



Increasing Arctic Tundra Flooding Threatens Wildlife Habitat and Survival: Impacts on the Critically Endangered Siberian Crane (*Grus leucogeranus*)

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Specialty section:

This article was submitted to
Global Biodiversity Threats,
a section of the journal
Frontiers in Conservation Science

Received: 22 October 2021

Accepted: 23 February 2022

Published: 14 April 2022

Citation:

Haverkamp PJ, Bysykatova-Harmey I,
Germogenov N and
Schaepman-Strub G (2022)
Increasing Arctic Tundra Flooding
Threatens Wildlife Habitat and
Survival: Impacts on the Critically
Endangered Siberian Crane (*Grus
leucogeranus*).
Front. Conserv. Sci. 3:799998.
doi: 10.3389/fcosc.2022.799998

Climate change is causing Arctic temperatures to increase at least twice as fast as the planet on average. Temperature and precipitation are predicted to continue increasing, such that flooding might become more prevalent in the new Arctic. Increased flooding frequency and extreme flooding events may pose new threats to Arctic biodiversity through habitat disturbance and decreased survival. We used the Siberian crane (*Grus leucogeranus*) as a model organism to investigate how flooding influences nesting habitat availability and juvenile counts. When spring flooding destroys eggs, adults either do not raise any chicks or have reduced time to prepare them for their long migration to China, thus years with extensive flooding could negatively impact future crane generations. We used nest site observation data from 14 surveys between 1995 and 2019, habitat mapping based on Landsat 8 imagery, and species distribution modeling to predict Siberian crane potential nesting habitat. Nesting habitat loss due to extreme flooding was calculated by overlaying this potential nesting habitat with Global Surface Water data. The percent of potential flooded nest sites varied between 6.7–55% across years, with a significant increase between 2001 and 2018. Extreme flood events, as experienced in 2017 and 2018, eliminated almost half of the potential nesting habitat. Importantly, we found that the percentage of flooded nest sites across years was negatively correlated with the number of observed juveniles. The Arctic lowlands are exposed to seasonal water level fluctuations that species have evolved with and adapted to. Siberian cranes and other species depending on Arctic ecosystems are expected to continue adapting to changing flood conditions, but extreme flood events further threaten the long-term survival of critically endangered species. It is imperative to assess how ecosystems and species respond to climatic extremes to support Arctic conservation strategies.

Keywords: extreme flooding, Siberian crane, Arctic, habitat suitability, flooding impact, conservation

INTRODUCTION

Around the world, extreme weather events such as storms, droughts, fires, and floods are increasing in frequency, a trend that has been attributed to climate change (Easterling et al., 2000; Cai et al., 2014). The Arctic is at heightened risk for such changes as air temperature in this region is increasing at least twice as fast as the rest of the planet on average, rising by 0.75°C in the past decade alone (Post et al., 2019). We are only recently beginning to monitor and understand how climate change in the Arctic is impacting species and biodiversity through shifting seasonality (Pastick et al., 2019; Mallory et al., 2020), changes in sea ice cover (Hunter et al., 2010; Peeters et al., 2020), and shifting plant and animal ranges to higher latitudes and associated displacement of endemic species (Sturm et al., 2001; Killengreen et al., 2007; Ksenofontov et al., 2019; Berner et al., 2020; Aronsson et al., 2021; Kubelka et al., 2022). However, it remains unexplored how changes in flooding will affect Arctic species.

Short- and long-term changes to flood regimes can impact wildlife population dynamics through habitat loss (Perotto-Baldivieso et al., 2011), changes in body condition (Jones et al., 2019), and breeding success (Van De Pol et al., 2010). As species adapt to an increasing frequency and extent of floods, many will rely on changing behavior, distribution, and habitat selection (Korosi et al., 2017; Bailey et al., 2019). However, phenotypic plasticity, for example in the timing or behavior of migration or breeding, can affect fitness (Przybylo et al., 2000; Réale et al., 2003; Charmantier et al., 2008). Further, changes in distribution can complicate survival if individuals expose themselves to novel conditions, including greater predation pressure (Ma et al., 2019).

Spring flooding in the Arctic coastal plains occurs mostly due to rapid snowmelt hundreds of kilometers away in combination with continuous permafrost, which is a poor buffer for hydrological variation (Kane et al., 2008). Greater snowfall in the Arctic is already leading to increased flooding (Woo, 2012) and a greater snow water equivalent is predicted by 2050 (Callaghan et al., 2011). With increasing temperatures, warm spells and rain-on-snow events, and an increasingly rain-dominated precipitation regime, increased flooding (Rennert et al., 2009; Bintanja and Andry, 2017; McCrystall et al., 2021), as well as extreme events such as 100 year floods (Hirabayashi et al., 2008, 2013; Shevnina et al., 2017) are expected. Recent changes in Siberian Arctic weather regimes suggest this area will face some of the largest impacts of ecosystem disturbance in the world (Tei et al., 2020).

Spring flooding is a normal occurrence in some areas of the Arctic that species here have evolved with. Meltwater causes flooding of the interconnected channel systems and wetlands between lakes every spring, with flooding intensity depending on snow abundance, thawing intensity, and distance to nearest water body (Germogenov et al., 2013). Ground-nesting birds, such as the Siberian crane (*Grus leucogeranus* Pallas, 1773) whose nests are located in wetlands along lake shores, are susceptible to egg destruction, while chicks are able to swim and thus avoid drowning (Germogenov et al., 2013). Siberian cranes have

adapted to flooding by building nests up to 15 cm above the water surface (Meine and Archibald, 1996) to allow for rising waters as snow melts, but this might not be enough with increasing flood height. The majority of the critically endangered Siberian crane population breeds in eastern Yakutia, Siberia, every summer before migrating about 5,000 km to lakes in eastern China (mostly Poyang Lake) for the winter (Harris et al., 1995). Siberian cranes typically arrive in Siberia in mid- to late-May, while snow is still on the ground and lakes are frozen, and remain until mid- to late-September, when snow begins to fall after the summer (Perfiliev, 1965; Johnsgard, 1983; Potapov and Flint, 1987). Pairs, and even individuals whose mates have died, are highly territorial and return to the same area each year, either using old nests, or building new ones (Germogenov et al., 2013). During late springs, snow melt and flooding occur during ideal nesting periods, when preferred nesting habitat and previous nest sites may already be flooded. In this case, cranes will build nests in higher locations within the microtopography of the wetlands (Flint and Sorokin, 1981; Johnsgard, 1983; Harris et al., 1995). Similarly, if nests are already built when flooding occurs, cranes will rebuild nests in other areas (Germogenov et al., 2013). Chicks are born in late-May to early-June but only have about 4 months to grow and gain enough strength for the long migration. If floods occur and new eggs are laid, chicks are born late and may not have enough time to mature for the migration, impacting reproduction success and hence population size of this already critically endangered species.

The aim of this study was to identify yearly flooding occurrence around previously identified Siberian crane nesting sites and examine flooding correlation with existing juvenile survival data in China. We also assess how extreme flooding decreases nesting habitat availability in their breeding grounds in the subarctic tundra in northeastern Yakutia, Siberia. The Siberian crane is used as a model organism for studying effects of changing environmental conditions and extreme flooding events on species that critically rely on Arctic ecosystems for their survival and reproduction.

MATERIALS AND METHODS

We use locations of observed Siberian crane nests and Global Surface Water (GSW) extent data (Pekel et al., 2016) to understand how yearly surface water is impacting nesting sites. We then used Siberian crane nest site locations, in combination with environmental variables and a maximum entropy (MaxEnt) species distribution model (Phillips and Dudík, 2008) to predict potential nesting habitat within the extent of their known breeding range in Siberia. Autumn juvenile counts at a migration stopover in China are then correlated to flooded nest sites to identify possible impacts on the population. Extreme flooding events are predicted to become more common, so we use the GSW maximum extent of surface water to represent an extreme flood event and examine how this would affect observed nest site locations and reduce potential nesting habitat. All statistics were run in R (R Core Team, 2021) using RStudio (RStudio Team, 2022) unless noted otherwise.

Study Species and Area

Siberian cranes are critically endangered with only 3,500–4,000 individuals remaining in the wild (Birdlife International, 2018). While their biggest threat is reported to be decreasing wintering grounds due to habitat flooding from the Three Gorges Dam and damming of the outlet of Poyang Lake in China (Jiang et al., 2014; Birdlife International, 2018), increasing flooding due to climate change could reduce the availability of suitable summer nesting grounds, and reduce nesting success and juvenile survival. Aerial surveys from the 1960s to 1980s identified three core sites in northern Siberia with high densities of nesting Siberian cranes: the westernmost population around the Khroma River; the central, and most dense population around the Indigirka River; and the eastern population around the Alazeya River (Figure 1; Degtyarev and Labutin, 1991). Optimal habitat includes wetlands along lakes and depressions between lakes, with cranes spending most time adjacent to large and medium lakes (Germogenov et al., 2013). This study applies to the area containing the majority of the breeding grounds in the open tundra wetlands in Yakutia (128,718 km²) as identified in previous studies (Figure 1). Within the study area, the Kytalyk Nature Reserve, containing the Indigirka breeding core area, was established in 1995 to protect Siberian cranes nesting grounds, and was elevated to Russian federal protection in 2019.

Observations of Nesting Sites and Juvenile Counts

Ornithologists have been researching rare and endangered birds in this area since the early 1990s, focusing on identifying the territorial distribution of Siberian cranes, searching for new and previously identified pairs, and mapping their nesting sites (Germogenov et al., 2013). 14 surveys were conducted in the Indigirka breeding range in northeastern Yakutia, Russia, between 1995 and 2019, with 37 Siberian crane nests identified in this time. Point surveys and transect surveys were done by boat, foot, and swamp-vehicle in the Yana and Indigirka interfluvium. Point surveys were performed from high hill peaks and from high river banks using 12–20x binoculars and a 60x telescope. Locations of nests and birds were recorded in the field, and nesting reliability was established in accordance with the criteria recommended by the European Ornithological Atlas Committee - EOAC (Hagemeijer and Blair, 1997). Nesting was considered confirmed after visiting nest sites and seeing nests, eggs, broods, or adults bringing food to chicks, and GPS coordinates of nest sites were taken. Nests were found at a range of elevations, 8–18 m [based on overlays of the Arctic DEM (Porter et al., 2018)], while the main habitats are located between 14–19 m above the Eastern Siberian Sea level (based on overlays of location data on topographic maps), as areas below 10 m are frequently flooded in the spring (Germogenov et al., 2013). We used these nest locations provided from stock materials of the Institute for Biological Problems of the Cryolithozone, Siberian Branch of Russian Academy of Sciences, Yakutsk.

Siberian crane juveniles were counted at the Momoge Nature Reserve, China, from 2007 to 2012 (Bysykatova, 2012; Hongxing, 2013), and 2017–2018 (Bysykatova, unpublished data). Momoge

Nature Reserve, in northeastern China (Jilin Province), is an important spring and autumn migration stop for Siberian cranes, where researchers are able to observe adults and juveniles (Bysykatova, 2012; Germogenov et al., 2013). We used autumn juvenile counts at Momoge Nature Reserve as a proxy for the reproductive success of the previous breeding season. This is only one possible spot for Siberian cranes to rest during migration and hence these numbers do not cover the entire Siberian crane population. However, the majority of the eastern population (up to 3,750 individuals) has been observed here, and it represents one of the highest concentrations of resting Siberian cranes in autumn (Bysykatova, 2012). Juveniles fly with the adults, and counts at this stopover can indicate population trends as this is a more compact area to count birds than Poyang Lake feeding grounds.

Environmental Variables of Nesting Habitat

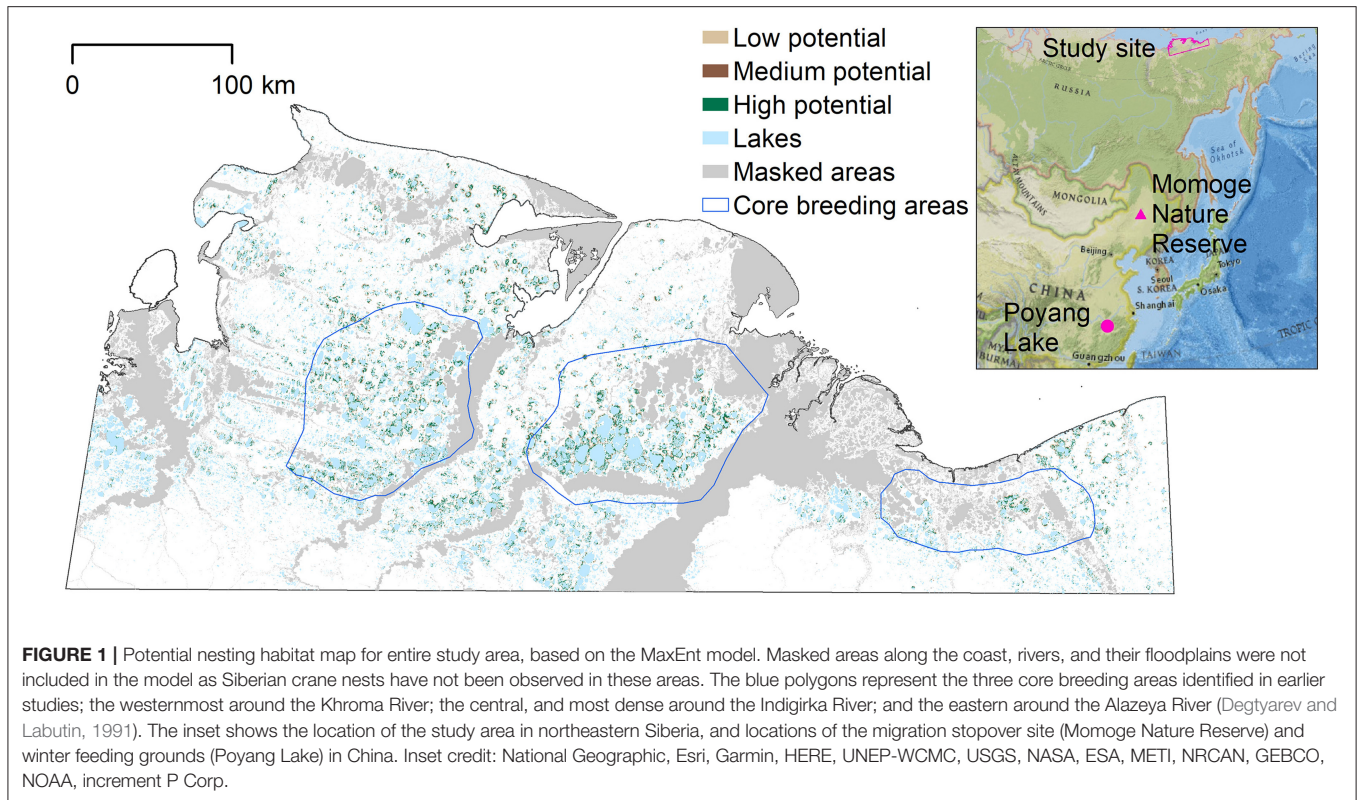
We identified three environmental variables to predict nesting habitat based on multiannual observational expertise of nesting locations of Siberian cranes in this area in combination with a review of the literature. The three identified environmental variables were landcover type, maximum topographical slope within 150 m, and distance to lakes. All variables were based on satellite data accessed and processed in Google Earth Engine (GEE; Gorelick et al., 2017) except where noted. Raster layers were exported from GEE to TIFF format at 30 m pixel resolution in the North Pole Lambert Azimuthal Equal Area projection to eliminate latitudinal land area bias.

Landcover Type

Siberian cranes prefer to nest in damp tidal flats around lakes with polygonal swamp vegetation dominated by the sedge species *Carex aquatilis* ssp. stans (Drejer) Hulténare, and occasionally by cottongrass *Eriophorum angustifolium* Honck., forming short, sparse stands (Johnsgard, 1983). A landcover map was developed based on spectral characteristics of wetlands, other vegetation, clear water, turbid water, and ice (as not all ice has typically melted in June, especially on larger lakes), using Landsat 8 surface reflectance (Bands 1–7) imagery with 30 m resolution as available in GEE and a random forest classifier (see **Supplementary Material A** for detailed methods).

Topographical Slope Within 150 m

Siberian cranes are fierce nest protectors, but when away from the nest can face nest predation pressure from arctic foxes (*Vulpes lagopus*), jaegers (*Stercorarius* spp.), glaucous gulls (*Larus hyperboreus*), and herring gulls (*Larus argentatus*) (Perfiliev, 1965). Thus, visibility around the nest (Flint and Sorokin, 1981) could be important to identify when predators are near and adults should not leave eggs unattended (Flint and Kischinski, 1975). To understand how topography affects visibility, we used the ArcticDEM 2 m mosaic dataset (Porter et al., 2018) from the Polar Geospatial Center downloaded from GEE to calculate the slope of each pixel, and then determined the maximum slope within 150 m of each pixel using the Focal Statistics tool in ArcMap 10.5 (Environmental Systems Research Institute, Redlands, CA), where steep slopes indicate reduced nest visibility.



Distance to Lakes

Surface water is important for shaping the tundra landscape and distribution of Siberian crane nesting sites. Previous research has highlighted the importance of distance to lakes for nest location (Bysykatova, 2012, 2016). Adult cranes rely on medium to large (minimum size of 0.35 km²), shallow (typically no deeper than 0.5 m) lakes surrounded by flat terrain for increased visibility and food resources, while nests are located in wetlands a mean of 300 m from the lake shore (Flint and Kischinski, 1975; Bysykatova, 2012, 2016). While Siberian crane nests are often built over shallow water (del Hoyo et al., 1996), they were rarely located in pixels classified as water in the habitat type map (see Section Landcover Type).

We used two layers from the Global Surface Water Explorer (Pekel et al., 2016) to develop environmental variables related to surface water. The Global Surface Water (GSW) layers are based on Landsat images (30 m resolution) obtained over more than 30 years. However, over the study site, Landsat imagery only exists since 2001. In May 2003, the Landsat 7 sensor experienced a permanent failure of the scan-line corrector (SLC-off images), resulting in a loss of ~22% of all data from this time forward (Arvidson et al., 2006; Chen et al., 2011). Thus, some data gaps exist in the GSW layers as well.

To identify typical June surface water extent, we used the GSW “monthly recurrence layer” for June (Pekel et al., 2016). This layer represents the frequency (in percent) at which each pixel has been identified as water in June between 2001 and 2018. We created a

binary image with pixels with values $\geq 50\% = 1$, indicating pixels that have been identified as water in June in more than 50% of the observations, and pixels with values $< 50\% = 0$, indicating areas identified as water in June in $< 50\%$ of the observations (June surface water map). Hence, the resulting map identifies all pixels that GSW identified as water in June in at least half of the years with observations, including river areas.

Shrubs form thickets on temporarily flooded river banks in the tundra. These shrubs are the tallest vegetation throughout the study site and can grow up to 2 m, restricting local visibility. To avoid flooding and tall shrubs, nests are located on average 2,938 m from river banks (Bysykatova, 2012, 2016). Consequently, to account for the fact that crane nesting site selection differs between lakes and rivers, we needed to exclude the river areas from the June surface water map. The GSW “maximum extent layer” shows all pixels that have ever been identified as water between 2001 and 2018, including river floodplains. We converted the GSW maximum extent to a vector file and selected and exported the river areas, which were mostly connected as polygons. The river polygons were then subtracted from the June surface water map, leaving the extent of lakes in June. To reduce noise in the analysis, we calculated the area of the polygons in the lakes layer, and deleted lakes smaller than 0.35 km², since cranes do not nest at lakes smaller than this.

We finally created the distance to lakes variable by converting the June lake vector map to raster format and calculating the Euclidean Distance (Spatial Analyst toolbox, ArcMap) to the closest lake for each pixel of the study area.

Modeling Potential Nesting Habitat

Maximum entropy species distribution modeling (MaxEnt) is a machine learning algorithm used for predicting potential species distributions using presence-only observations and a set of environmental variables (Phillips et al., 2006; Morales et al., 2017). MaxEnt was used to identify potential nesting habitat given it has high accuracy under two restrictions of our field observational data, i.e., low sample numbers (Pearson et al., 2007; Thibaud et al., 2014; Guisan et al., 2017) and presence only data (Phillips et al., 2006; Wisz et al., 2008; Elith et al., 2011). We followed several measures to reduce overfitting and bias, and optimize our MaxEnt models, including masking areas where cranes are not expected to nest (see **Supplementary Material B** for detailed explanations). To reduce the influence of spatial autocorrelation at nest sites (Wisz et al., 2008; Phillips et al., 2017), we thinned observed nest sites used to train our MaxEnt model by only choosing one nest per known breeding pair, unless nests from different years were located at least 2 km away from other nest sites of that pair. This left us with 20 of 37 observed nest locations to use in our final models. We used this subset of 20 observed nest locations as input to the MaxEnt model.

We imported the nest location and environmental variables into R version 3.6.0 (R Core Team, 2021) and evaluated several model tuning runs using the ENMeval package (Kass et al., 2021). We applied different regularization multipliers (0.75, 1.00, 1.25), which penalize more complex models, in order to optimize model performance and limit the effects of overfitting (Radosavljevic and Anderson, 2014). We chose 10,000 random background points as input to the model. We did not constrain features to remain within values in the training data (clamping), and only used values at presence and background points, instead of the entire rasters. We used the “ENMevaluate” function in ENMeval to run models with four different combinations of the three selected variables (all combinations with at least two variables) to allow us to compare results and choose the best model (Kass et al., 2021), with only linear and quadratic features since there were few sample points.

We used “jackknife” partitioning to validate the training and validation data, which used k -fold cross validation where k (the number of bins) is equal to the number of samples in the data, which is 20 here. This validation method is recommended for occurrence datasets with <25 observations (Pearson et al., 2007; Shcheglovitova et al., 2013). This method uses each occurrence as a testing point once, while it uses the remaining occurrence points as training data for each iteration. A total of 20 cross validation models were run for each model, with evaluation metrics calculated based on all iterations.

All models were evaluated using Akaike information criterion corrected for small sample sizes (AICc; Akaike, 1974; Burnham and Anderson, 2004; Warren and Seifert, 2011). AICc is a measure of model goodness-of-fit and complexity. The model with the lowest AICc is considered the best model and all models with $\Delta\text{AICc} < 2$ are considered to be statistically equal. In ENMevaluate, when rasters are not used AICc is calculated using the predicted background occurrences, compared to the original data, with the assumption that background records have adequately represented presence records (Kass et al., 2021). We

also examined the area under the curve of the receiver operating characteristic plot (AUC), which was calculated using both training and validation background data based on the jackknife cross validation data partitions (Radosavljevic and Anderson, 2014). The AUC measures how well the model predicts output compared to a random model on a scale from 0 to 1, with values close to 1 considered highly accurate, and values around 0.5 considered to be no better than random, and values < 0.5 considered to be worse than random (Elith et al., 2006; Phillips et al., 2006). MaxEnt models selected by AICc have been found more accurate than AUC at estimating the relative importance of variables and habitat suitability in training and predicted models, when samples sizes are low (Warren and Seifert, 2011). Jackknife tests were used to determine variable percent contribution and permutation importance and to develop variable response curves. High values of percent contribution indicate the variable adds more to fitting the final model, while high values of permutation importance (%) indicate that the variable influences the final model AUC more (Phillips, 2005). We checked for overfitting by examining the absolute difference in AUC (AUCdiff) between the training and validation data, given in the output of the ENMevaluate command. We used the AUC to choose between model groupings, and used AICc to evaluate models and choose our final model. The final model was used to create a map of potential nesting habitat using the “predict” function in ENMeval with a complementary log-log output, which is more appropriate for estimating probability of presence (Phillips et al., 2017). This created a raster map with output probability values between 0 and 1 (Phillips et al., 2017). The mapped probabilities were classified to represent no nesting potential (probability < 0.50), low nesting potential ($0.5 \leq \text{probability} < 0.66$), medium nesting potential ($0.66 \leq \text{probability} < 0.75$), and high nesting potential ($0.75 \leq \text{probability}$). Neighboring pixel areas belonging to the same class were converted to polygons in ArcMap. To get an understanding of average nesting habitat availability in most years, we erased the June surface water map (Section Distance to Lakes) from the predicted map to remove areas covered by water in June more than 50% of the time. Land surface areas were then calculated for low, medium, and high nesting potential. Nest locations were overlaid on the map, and all nests found within suitable habitat were counted and divided by total number of nests to get a measure of the predicted map accuracy.

Impacts of Yearly Flooding on Siberian Cranes

Flooded Nest Sites

We first aggregated observed nest sites across all surveys into a single layer, representing all known used nest sites for all years. To estimate how many of these used nest sites were affected by flooding in a given year, we overlaid these observed nest sites on the GSW monthly history (Pekel et al., 2016) extent in June and determined if each nest was located within a pixel of water, non-water, or had no observation. We calculated the percent of flooded nest sites per year based on the number of nest sites that had a water observation divided by the total number of observations. Nest sites with no GSW observation could have

been located in ice or snow (which are not indicated in GSW layers), behind a cloud, or within a Landsat 7 SLC-off data gap, and were thus excluded from calculating the percent of flooded nest sites. If a nest site was located within a water observation of the GSW monthly history layer, there is a high potential that the nest was flooded that year. However, it has to be noted that nests can be built on small outcroppings higher than the surrounding areas. Depending on the microtopography of the wetland and the level of the flood, there is a chance that the nest and eggs survive even if the nest site is flooded. We determined if there was a significant relationship between flooded nest sites and year from 2001 to 2018 using the “lm” function in the stats package of R (R Core Team, 2021) and plotted in ggplot2 (Wickham, 2016). We used the “grubbs.test” function in the outliers package (Komsta, 2011) to check for outliers.

Flooding Impact on Juvenile Counts

To examine the relationship between juvenile survival and flooding, we calculated the Pearson correlation between the percent of nest sites in flooded areas and the juvenile counts at Momoge Nature Reserve in the same year using the “cor.test” function in the stats package of R (R Core Team, 2021). To verify normality of variables, we examined the residuals of a linear model with numbers of juveniles as the dependent variable and the percent of flooded nest sites as the independent variable, using the “qqnorm” function in the stats package of R (R Core Team, 2021), and plotted the relationship using ggplot with a “lm” smoothing line from the ggplot2 package (Wickham, 2016).

Impacts of Extreme Flooding on Observed Nest Sites and Potential Nesting Habitat

We used the GWS maximum extent layer (Pekel et al., 2016) to represent an extreme flooding event across the study area. The maximum extent layer shows all pixels that have ever been identified as water by GSW between 2001 and 2018.

We overlaid the observed nest locations on the GSW maximum extent layer in ArcMap to determine which nest sites might be affected during an extreme flood. We subtracted the GSW maximum extent from the predicted nesting habitat map for the study area to get an estimate of how extreme flooding would reduce potential nesting habitat (see Section Modeling Potential Nesting Habitat).

RESULTS

Potential Nesting Habitat

We chose the MaxEnt model with the second lowest AICc. This model included all three environmental variables, as this model grouping had the highest average AUC values (Supplementary Table C.1). The linear models had the lowest AICc values, all within $\Delta AICc < 2$ suggesting they are statistically equivalent, while the lowest AICc had a regularization multiplier of 0.75, allowing more complex models (Elith et al., 2010, 2011). However, AUC values (average AUC = 0.96) within this grouping were approximately equal in the linear and linear-quadratic models (Supplementary Table C.1). We chose the model with a regularization multiplier of 1 as we chose to

TABLE 1 | Average area of nesting habitat suitability and reduced area due to extreme flooding within the study area.

Potential nesting habitat	Average available area (km ²)	Extreme flood available area (km ²)	Decrease in area (km ²)	Decrease in area (%)
Low	1,169.9	643.2	526.7	45.0
Medium	666.7	390.4	276.3	41.4
High	1,970.8	1,035.0	935.8	47.5
All suitable	3,807.4	2,068.6	1,738.8	45.7
Unsuitable and masked	124,910.6	126,649.4		

use the least complex model. All models had an AUCdiff of 0.03, suggesting the model was not overfit. Response curves for the predictor variables of the chosen model are shown in Supplementary Figure C.1.

The final model showed the three variables to contribute to both model fitting (percent contribution) and model accuracy (permutation importance): landcover type (highest probability associated with the wetland class, percent contribution = 66.9, permutation importance = 14.6), distance to lakes (highest probability associated with shorter distances, percent contribution = 27.3, permutation importance = 45.0), and maximum slope within 150 m (highest probability associated with lower slopes, percent contribution = 5.9, permutation importance = 40.4; Supplementary Table C.1).

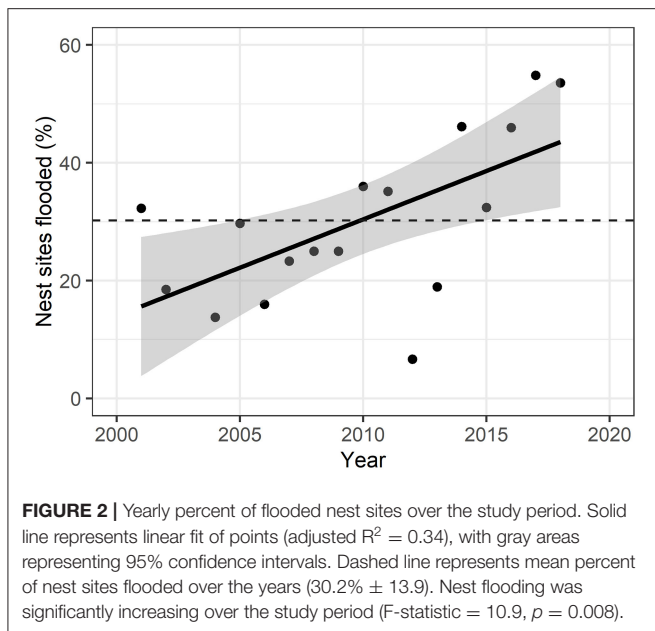
The potential nesting habitat map (Figure 1) shows the area of high nesting potential (1970.8 km²) was found to contribute most to the total suitable area, more than low (1,169.9 km²) and medium (666.7 km²) suitability combined (Table 1). In general, high potential habitat was identified closest to large lakes, with lower potential habitat further away. Unsuitable areas (124,910.6 km²) include the areas masked from the analysis where cranes are not expected to nest.

We overlaid the 37 observed nest sites on the potential nesting habitat map to determine in which potential habitat they were located: two were found in predicted areas of low potential habitat, three in medium potential habitat, and 26 nests were located in high nesting potential habitat. Six nest sites were not located within potential nesting territory, but within 485 m of at least low potential habitat. Thus, the accuracy of the predicted map, based on the number of nest locations found in predicted suitable nesting habitat, was 84%.

Impacts of Yearly Flooding on Siberian Cranes

Flooded Nest Sites

We examined the extent of surface water in June each year from 2001 to 2018 (except 2003) to determine how many observed nest sites were potentially affected by flooding (Figure 2; Supplementary Table C.2). 30.2% (s.d. = 13.9) of the nest sites were flooded on average across years, with a significant positive relationship from 2001 to 2018 (F-statistic = 9.21, *p*-value = 0.008). The peak of flooded nest sites (55.0%) was reached in



2017, but also in 2018 54.8% of the nest sites were located within water-covered pixels. 2012 was the year with the lowest percent of nest sites flooded (6.7%).

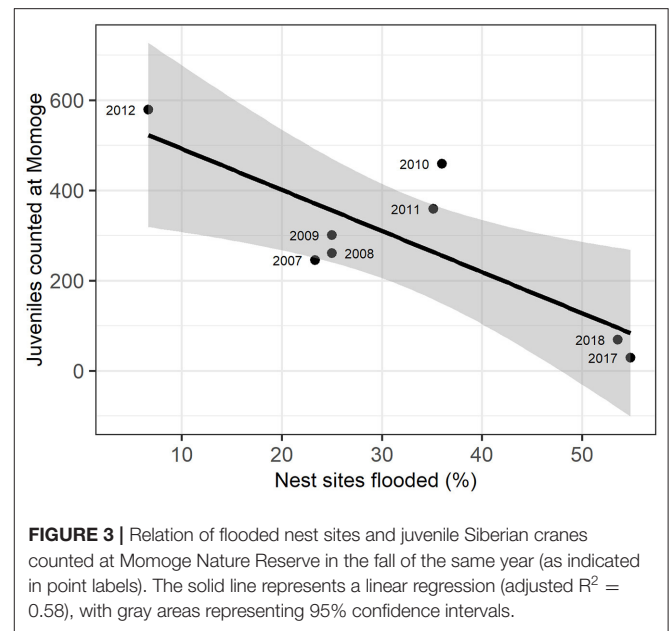
Flooding Impact on Juvenile Counts

We examined the relationship between the number of juveniles counted at Momoge Nature Reserve and the percent of flooded nest sites for 8 years during the study (Figure 3; Supplementary Table C.2). We found a significant negative correlation ($R = -0.80$, t -value = -3.27 , p -value = 0.02) indicating lower numbers of observed juveniles in years with a greater percentage of nest sites flooded (Figure 2). In 2017, which had extreme flooding conditions (Tei et al., 2020), 55% of the nest sites were flooded, and the lowest number of juveniles were counted in Momoge Nature Reserve (29). The greatest numbers of juveniles counted (579) occurred in 2012, which also had the lowest percent of flooded nest sites (6.67%).

Impacts of Extreme Flooding on Observed Nest Sites and Potential Nesting Habitat

We used the GSW maximum extent layer to determine how extreme flooding could impact observed Siberian crane nest sites and potential nesting habitat. We found 17 nest sites to be flooded under maximum water extent. Only two of the six nests located outside of the predicted potential habitat would be flooded at this level, while 12 nests located in high potential habitat would be flooded. This extreme flooding situation affects almost half of all suitable nesting habitat, eliminating over 1,700 km² and reducing high potential nesting habitat by more than 47%, to just over 2,000 km² (Table 1).

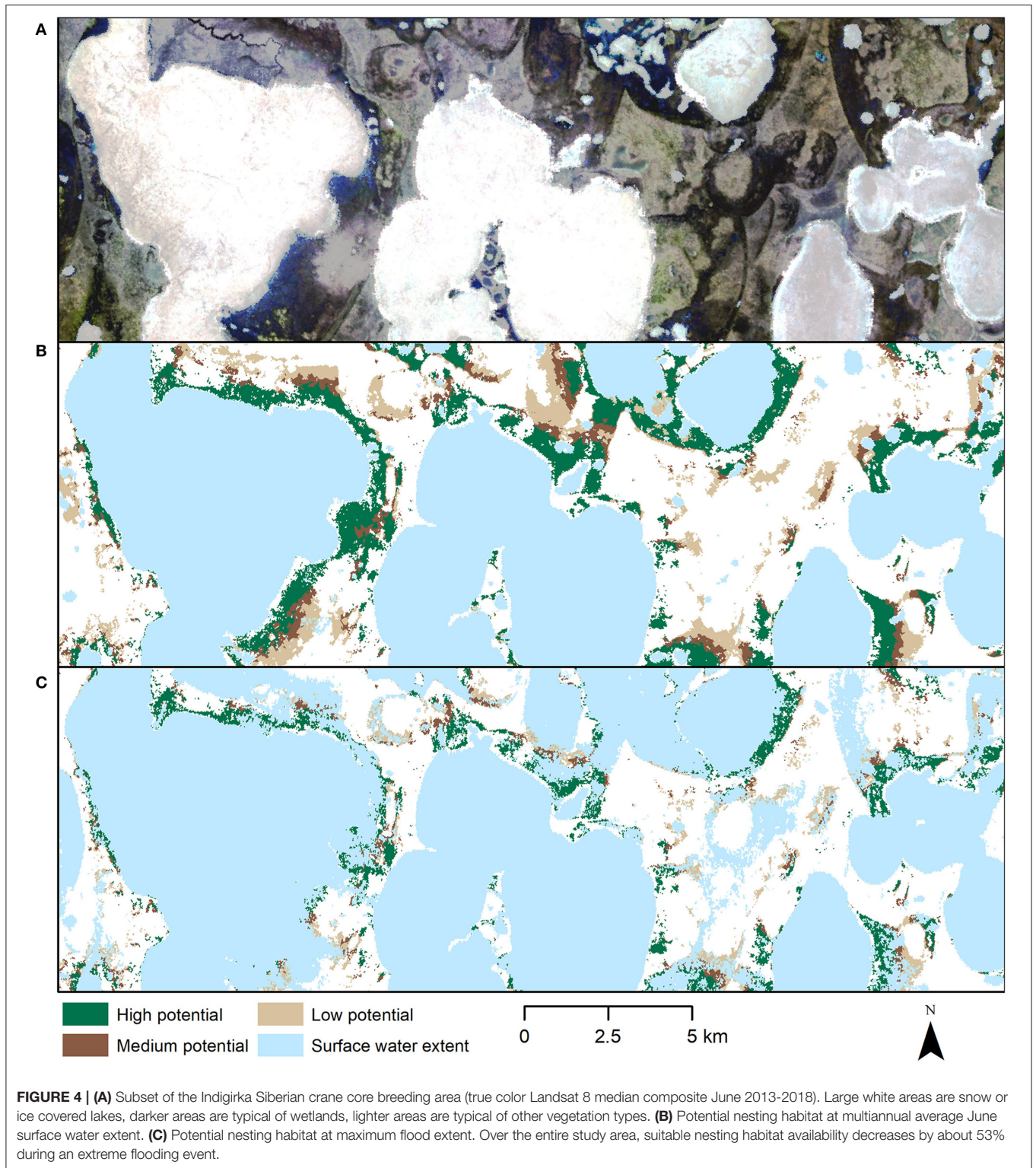
During extreme flooding, lake boundaries expand and can merge to form larger lakes (Figure 4C). These larger lakes often expand into the high potential nesting habitat that are surrounding the lakes, making much of the area unsafe for



nesting. However, some large lakes maintain their shores (see large lake in the center of Figure 4), due to higher banks surrounding them, which at the same time make these areas less suitable for crane nesting due to reduced visibility related to steep slopes.

DISCUSSION

The occurrence of extreme flooding in Arctic lowlands in recent years (Kane et al., 2003; Tei et al., 2020) highlights the importance of conservation planning for extreme weather impacts on threatened and endangered species (Maxwell et al., 2019). This study investigates how flooding events might impact critical wildlife habitat in the Arctic, i.e., potential nesting habitat of the critically endangered Siberian crane. We found that extreme flooding causes a strong decrease in availability of vital habitat, showing a correlated decrease in reproductive success. Based on our modeling results, Siberian cranes can only utilize nesting areas in a small fraction (2.96%; Table 1) of the landscape during years with average surface water extent. Yearly flooding of previously observed nest sites significantly increased over the past 18 years, with more than 50% of sites flooded in the last 2 years of the study (Supplementary Table C.2). We found autumn counts of juvenile cranes to significantly decrease with increasing percent of flooded nest sites, suggesting that the increasing frequency of flood events could have important long-term effects on population viability. Depending on the microtopography and flood level, nests and eggs may not necessarily be destroyed even if a nest location is indicated as flooded by the GSW data. But, when nests do flood, eggs can be destroyed. If adults try to build a new nest and have a successful hatching, surviving chicks have less time to develop and gain strength before their migration to China, and shortened development periods could lead to reduced juvenile survival and consequently decreasing population size.



During times of extreme flooding, as was seen in 2017, almost half of all high nesting potential areas could flood, forcing cranes to choose medium or low potential nesting habitat instead, which can result in lower numbers of surviving juveniles.

Our model confirmed the importance of wetlands along lakes for Siberian crane nesting. These swampy tidal flats in water up to 0.5 m deep provide easy access to lake resources, along with added protection from predators due to high visibility and tall grasses to

hide nests (Vorobyov, 1963; Flint and Kischinski, 1975; Flint and Sorokin, 1981; Johnsgard, 1983; del Hoyo et al., 1996; Bysykatova et al., 2014). Although no nests have been directly observed in the western region of the study site, cranes here are also typically seen in shallow wetlands along lakes, with extensive pendant grass (*Arctophila fulva*) and surrounded by sedges (Bysykatova et al., 2014). Similarly, temporary wetland habitats are avoided, further highlighting the importance of being close to lakes (Germogenov et al., 2013; Bysykatova et al., 2014).

Some high potential nesting habitat was identified along small river channels, which is expected to actually be surrounded by tall shrubs. Nesting habitat has a similar spectral signal to shrubs along rivers in the Landsat 8 imagery due to a high amount of green vegetation in close proximity to water, and thus the shrubs were misclassified as nesting habitat. While we were able to mask out large rivers, we were not able to mask the smaller channels, as the width of these channels is often smaller than the resolution of the GSW layers. We expect that this is a very small fraction of the overall area and the high nesting potential area. Another possible source of uncertainty was in masking where cranes are not known to nest. Using the GSW maximum extent layer to remove coasts, rivers, and their floodplains, some rivers were connected to larger wetlands and coastal areas along the East Siberian Sea and Laptev Sea that flood extensively. These areas were not analyzed, but nest sites might be located here. Previous research found breeding pairs in coastal wetlands and wetlands located on river floodplains near the sea (Germogenov et al., 2013; Bysykatova et al., 2014), and thus the total potential nesting habitat might be slightly underestimated, but might also be subject to frequent flooding.

Species will have to adapt their behavior or disperse to better habitat to survive rapidly changing climate conditions (Gilg et al., 2012; Beever et al., 2017; Descamps et al., 2017; Noonan et al., 2018). In the Arctic, there are few studies examining extreme flooding impacts on wildlife, but increasing temperatures, changing precipitation dynamics and landscape phenology, more frequent rain-on-snow events, and melting sea ice are affecting trophic dynamics (Rockwell et al., 2011; Hansen et al., 2013), breeding (Descamps et al., 2017; Mallory et al., 2020), and population genetics (Peeters et al., 2020). Extreme weather events are predicted to increase in extent and frequency worldwide (Cai et al., 2014), and flooding has been linked with local extinctions (Maxwell et al., 2019), impacts to population and community structure (Thibault and Brown, 2008), and greatly decreased survival (Korslund and Steen, 2006; Tryjanowski et al., 2009). Previous studies have highlighted the impacts of extreme floods on coastal birds, which are generally threatened from sea level rise and increasing salinity (Van De Pol et al., 2010). While some birds shift habitat selection from traditional areas in response to long-term changes in flood extent (Bailey et al., 2017, 2019), shifts right after extreme flooding can also lead to increased nest predation (Ma et al., 2019), further threatening breeding success. Thus, it will be important to monitor Siberian cranes, and other Arctic species, responses to continued flooding, as there is

little research investigating the effects of extreme flooding in the tundra.

During the study period, maximum snow depth increased significantly and was correlated with the percent of nests in flooded areas (see **Supplementary Figures B.2, C.1, C.2**), suggesting that precipitation and flooding patterns are already changing and disturbing Siberian crane nesting. Heavy snowfall caused the extreme flooding in 2017 (Tei et al., 2020), which was also the year with the fewest juveniles at Momoge Nature Reserve. Siberian cranes may be well suited to adapting distribution to changing climate conditions. Since the 1950s, lake extents within the study site have experienced significant change, including flooding of islands, peninsulas and isthmuses, and destroying high potential nesting habitat along lake shores (Pshennikov and Germogenov, 2008; Germogenov et al., 2013). As temperatures have increased over the past 40 years, population numbers have increased with higher reproductive success in warmer years (Germogenov et al., 2013; Birdlife International, 2018), and Siberian cranes in the western extent of their breeding range have moved closer to the sea (Bysykatova et al., 2014). With increased flooding, cranes may begin shifting nesting habitat to lower potential areas with higher microtopography or further from lake shores to limit flooding risk. However, these adaptations might expose chicks to higher predation. Future monitoring of habitat, snowfall, flooding, nesting, and juvenile counts may hint at further modifications, as Siberian cranes have proven very adaptable to living in this highly dynamic system, where surface water extent can change at a yearly scale (Vladimirtseva et al., 2012).

Siberian cranes are critically endangered, with their current greatest perceived threat being loss of winter habitat, mostly due to changing landscapes caused by the Three Gorges Dam along the Yangtze River in China, and potential habitat loss through a proposed dam at the outlet of Poyang lake, their largest wintering grounds (Birdlife International, 2018). Flooding in their wintering lakes has already caused cranes to feed outside of normal habitats (Jia et al., 2013; Burnham et al., 2017). Additionally, as climate change reduces tundra permafrost, and changes precipitation dynamics and ice cover, increased opportunities for natural resources exploration and extraction will lead to increasing pressure for development in the Arctic (Kumpula et al., 2011). With threats to important habitat in both breeding and wintering grounds, it will be vital to coordinate conservation and research efforts for Siberian cranes in their breeding range in Siberia and their winter feeding habitats in China, and understand how their changing habitats are affecting population dynamics.

DATA AVAILABILITY STATEMENT

The nest GPS locations will not be made available to protect the locations of these critically endangered species, but the environmental variable values determined from the nest sites,

and R code, are available at doi: 10.17605/OSF.IO/B7328. Requests for further access should be directed to pjhav17@gmail.com.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because research involved only observations and counts of individuals in the field.

AUTHOR CONTRIBUTIONS

PH: conceptualization, methodology, formal analysis, investigation, data curation, data interpretation, writing—original draft, and writing—reviewing and editing. IB-H: conceptualization, investigation, data curation, data interpretation, writing—reviewing and editing, supervision, and funding acquisition. NG: investigation, data curation, data interpretation, writing—reviewing and editing, and funding acquisition. GS-S: conceptualization, methodology, investigation, data interpretation, writing—reviewing and editing, supervision, and funding acquisition. All authors contributed to the article and approved the submitted version.

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FUNDING

All funding was provided by the University of Zurich, Department of Evolutionary Biology and Environmental Studies, and the Institute for Biological Problems of the Cryolithozone, Siberian Branch of the Russian Academy of Sciences.

ACKNOWLEDGMENTS

The authors would like to thank Mr. Zhou Chanling and Chan Fawen for Siberian crane juvenile count data at Momoge Nature Reserve. We appreciate the Polar Geospatial Center for freely available access to the ArcticDEM. The contribution by GS-S was supported by the University of Zurich Research Priority Programme on Global Change and Biodiversity.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fcsc.2022.799998/full#supplementary-material>

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