 35.64×10^4 km^2, respectively. Additionally, our observations varied considerably with these two climate change scenarios. For example, under the SSP126 and SSP585 climate change scenarios, the range overlap areas derived from MPI-ESM1-2-HR were 35.64×10^4 km^2 and 141.88×10^4 km^2, respectively. In summary, although we have observed increases in the potential ranges of grey squirrels and red squirrels and their overlap from current conditions to the future, the observations may vary considerably with the GCM and the climate change scenario.

5. Conclusions

The present study detected expansions in the grey squirrel and red squirrel ranges under both the most optimistic and pessimistic climate change scenario in the future. Despite the considerable variation, overlapped ranges between grey squirrels and red squirrels in the future showed larger sizes than those under current conditions. Therefore, the range dynamics of grey squirrels and red squirrels and their overlap suggest increasing threats of grey squirrels against red squirrels in Europe, which may result in the accelerating decline of red squirrel populations in Europe and impact the biodiversity and ecological equilibrium of European forest ecosystems, although great uncertainty remains, and further investigations are needed.

Supplementary Materials: The data (Online dataset 1) that support the findings of this study are available at https://doi.org/10.6084/m9.figshare.23180948 (accessed on 25 May 2023). The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14061150/s1, Table S1: Importance value of each predictor in the preliminary ecological niche models. Table S2: Correlations among the 19 climatic predictors. Table S3: The retained predictors in the final ecological niche models.

Author Contributions: Conceptualization, J.F.; methodology, J.F. and P.N.; software, P.N. and R.Y.; validation, P.N. and R.Y.; formal analysis, P.N.; investigation, P.N. and R.Y.; resources, P.N.; data curation, P.N.; writing—original draft preparation, P.N. and J.F.; writing—review and editing, P.N., J.F., and R.Y.; visualization, P.N. and R.Y.; supervision, J.F.; project administration, J.F.; funding acquisition, J.F. All authors have read and agreed to the published version of the manuscript.

Funding: This study was funded by the National Science Foundation of China (Grant ID: 31560178).

Data Availability Statement: Not applicable.

Acknowledgments: We are grateful to Youjun Chen and Junjie Wu for their valuable comments on this study. We would also like to thank the anonymous reviewers' valuable comments.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Vila, M.; Basnou, C.; Pyšek, P.; Josefsson, M.; Genovesi, P.; Gollasch, S.; Hulme, P.E. How well do we understand the impacts of alien species on ecosystem services? A pan–European, cross–taxa assessment. *Front. Ecol. Environ.* **2010**, *8*, 135–144. [CrossRef]
2. Vila, M.; Hulme, P.E. *Impact of Biological Invasions on Ecosystem Services. Invading Nature–Springer Series in Invasion Ecology*, 1st ed.; Springer: Cham, Switzerland, 2017.
3. Early, R.; Bradley, B.A.; Dukes, J.S.; Lawler, J.J.; Olden, J.D.; Blumenthal, D.M.; Gonzalez, P.; Grosholz, E.D.; Ibañez, I.; Miller, L.P.; et al. Global threats from invasive alien species in the twenty first century and national response capacities. *Nat. Commun.* **2016**, *7*, 12485. [CrossRef]

4. Diagne, C.; Leroy, B.; Vaissiere, A.C.; Gozlan, R.E.; Roize, D.; Jarić, I.; Salles, J.M.; Bradshaw, C.J.A.; Courchamp, F. High and rising economic costs of biological invasions worldwide. *Nature* **2021**, *592*, 571–576. [CrossRef] [PubMed]
5. Barney, J.N.; Tekiela, D.R.; Barrios-Garcia, M.N.; Dimarco, R.D.; Hufbauer, R.A.; Leipzig-Scott, P.; Nuñez, M.A.; Pauchard, A.; Pyšek, P.; Vítková, M.; et al. Global Invader Impact Network (GIIN): Toward standardized evaluation of the ecological impacts of invasive plants. *Ecol. Evol.* **2015**, *5*, 2878–2889. [CrossRef] [PubMed]
6. Blackburn, T.M.; Bellard, C.; Ricciardi, A. Alien versus native species as drivers of recent extinctions. *Front. Ecol. Environ.* **2019**, *17*, 203–207. [CrossRef]
7. Van Kleunen, M.; Dawson, W.; Maurel, N. Characteristics of successful alien plants. *Mol. Ecol.* **2015**, *24*, 1954–1968. [CrossRef]
8. Bellard, C.; Thuiller, W.; Leroy, B.; Genovesi, P.; Bakkenes, M.; Courchamp, F. Will climate change promote future invasions? *Glob. Chang. Biol.* **2013**, *19*, 3740–3748. [CrossRef]
9. Bellard, C.; Jeschke, J.M.; Leroy, B.; Mace, G.M. Insights from modelling studies on how climate change affects invasive alien species geography. *Ecol. Evol.* **2018**, *8*, 5688–5700. [CrossRef]
10. Jia, J.; Dai, Z.; Li, F.; Liu, Y. How will global environmental changes affect the growth of alien plants? *Front. Plant Sci.* **2016**, *7*, 1623. [CrossRef]
11. Hulme, P.E. Climate change and biological invasions: Evidence, expectations, and response options. *Biol. Rev.* **2017**, *92*, 1297–1313. [CrossRef]
12. Hernández-Lambraño, R.E.; González-Moreno, P.; Sánchez-Agudo, J.Á. Towards the top: Niche expansion of Taraxacum officinale and *Ulex europaeus* in mountain regions of South America. *Austral Ecol.* **2017**, *42*, 577–589. [CrossRef]
13. Christina, M.; Limbada, F.; Atlan, A. Climatic niche shift of an invasive shrub (*Ulex europaeus*): A global scale comparison in native and introduced regions. *J. Plant Ecol.* **2019**, *13*, 42–50. [CrossRef]
14. Sutherland, W.J.; Armstrong-Brown, S.; Armsworth, P.R.; Tom, B.; Brickland, J.; Campbell, C.D.; Chamberlain, D.E.; Cooke, A.I.; Dulvy, N.K.; Dusic, N.R.; et al. The identification of 100 ecological questions of high policy relevance in the UK. *J. Appl. Ecol.* **2006**, *43*, 617–627. [CrossRef]
15. Chapman, D.S.; Haynes, T.; Beal, S.; Essl, F.; Bullock, J.M. Phenology predicts the native and invasive range limits of common ragweed. *Glob. Chang. Biol.* **2014**, *20*, 192–202. [CrossRef] [PubMed]
16. Wagner, N.K.; Ochocki, B.M.; Crawford, K.M.; Compagnoni, A.; Miller, T.E.X. Genetic mixture of multiple source populations accelerates invasive range expansion. *J. Anim. Ecol.* **2017**, *86*, 21–34. [CrossRef] [PubMed]
17. Liu, T.M.; Wang, J.M.; Hu, X.K.; Feng, J.M. Land–use change drives present and future distributions of Fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae). *Sci. Total Environ.* **2020**, *706*, 135872. [CrossRef]
18. Tang, X.G.; Yuan, Y.D.; Liu, X.F.; Zhang, J.C. Potential range expansion and niche shift of the invasive *Hyphantria cunea* between native and invasive countries. *Ecol. Entomol.* **2021**, *46*, 910–925. [CrossRef]
19. Thomas, S.M.; Moloney, K.A. Combining the effects of surrounding land–use and propagule pressure to predict the distribution of an invasive plant. *Biol. Invasions* **2015**, *17*, 477–495. [CrossRef]
20. Gong, X.; Chen, Y.J.; Wang, T.; Jiang, X.F.; Hu, X.K.; Feng, J.M. Double–edged effects of climate change on plant invasions: Ecological niche modeling global distributions of two invasive alien plants. *Sci. Total Environ.* **2020**, *740*, 139933. [CrossRef]
21. Cao, R.Y.; Gong, X.; Feng, J.M.; Yang, R.J. Niche and range dynamics of Tasmanian blue gum (*Eucalyptus globulus* Labill.) a globally cultivated invasive tree. *Ecol. Evol.* **2022**, *12*, e9305. [CrossRef]
22. Colautti, R.I.; Barrett, S.C.H. Rapid Adaptation to Climate Facilitates Range Expansion of an Invasive Plant. *Science* **2013**, *342*, 364–366. [CrossRef]
23. Jourdan, J.; Riesch, R.; Cunze, S. Off to new shores: Climate niche expansion in invasive mosquitofish (*Gambusia* spp.). *Ecol. Evol.* **2021**, *11*, 18369–18400. [CrossRef] [PubMed]
24. Osland, M.J.; Feher, L.C. Winter climate change and the poleward range expansion of a tropical invasive tree (Brazilian pepper–*Schinus terebinthifolius*). *Glob. Chang. Biol.* **2020**, *26*, 607–615. [CrossRef] [PubMed]
25. de Albuquerque, F.S.; Macias-Rodriguez, M.A.; Burquez, A.; Astudillo-Scalia, Y. Climate change and the potential expansion of buffelgrass (*Cenchrus ciliaris* L., Poaceae) in biotic communities of Southwest United States and northern Mexico. *Biol. Invasions* **2019**, *21*, 3335–3347. [CrossRef]
26. Kelly, B.P.; Whiteley, A.; Tallmon, D. The arctic melting pot. *Nature* **2010**, *468*, 891. [CrossRef]
27. Schmidt, N.M.; Hardwick, B.; Gilg, O.; Høye, T.T.; Krogh, P.H.; Meltofte, H.; Michelsen, A.; Mosbacher, J.B.; Raundrup, K.; Reneerkens, J.; et al. Interaction webs in arctic ecosystems: Determinants of arctic change? *Ambio* **2017**, *46*, 12–25. [CrossRef]
28. Bryce, S.J.; Johnson, P.J.; Macdonald, D.W. Can niche use in red and grey squirrels offer clues for their apparent coexistence? *J. Appl. Ecol.* **2002**, *39*, 875–887. [CrossRef]
29. Elsen, M.P.R.; Monahan, W.B.; Dougherty, E.R.; Merenlender, A.M. Keeping pace with climate change in global terrestrial protected areas. *Sci. Adv.* **2020**, *6*, e0814. [CrossRef]
30. Bamber, J.A.; Shuttleworth, C.M.; Hayward, M.W.; Everest, D.J. Reinstating trophic cascades as an applied conservation tool to protect forest ecosystems from invasive grey squirrels (*Sciurus carolinensis*). *Food Webs* **2020**, *25*, 00164. [CrossRef]
31. Middleton, A.D. The grey squirrel: The introduction and spread of the American grey squirrel in the British Isles, its habits, food, and relations with the native fauna of the country. *Nature* **1933**, *131*, 45. [CrossRef]
32. Wauters, L.A.; Gurnell, J.; Martinoli, A.; Tosi, G. Interspecific competition between native Eurasian red squirrels and alien grey squirrels: Does resource partitioning occur? *Behav. Ecol. Sociobiol.* **2002**, *52*, 332–341. [CrossRef]

33. Wauters, L.A.; Mazzamuto, M.V.; Santicchia, F.; Van, D.; Preatoni, D.G.; Martinoli, A. Interspecific competition affects the expression of personality–traits in natural populations. *Sci. Rep.* **2019**, *9*, 11189. [CrossRef] [PubMed]
34. Johnston, A.N.; Vander Haegen, W.M.; West, S.D. Differential Resource Use between Native and Introduced Gray Squirrels. *J. Wildl. Manag.* **2020**, *84*, 726–738. [CrossRef]
35. Santicchia, F.; Wauters, L.A.; Piscitelli, A.P.; Dongen, S.V.; Martinoli, A.; Preatoni, D.; Romeo, C.; Ferrari, N. Spillover of an alien parasite reduces expression of costly behaviour in native host species. *J. Anim. Ecol.* **2020**, *89*, 1559–1569. [CrossRef]
36. Romeo, C.; Piscitelli, A.P.; Santicchia, F.; Martinoli, A.; Ferrari, N.; Wauters, L.A. Invading parasites: Spillover of an alien nematode reduces survival in a native species. *Biol. Invasions* **2021**, *23*, 3847–3857. [CrossRef]
37. White, A.; Bell, S.S.; Lurz, P.W.W.; Boots, M. Conservation management within strongholds in the face of disease–mediated invasions: Red and grey squirrels as a case study. *J. Appl. Ecol.* **2014**, *51*, 1631–1642. [CrossRef]
38. Chantrey, J.; Dale, T.; Jones, D.; Begon, M.; Fenton, A. The drivers of squirrelpox virus dynamics in its grey squirrel reservoir host. *Epidemics* **2019**, *28*, 100352. [CrossRef] [PubMed]
39. Shuttleworth, C.M.; Robinson, N.; Halliwell, E.C.; Clews-Roberts, R.; Peek, H.; Podgornik, G.; Stinson, M.; Rice, S.; Finlay, C.; McKinney, C.; et al. Evolving grey squirrel management techniques in Europe. *Manag. Biol. Invasions* **2020**, *11*, 747–761. [CrossRef]
40. Schuchert, P.; Shuttleworth, C.M.; McInnes, C.J.; Everest, D.J.; Rushton, S.P. Landscape scale impacts of culling upon a European grey squirrel population: Can trapping reduce population size and decrease the threat of squirrelpox virus infection for the native red squirrel? *Biol. Invasions* **2014**, *16*, 2381–2391. [CrossRef]
41. Goldstein, E.A.; Butler, F.; Lawton, C. Modeling future range expansion and management strategies for an invasive squirrel species. *Biol. Invasions* **2016**, *18*, 1431–1450. [CrossRef]
42. Jessen, T.; Wang, Y.; Wilmers, C.C. Habitat fragmentation provides a competitive advantage to an invasive tree squirrel, *Sciurus carolinensis*. *Biol. Invasions* **2018**, *20*, 607–618. [CrossRef]
43. Wauters, L.A.; Lurz, P.W.W.; Santicchia, F.; Romeo, C.; Ferrari, N.; Martinoli, A.; Gurnell, J. Interactions between native and invasive species: A systematic review of the red squirrel-gray squirrel paradigm. *Front. Ecol. Evol.* **2023**, *11*, 1083008. [CrossRef]
44. Di Febbraro, M.; Martinoli, A.; Russo, D.; Preatoni, D.; Bertolino, S. Modelling the effects of climate change on the risk of invasion by alien squirrels. *Hystrix* **2016**, *27*, 1–8. [CrossRef]
45. Di Febbraro, M.; Menchetti, M.; Russo, D.; Ancillotto, L.; Aloise, G.; Roscioni, F.; Preatoni, D.G.; Loy, A.; Martinoli, A.; Bertolino, S.; et al. Integrating climate and land–use change scenarios in modelling the future spread of invasive squirrels in Italy. *Divers. Distrib.* **2019**, *25*, 644–659. [CrossRef]
46. Gurnell, J.; Clark, M.J.; Lurz, P.W.W.; Shirley, M.D.F.; Rushton, S.P. Conserving red squirrels (*Sciurus vulgaris*): Mapping and forecasting habitat suitability using a Geographic Information Systems Approach. *Biol. Conserv.* **2002**, *105*, 53–64. [CrossRef]
47. Rushton, S.P.; Lurz, P.W.W.; Fuller, R.; Garson, P.J. Modelling the distribution of the red and grey squirrel at the landscape scale: A combined GIS and population dynamics approach. *J. Appl. Ecol.* **1997**, *34*, 1137–1154. [CrossRef]
48. Rushton, S.P.; Lurz, P.W.W.; South, A.B.; Mitchell-Jones, A. Modelling the distribution of red squirrels (*Sciurus vulgaris*) on the Isle of Wight. *Anim. Conserv.* **1999**, *2*, 111–120. [CrossRef]
49. Lurz, P.W.W.; Rushton, S.P.; Wauters, L.A.; Bertolino, S.; Currado, I.; Mazzoglio, P.; Shirley, M.D.F. Predicting grey squirrel expansion in North Italy: A spatially explicit modelling approach. *Landsc. Ecol.* **2001**, *16*, 407–420. [CrossRef]
50. Tattoni, C.; Preatoni, D.G.; Lurz, P.W.W.; Rushton, S.P.; Tosi, G.; Bertolino, S.; Martinoli, A.; Wauters, L.A. Modelling the expansion of a grey squirrel population: Implications for squirrel control. *Biol. Invasions* **2006**, *8*, 1605–1619. [CrossRef]
51. Bertolino, S.; Lurz, P.W.W.; Sanderson, R.; Rushton, S. Predicting the spread of the American grey squirrel (*Sciurus carolinensis*) in Europe: A call for a co–ordinated European approach. *Biol. Conserv.* **2008**, *141*, 2564–2575. [CrossRef]
52. Anav, A.; Mariotti, A. Sensitivity of natural vegetation to climate change in the Euro–Mediterranean area. *Clim. Res.* **2011**, *46*, 277–292. [CrossRef]
53. Garamvoelgyi, A.; Hufnagel, L. Impacts of climate change on vegetation distribution No. 1 climate change induced vegetation shifts in the palearctic region. *Appl. Ecol. Environ. Res.* **2013**, *11*, 79–122. [CrossRef]
54. Ward, D.S.; Mahowald, N.M.; Kloster, S. Potential climate forcing of land use and land cover change. *Atmos. Chem. Phys.* **2014**, *14*, 12701–12724. [CrossRef]
55. Gurnell, J. *The Natural History of Squirrels*, 1st ed.; Christopher Helm Publishers: Bromley, UK, 1987.
56. Wauters, L.A.; Gurnell, J.; Currado, I.; Mazzoglio, P. Grey squirrel *Sciurus carolinensis* management in Italy–squirrel distribution in a highly fragmented landscape. *Wildl. Biol.* **1997**, *3*, 117–124. [CrossRef]
57. Brown, J.L. SDMtoolbox: A python–based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods Ecol. Evol.* **2014**, *5*, 694–700. [CrossRef]
58. Brown, J.L.; Bennett, J.R.; French, C.M. SDMtoolbox 2.0: The next generation Python–based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ* **2017**, *5*, e4095. [CrossRef]
59. Fick, S.E.; Hijmans, R.J. WorldClim2: New 1km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **2017**, *37*, 4302–4315. [CrossRef]
60. Zhang, M.Z.; Xu, Z.F.; Han, Y.; Guo, W.D. Evaluation of CMIP6 models toward dynamical downscaling over 14 CORDEX domains. *Clim. Dyn.* **2022**, *2022*, 1–15. [CrossRef]
61. Myers, P.; Lundrigan, B.L.; Hoffman, S.M.G.; Haraminac, A.P.; Seto, S.H. Climate-induced changes in the small mammal communities of the Northern Great Lakes Region. *Glob. Chang. Biol.* **2009**, *15*, 1434–1454. [CrossRef]

62. Thuiller, W.; Lafourcade, B.; Engler, R.; Araújo, M.B. BIOMOD–A platform for ensemble forecasting of species distributions. *Ecography* **2009**, *32*, 369–373. [CrossRef]
63. Dormann, C.F.; Elith, J.; Bacher, S.; Buchmann, C.; Carl, G.; Carré, G.; García Marquéz, J.R.; Gruber, B.; Lafourcade, B.; Leitão, P.J.; et al. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **2013**, *36*, 7–46. [CrossRef]
64. Barbet-Massin, M.; Jiguet, F.; Albert, C.H.; Thuiller, W. Selecting pseudo–absences for species distribution models: How, where and how many? *Methods Ecol. Evol.* **2012**, *3*, 27–338. [CrossRef]
65. Gallien, L.; Douzet, R.; Pratte, S.; Zimmermann, N.E.; Thuiller, W. Invasive species distribution models–how violating the equilibrium assumption can create new insights. *Glob. Ecol. Biogeogr.* **2012**, *21*, 1126–1136. [CrossRef]
66. Cantor, S.B.; Sun, C.C.; Tortolero-Lunaet, G.; Richards-Kortum, R.; Follen, M. A comparison of C/B ratios from studies using receiver operating characteristic curve analysis. *J. Clin. Epidemiol.* **1999**, *52*, 885–892. [CrossRef]
67. Liu, C.R.; Berry, P.M.; Dawson, T.P.; Pearson, R.G. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **2005**, *28*, 385–393. [CrossRef]
68. Yang, R.J.; Cao, R.Y.; Gong, X.; Feng, J.M. Large shifts of niche and range in the golden apple snail (*Pomacea canaliculata*), an aquatic invasive species. *Ecosphere* **2023**, *14*, e4391. [CrossRef]
69. Stapp, P.; Pekins, P.J.; Mautz, W.W. Winter Energy-Expenditure and The Distribution Of Southern Flying Squirrels. *Can. J. Zool.* **1991**, *69*, 2548–2555. [CrossRef]
70. Jokinen, M.; Hanski, I.; Numminen, E.; Valkama, J.; Selonen, V. Promoting species protection with predictive modelling: Effects of habitat, predators and climate on the occurrence of the Siberian flying squirrel. *Biol. Conserv.* **2019**, *230*, 37–46. [CrossRef]
71. Aidoo, O.F.; Souza, P.G.C.; da Silva, R.S.; Santana, P.A.; Picanco, M.C.; Kyerematen, R.; Setamou, M.; Ekesi, S.; Borgemeister, C. Climate-induced range shifts of invasive species (*Diaphorina citri* Kuwayama). *Pest Manag. Sci.* **2022**, *78*, 2534–2549. [CrossRef]
72. Johovic, I.; Gama, M.; Banha, F.; Tricarico, E.; Anastacio, P.M. A potential threat to amphibians in the European Natura 2000 network: Forecasting the distribution of the American bullfrog *Lithobates catesbeianus*. *Biol. Conserv.* **2020**, *245*, 108551. [CrossRef]