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POPULATION ECOLOGY – ORIGINAL RESEARCH

Extreme climate events limit northern range expansion of wild turkeys

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Abstract
For species inhabiting areas at the limit of their environmental tolerance, extreme events often drive population persistence. However, because extreme events are uncommon, their effects on population dynamics of expanding species are poorly known. We examined how extreme climate events in winter and summer affected three populations of wild turkeys occupying a natural climate gradient at the northern edge of their range. First, we examined the mechanism by which vital rates affect the population growth rate. Second, we developed a climate-dependent structured population model. Finally, by linking this population model to IPCC-class climate projections, we projected wild turkey population abundance in response to the frequency of extreme snow events by 2100 for the northernmost population. We showed that the population dynamics of the three populations is driven through different pathways expected from the theory of invading population dynamics; that those populations were mainly limited by heavy snow that decreases winter survival by restraining food access; and that a population of immigrant is projected to decline at the northern species range. This study exemplifies how extreme events affect population dynamics and range expansion of temperate species at the northern edge of the distribution.

Keywords Climate change · Expansion range · *Meleagris gallopavo* · Population dynamics · Population projection

Introduction

A range contraction or expansion for many animal populations has been observed because of climate changes (Walther et al. 2002; Parmesan et al. 2013). The range shift of these populations also varies according to their geographical location. For example, terrestrial species inhabiting temperate zones are more sensitive to environmental improvement towards their leading than their trailing edge range boundaries (Sunday et al. 2012). This situation is resulting in a global increase in their abundance and distribution (Parmesan et al. 1999) and contributed to average changes of 17 km per decade toward the poles for more than 1300 species (Chen et al. 2011) (Figs. 1, 2, 3, 4, 5, 6, 7, 8, 9, 10).

Populations at the edge of their geographical range are especially sensitive to variation in their environment (Thompson et al. 2013) and extreme events, not average climate, often better predict species distribution of both animals (Bateman et al. 2012) and plants (Reyer et al. 2013). For example, the northern boundary of the evergreen bagworm moth (*Thyridopteryx ephemeraeformis*) is limited by winter temperature dropping under the physiological limit of overwintering eggs during extreme years (Lynch et al. 2014). Similarly, in the southern hemisphere, the northern boundary of the seaweed *Scytothalia dorycarpa* retracted by 100 km following an unusual heat wave (Smale and Wernberg 2013). However, because extreme events are uncommon, assessing their impact on wildlife remains a challenge

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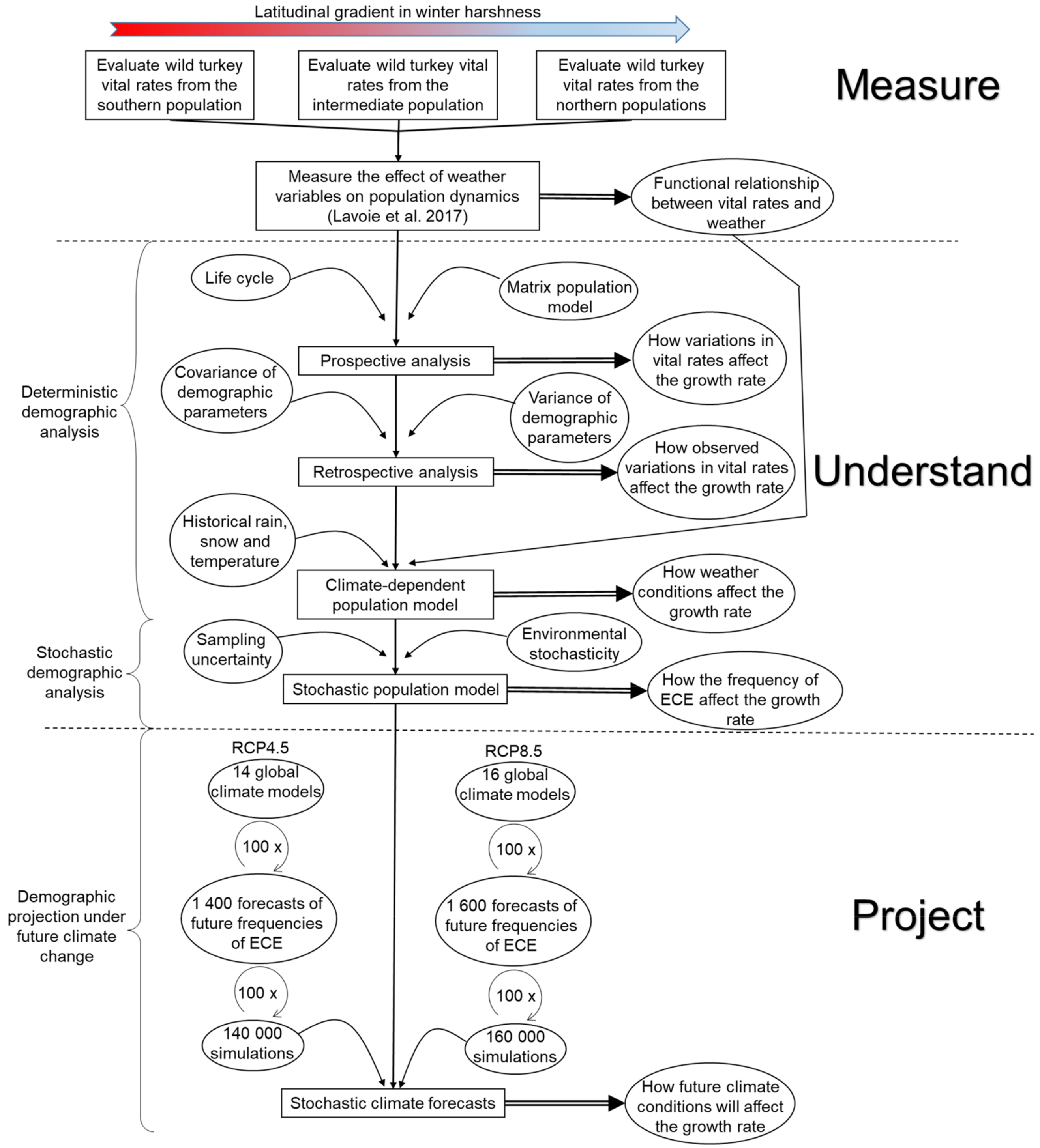


Fig. 1 Analytical process used to implement the Measure-Understand-Project (MUP) approach to model population changes of wild turkeys at the northernmost limit of their range

(Jenouvrier et al. 2015, 2021, van de Pol et al. 2017, Latimer et al. 2019, Jenouvrier et al. 2021).

To understand change in species distribution, it is important to account for multiple seasonal and carry over effects of climate on the complete life cycle of the studied species that drive population dynamics. The biogeographic limit may also be imposed by different seasons, such as summer weather. Indeed, rainfall usually impacts bird populations by reducing chick survival (Guttery et al. 2013). During the first weeks of life, chicks are more vulnerable to weather-induced

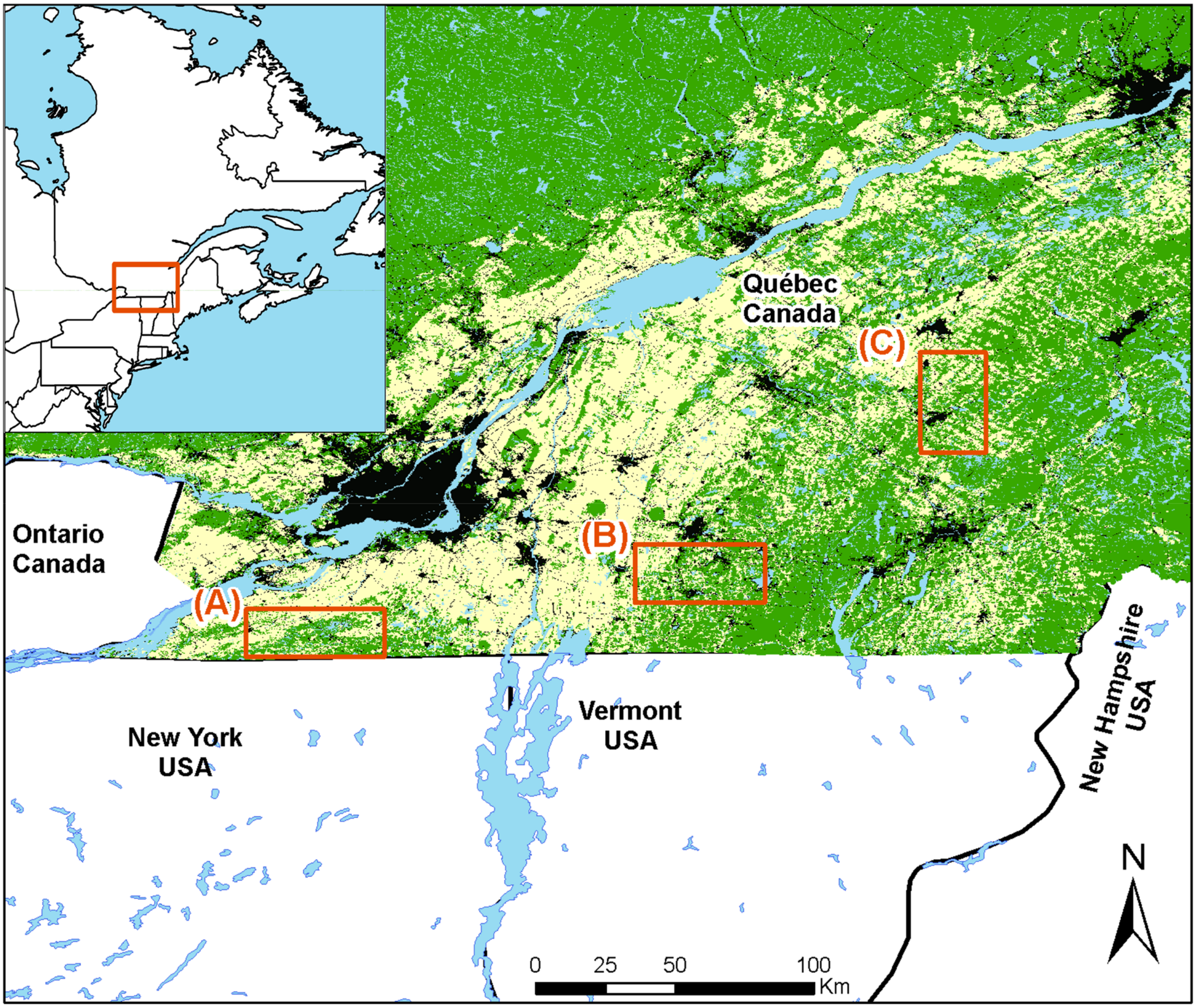
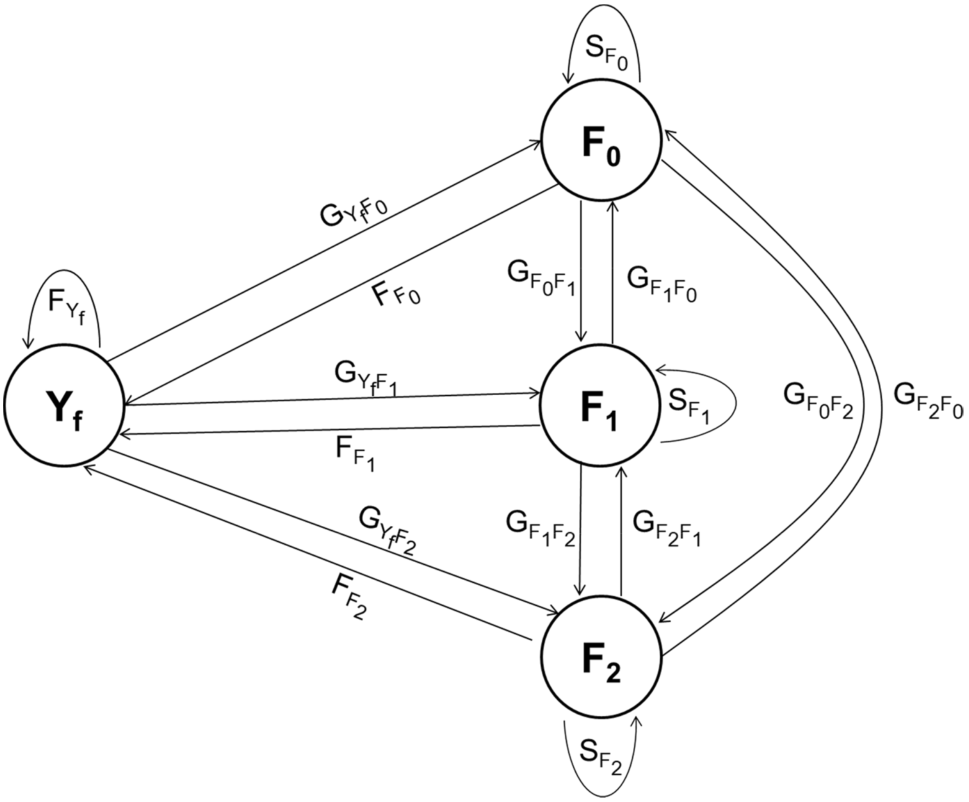


Fig. 2 Location of the three study areas representing the latitudinal gradient in winter harshness: **a** southernmost, **b** intermediate, and **c** northernmost. The proportion of forested cover (green) is slightly lower and the proportion of crops lands (yellow) is slightly higher in the southernmost area

mortality before additional thermo-protective plumage is developed (Roberts and Porter 1998) and endothermy is acquired (Dégletagne et al. 2013). For example, during an extreme warm and wet summer, > 50% of the chicks of Adélie penguin (*Pygoscelis adeliae*) from a colony in Antarctica died from hypothermia (Ropert-Coudert et al. 2015).

In Canada, the wild turkey (*Meleagris gallopavo*) is at the northern limit of its distribution, yet the species continues to expand its range. Historically, wild turkeys were limited to latitudes below 45°. However, they now occur above 50° of latitude in Canada, which is approximately 550 km northerly of their historical limit, and their numbers have been increasing since the 1950s (Hughes and Lee 2015). The widespread reintroduction programs of state game agencies have accelerated this northward expansion (Mock et al. 2001) but environmental changes, especially reversion of farms to natural habitat (Hughes and Lee 2015) and reduction of snow cover caused by global warming (Ogden 2015), likely helped. Indeed, populations of wild turkeys in northern areas are limited by snow accumulation that restricts access to food (Kane et al. 2007), resulting in lower survival when snow depth exceeds 30 cm for more than 10 days (Lavoie et al. 2017). Furthermore, as wild turkeys need to find additional food resources when temperature decreases, the effect of temperature gets more significant above the 30 cm threshold in snow depth. Weather conditions also affect reproductive parameters as an increase in rainfall quantity reduces nesting success at a faster rate for first than second nesting attempt (Lavoie et al. 2017, Fig. 1 Step 1: Measure). Consequently, to understand the mechanisms by

Fig. 3 Annual life cycle model for the wild turkey. The four stages are yearlings (Y_f), non-nesting adults (F_0), adults attempting one nest (F_1), and adults attempting two nest (F_2). Each year, birds produce offspring with probability F, remain in the same stage with the probability S or move to another stage with the probability G



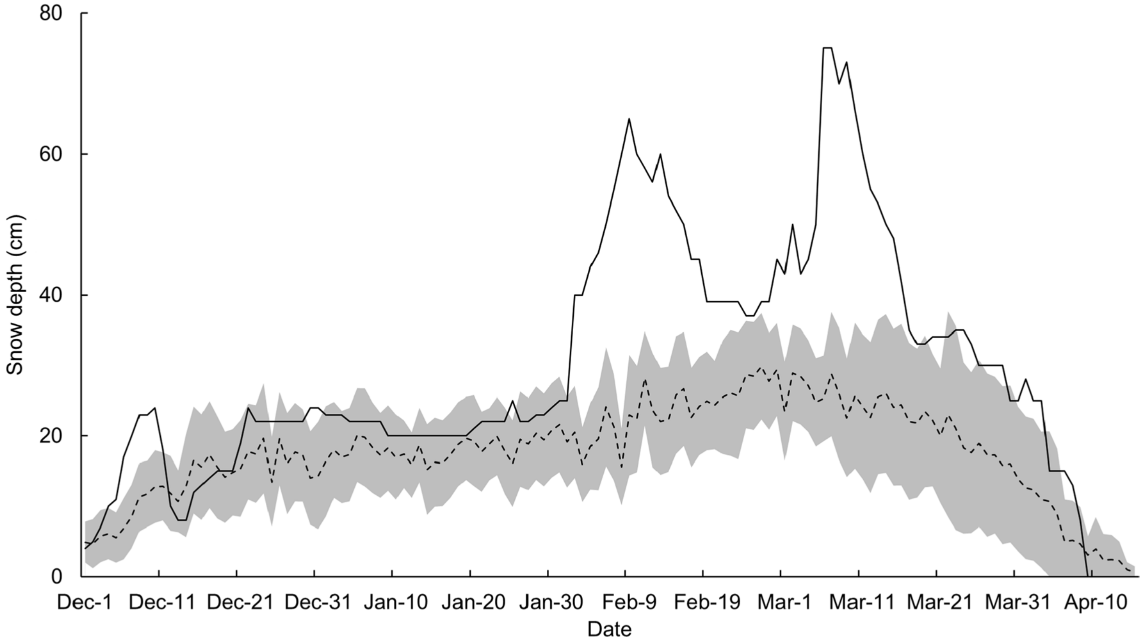


Fig. 4 Average historical snow depth (hatched line) compared to the extreme climatic event (plain line) of 2011 in the northernmost study area in Quebec, Canada. The historical (1994–2009) 95% confidence interval is shown in gray

which population respond to those climate variables, occurring at different seasons and affecting various part of the life cycle in non-linear ways, it is necessary to incorporate those climate–demographic relationships into population models (Fig. 1 Step 2: Understand). The final step, which is to project population changes and range expansion require

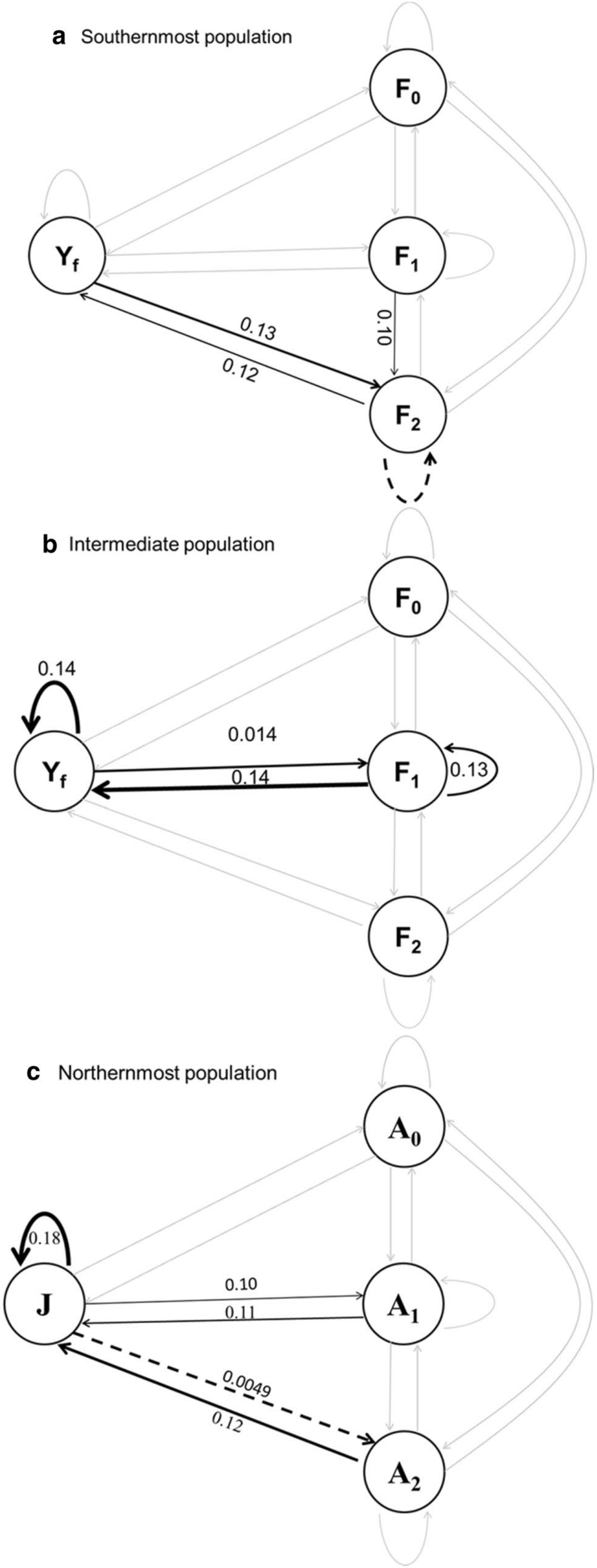


Fig. 5 Life cycle model of wild turkey from three populations representing a gradient of climate harshness in southern Quebec, Canada: **a** southernmost, **b** intermediate, and **c** northernmost. The four stages are yearlings (Y_f), non-nesting adults (F_0), adults attempting one nest (F_1), and adults attempting two nest (F_2). Arrows represent the transitions that had the highest elasticities from the prospective (plain) and retrospective (hatched) analysis. The width of the arrow corresponds to the magnitude of the elasticity, which is specified above arrows

to link these population models to climate outputs projected by climate models (Fig. 1 Step 3: Project, see more details in Jenouvrier 2013, Iles and Jenouvrier 2019).

Heretofore, the effect of climate and extreme events on the population growth rate of wild turkey remains unexplored. Here, we aimed to assess the impact of extreme winter and summer events on the whole life cycle of the wild turkey and how these events can limit the expansion of the population northward. We predict that if the future frequency of extreme events exceeds the population tolerance, wild turkeys will not persist at their northernmost range boundary. To test this prediction, first we examine the demographic mechanisms driving the wild turkey expansion in the context of life history and biological invasion theory. Second, we project the population growth and thus the likelihood of the northern expansion range of wild turkey using future climate conditions projected by IPCC-class models. Finally, we discuss our results and stressed the importance of developing climate-dependent population models to assess the persistence of populations and help implementing conservation and management strategies.

Materials and methods

Figure 1 describes our overall approach following the MUP approach developed by Jenouvrier (2013). The first step is measuring the effect of climate on the complete life cycle of the studied species, thereby accounting for multiple seasonal and carry-over effects of climate (Iles and Jenouvrier 2019). The second step is examining the demographic pathways through which climate influences overall population dynamics. This step requires integrating the statistical relationships between climate and vital rates (found in step one) into population models. At this step, population models become climate dependent. Climate can be modelled as deterministic or stochastic. The third and final step is fusing climate-dependent population models with projections of future climate from IPCC-class climate projection.

Here, we build on previous studies characterizing the impact of snow, rain and temperature on the life cycle of the wild turkey for three populations of wild turkey along a climate gradient (Figs. 1 and 2, step 1 of the MUP approach) to understand the population responses to extreme climate events (step 2 of the MUP approach). We

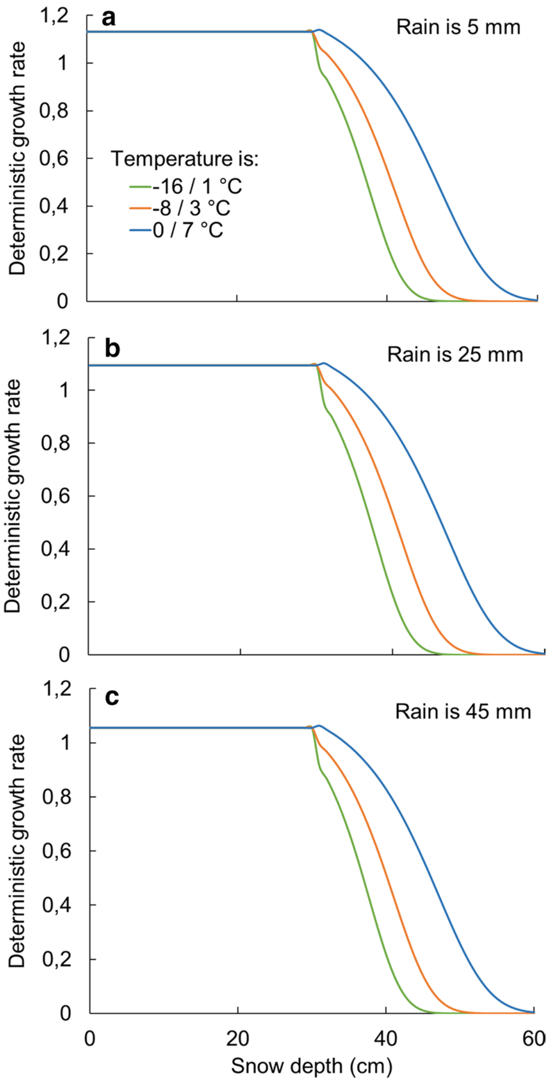


Fig. 6 Relationship between the deterministic population growth rate of wild turkeys at the northern limit of their range in southern Quebec, Canada and environmental conditions (snow depth, temperature and rain) for 3 level of rain: **a** 5 mm, **b** 25 mm, and **c** 45 mm

first characterize the demographic mechanisms by which vital rates affect the population growth rate by performing a deterministic analysis for each of the three populations using a structured population model. Second, we include the effect of climate to predict the deterministic population growth rate across the latitudinal gradient of climate conditions and years. We then developed a climate-dependent stochastic population model accounting for sampling uncertainty and environmental stochasticity to study the impact of an increased frequency of extreme climatic events (ECEs) on the population growth rate. Finally, we coupled this demographic stochastic model to IPCC-class climate projections and project wild turkey population abundance in response to the forecasted frequency of extreme snow events by 2100 for the northernmost population (step 3 of the MUP approach, Fig. 1).

Study area

Our study area was located in southern Quebec, Canada, where the landscape is characterized by a mosaic of farmland and privately owned forest from the deciduous Nordic temperate zone (Fig. 2). This represents the northeastern range limit of wild turkeys (Hughes and Lee 2015). Within this region, we selected three study areas (Table 1; Lavoie et al. 2014) that offered a latitudinal gradient in winter harshness: Huntingdon (southernmost; approximate centroid 45.078792, − 74.170543), Dunham (intermediate; approximate centroid 45.141063, − 72.678462), and Asbestos (northernmost; approximate centroid 45.763869, − 71.978084). The northernmost area annually receives more than twice the snowfall from the southernmost area and has a higher proportion of forested cover (Table 1). Physical characteristics and the gradient in climate harshness are described in Lavoie et al. (2017).

Capture methodology

To quantify the impact of snow, rain and temperature on wild turkey, we previously estimated the functional relationship between these climate variables and vital rates using capture-recapture data (Lavoie et al. 2017). During our 3-year study (2010–2013), we captured a total of 344 wild turkeys and classified individuals as adult (> 1 year) or yearlings (< 1 year) and determined sex based on feather coloration. We used Teflon cord looped underneath each wing to radiotagged 161 females (Table 1) with a very high frequency (VHF) radiotransmitters (Advance Telemetry Systems, Isanti, Minnesota, USA; Sirtrack, Havelock North, New Zealand) and 24 with an Argos/GPS transmitters (Microwave Telemetry Inc., Columbia, Maryland, USA; Lavoie et al. 2017). We used ground triangulation to localise VHF radiotagged birds at least twice per week during nesting and once per week the rest of the year. We schedule Argos/GPS transmitters to collect 5 locations during a period of 24 h. We followed some individuals for more than 4 years but the average was 270 and 253 days for VHF and Argos/GPS transmitters, respectively (Lavoie et al. 2017). More details on capture methodology are given in Lavoie et al. (2014, 2017).

Life cycle

The wild turkey is a relatively short-lived species (life expectancy at birth between 2 and 5 years; Pollentier et al 2014, this study). Females reproduce during their second summer from April to August and may attempt a second brood if the first

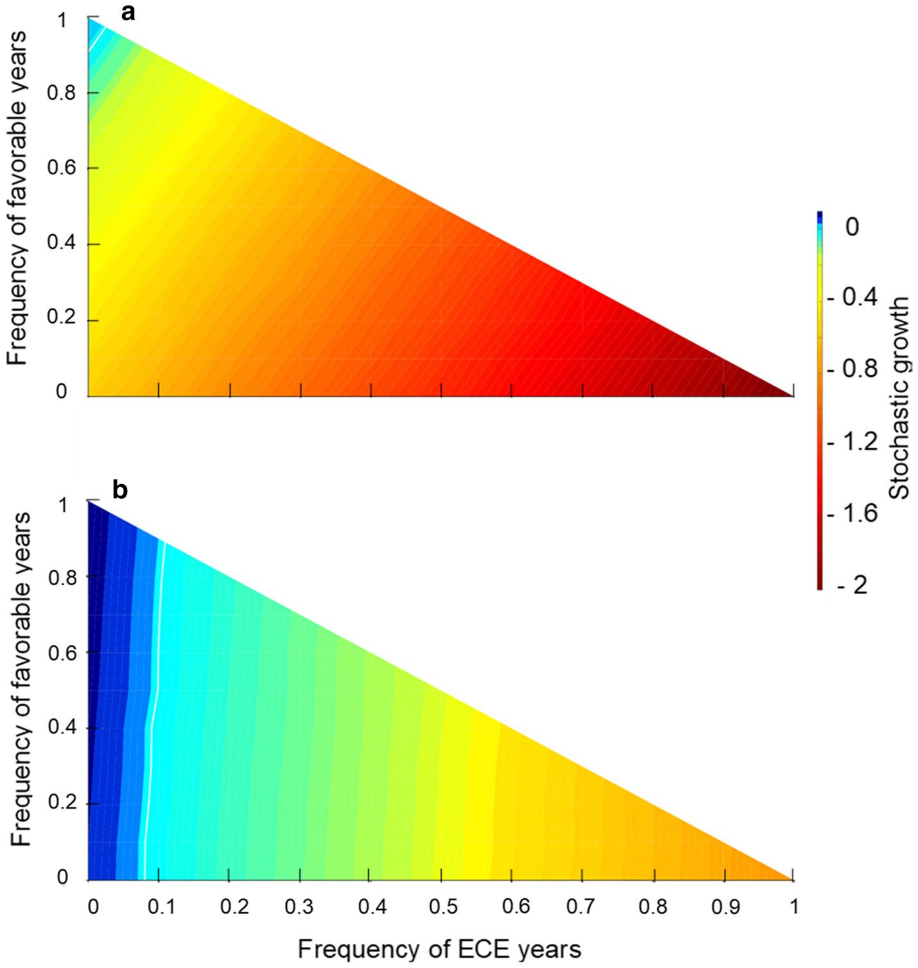


Fig. 7 Stochastic analysis of the effect of extreme harsh and favourable conditions for **a** temperature and rain variations within the historical and **b** for most favorable temperature and rain variations observed on the stochastic population growth rate of wild turkeys at the northern limit of their range in southern Quebec, Canada. The white contour represents the stable population (stochastic growth rate of zero)

clutch of eggs is depredated. Female lay on average 10 eggs, and although clutch size does not differ between broodings, hatching success is higher for first nesting attempts (Lavoie et al. 2017). However, nest and hen survival on the nest is lower for first nesting attempts. Because the number of nests produced influences vital rates (Lavoie et al. 2017), the annual life cycle includes four stages based on reproductive status: (1) yearlings, (2) non-nesting adults, (3) adults attempting one nest and, (4) adults attempting two nests (Fig. 3).

The transitions between these stages are conditional on vital rates during multiple seasons through the year (Supplementary Appendix S1). Specifically, the transitions are function of 15 vital rates for each reproductive stages for a total of 60 demographic parameters (Supplementary Appendix S2).

The life cycle describes a pre-breeding population model structured by reproductive stages that projects the population just after winter between year t and $t+1$ using:

$$\boldsymbol{n}(\boldsymbol{t}+1)=\boldsymbol{A}\boldsymbol{n}(\boldsymbol{t}), \tag{1}$$

where $\mathbf{A}$ is the annual population transition matrix and contains the 60 demographic parameters, and $\mathbf{n}(t)$ a vector giving the number of individuals in each reproductive status stages (Caswell 2001).

Climate data

Snow (S) and rain (R) accumulation, and temperature (T) affect the life history of wild turkey (Lavoie et al. 2017). Specifically, survival of wild turkeys decreases sharply when snow cover remains above 30 cm and at a faster rate as temperature decreases (Lavoie et al. 2017). Additionally, an increase in daily rain over the previous 9 to 14 days decreases nest survival (Lavoie et al. 2017). We used these relationships to perform our analysis. Weather data were acquired from a meteorological station located in the middle of each study area (southernmost = 45.05, − 74.16667; intermediate = 45.15, − 72.81667; northernmost = 45.66667, − 71.73333), obtained from Environment Canada. These stations were located in a similar habitat and are not under forested cover but in open fields. Furthermore, as weather stations in southern Quebec are not evenly distributed across the landscape and between our three study areas, we believe

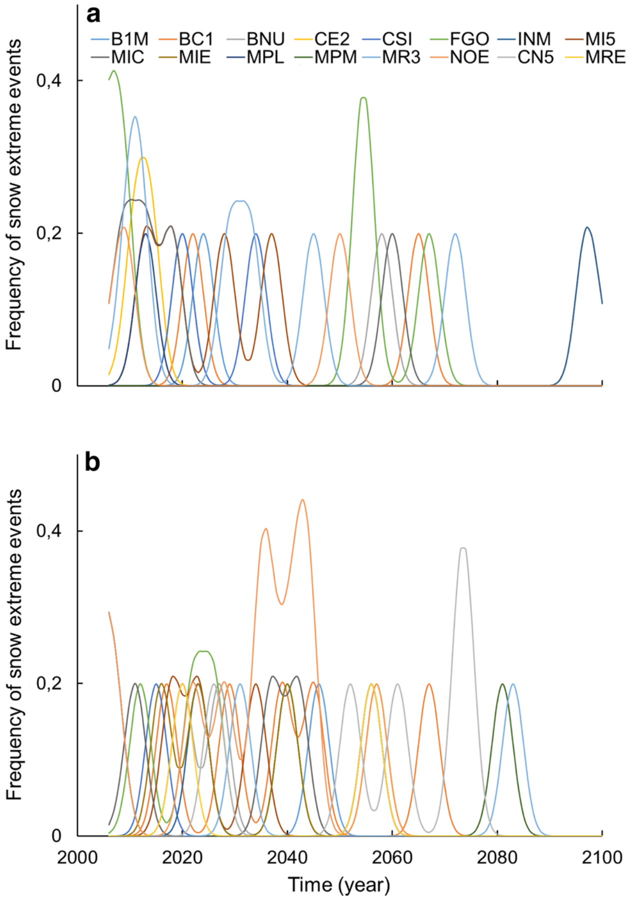


Fig. 8 Frequency of extreme snow events in January produced by **a** 14 CMIP5 models forced using RCP4.5 and **b** 16 CMIP5 models forced using RCP8.5. Each line represents a different CMIP5 model

that using only one station located in the middle of each study area our analysis would be more comparable.

Furthermore, we studied the impact of Extreme Climatic Event (ECE) using an impact-related definition: a climatic episode in which a statistically unusual or rare weather alters the demographic response well outside the boundary of what is considered normal variability (Smith 2011). Defining an extreme event is a challenge (de Pol et al. 2017; Latimer et al. 2019), and we combined the functional response of the vital rates and population growth to environmental conditions with our observations to define an extreme snow fall event as the one observed in 2011 (Lavoie et al. 2017, Table 2). We thus distinguish favorable conditions as conditions that do not impact the winter survival (snowfall < 30 cm), from harsh conditions with snow conditions that reduce winter survival (2011 value > snow > 30 cm) to extreme persistent snow cover that dramatically decrease winter survival (extreme snow cover observed in 2011 for three consecutive months; Fig. 4). As temperature and rain alone cannot limit wild turkey populations, we only used snow depth to define an ECE (see Results, Fig. 6, Supplementary Appendix S8). However, temperature and rain were also included as a component of the ECE analysis.

Deterministic demographic analysis

We performed a deterministic analysis to understand the demographic mechanisms for each of the three populations and their response to climate variables. A deterministic analysis for a given year or set of environmental conditions describes the consequences of maintaining those conditions permanently. Specifically, we (1) calculated the life expectancy of individuals for each population, (2) calculated the population growth and structure, (3) performed a prospective analysis to project how variations in vital rates, independently of their past variations, would affect the growth rate (Caswell 2000), (4) performed a retrospective analysis to evaluate how the inter-annual variations in vital rates we observed influenced the variability in the growth rate (Caswell 2000), and (5) incorporated the effect of climate on the life cycle to project the impact of snowfall, rainfall and temperature on the growth rate (Fig. 1).

First, we evaluated the life expectancy using absorbing Markov chain (AMC) models that only contain the transitions of individuals alive in the population (see Caswell 2009). We used the data averaged from 2010 to 2013 to parameterize the AMC at each location.

Second, we calculated the deterministic growth rate and stable age distribution as the dominant eigenvalue and right eigenvector of the population matrix $\mathbf{A}$. We used the data averaged from 2010 to 2013 to parameterize the population matrix $\mathbf{A}$ at each location. We calculated the deterministic growth rate each year using a population matrix $\mathbf{A}_t$ with t varying from 2011 to 2013 for each population, using the demographic data observed.

Third, we applied a prospective analysis to identify vital rates with high proportional sensitivities (i.e., elasticities), which have the potential to produce the largest changes in the growth rate. The elasticity of the population growth rate to a given demographic rate is provided by analytical matrix formula described in Caswell (2001).

Fourth, we used a retrospective analysis to estimate past contribution of each vital rate to observed changes in the growth rate. We included the variance and covariance of each demographic parameter into a random design Life Table Response Experiment (LTRE) for the three areas and 4 years of our study (Caswell 2001). This analysis decomposes the variance of the growth rate into contributions from the variability of each matrix entries and vital rates and details are provided in Caswell (2001).

Fifth, to understand the impact of weather conditions on the population growth rate, we developed a climate-dependent population model by incorporating the functional relationship between vital rates and weather.

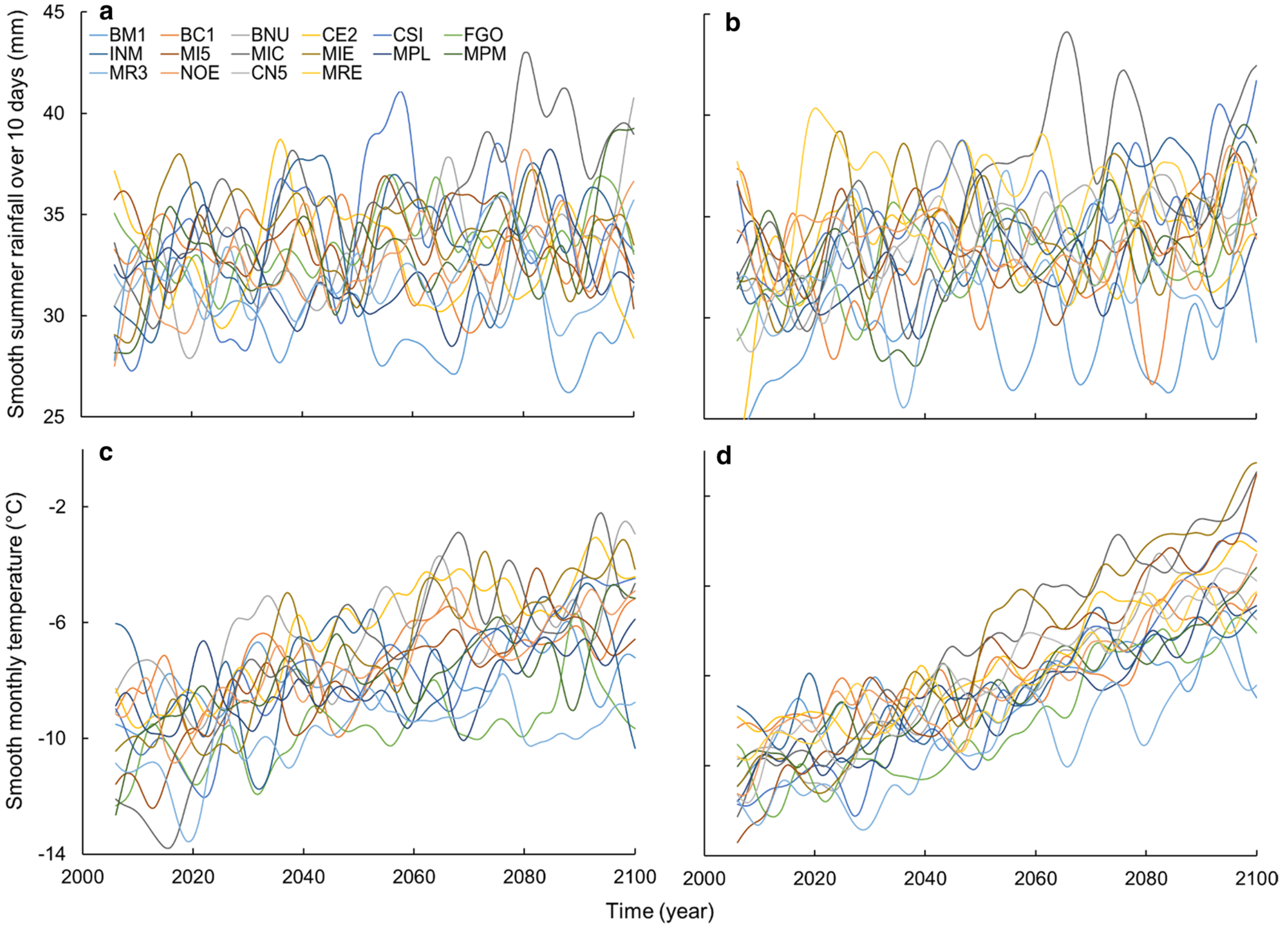


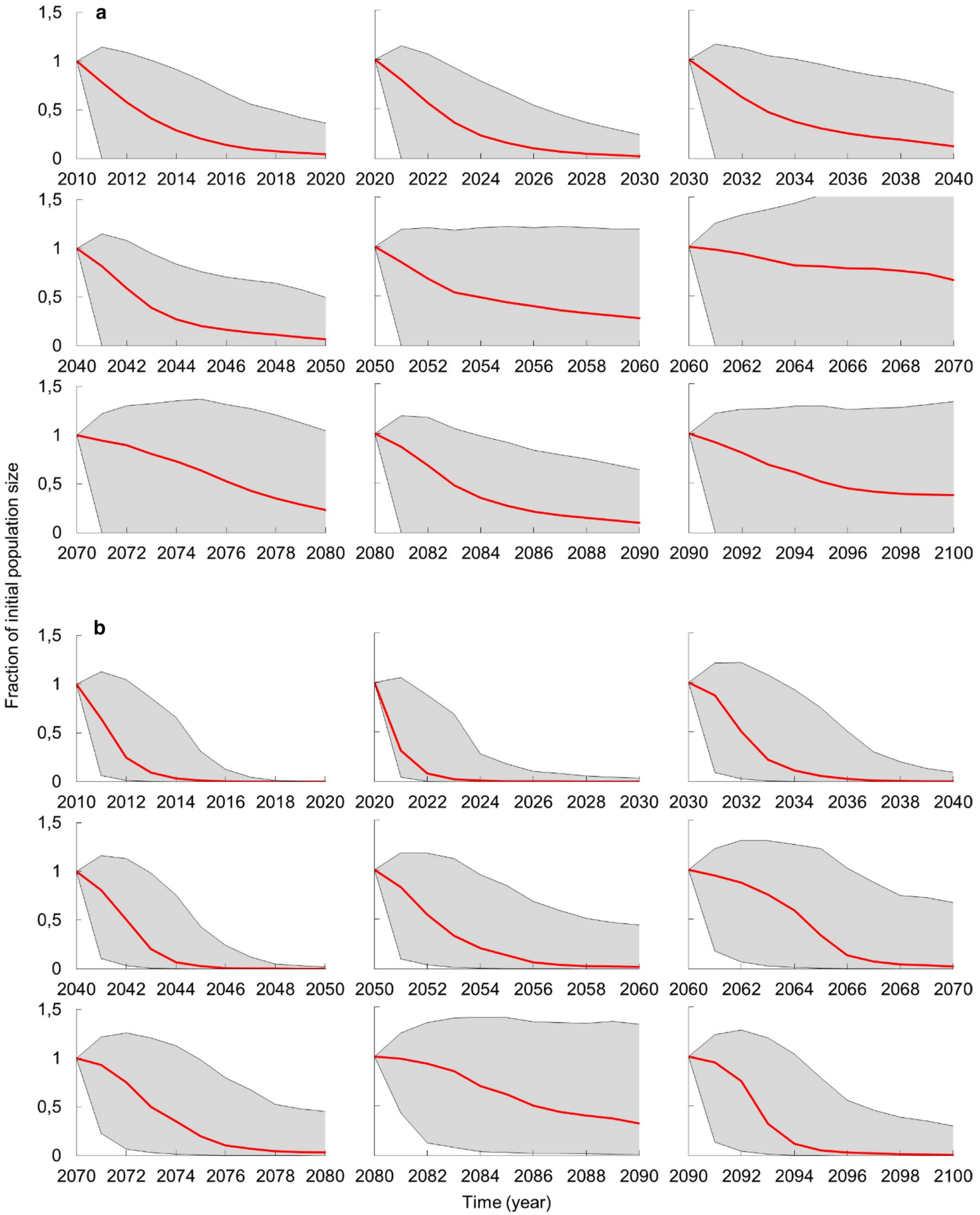
Fig. 9 Forecasted **a**, **b** rain and **c**, **d** temperature in January produced by **a**, **c** 14 CMIP5 models forced using RCP4.5 and **b**, **d** 16 CMIP5 models forced using RCP8.5. Each line represents a different CMIP5 model

Specifically, we projected the matrix **A** using daily weather data averaged for the whole period from 1999 to 2014 using historical weather data and calculating the population growth rate. This 15-year period was used to evaluate the recent population trend as there is no time series of population size of wild turkey available.

Then we studied the respective impact of snow, rain and temperature on the growth rate by varying these climate variables within a range set by their historical variations. The value used for snow is only applied from January to March as the snow cover during other months does not reach 30 cm and thus has no effect on winter survival (Lavoie et al. 2017). For rain, the daily value used remains constant for the 28 days that affect nest success. We only held rain constant for the deterministic demographic analysis. This allowed to understand the impact of rain conditions on the population growth rate. However, when we performed the subsequent analyses, rain varied from year to year. Then we projected the set of vital rates from the functional relationship and calculated the deterministic growth rates from the population matrix **A**.

Stochastic demographic analysis

We developed a stochastic population model to study the impact of an increase frequency of ECE on the population growth rate by accounting for the variation associated with the capture-recapture estimation procedure (sampling uncertainty; Link and Nichols 1994) and the variation in environmental conditions (environmental stochasticity; Fig. 1). The environmental stochasticity includes the influence of the combined seasonal and inter-annual variations of climate and environmental stochasticity not related to our specific weather variables. As snow cover is the main driver of population dynamics, we developed a model projecting the stochastic population growth rate as a function of the frequency of harsh and extreme snowfall. Thus, we distinguished three environments: favorable, harsh and extreme depending on


a
b
Fraction of initial population size
Time (year)
0
0,5
1
1,5
2010 2012 2014 2016 2018 2020
2020 2022 2024 2026 2028 2030
2030 2032 2034 2036 2038 2040
2040 2042 2044 2046 2048 2050
2050 2052 2054 2056 2058 2060
2060 2062 2064 2066 2068 2070
2070 2072 2074 2076 2078 2080
2080 2082 2084 2086 2088 2090
2090 2092 2094 2096 2098 2100

◂**Fig. 10** Projection of the total population size of the wild turkey at the northern limit of their range in southern Quebec, Canada, produced by **a** 14 CMIP5 models forced using RCP4.5 and **b** 16 CMIP5 models forced using RCP8.5. Each panel shows the population projections of an immigrant population (size scaled relative to 1) which expanded the northern range a given year (panels are for every 10 years). To compare the panels, only the 10 first years after expansion are shown (xlabel). The thick red line represents the median of, respectively, 1,400,000 (RCP4.5) and 1,600,000 (RCP8.5; 100,000 each model) stochastic projections based on snow, temperature and rain forecasts. The 95% confidence envelope is shown in gray

whether snow conditions would trigger a negative threshold-like (non-linear) growth rate response (harsh environment) or would alter growth rate well outside the bounds of what is considered ordinary variability (extreme environment). After selecting the main environment based on snow cover, we accounted for environmental stochasticity by integrating rain and temperature randomly over the historical range.

We evaluated the stochastic growth rate numerically. We began with an initial vector where the numbers in the four stages of the annual life cycle (Fig. 3) were based on the stable age distribution obtained from the left eigenvector of the matrix A for an environment characterized by favorable conditions. At each time step, we draw independently an environment with probability f of a favorable year and e of an extreme year, and 1-f-e for a harsh year. For favorable and harsh environments, the population matrix was parameterized randomly by sampling the vital rates from 2010 to 2013 or projecting the vital rates from their response to weather within the range set by the given environment; i.e. $0 < snow\ cover < 30$ cm for favorable, $30 < snow <$ extreme threshold for harsh or $>$ extreme for extreme conditions; and randomly over the historical range for temperature/rain. For the extreme environment we used the population matrix of 2011, an extreme year in term of snow cover as it stand out from the 95% envelope of historical variability (Fig. 4). This model avoids extrapolating the response of the vital rates to environmental factor beyond the observed range of snow, rain and temperature and our projection are conservative in the sense that they do not project worse demography than the one observed in 2011.

We used Monte Carlo simulation using $T = 20{,}000$ iterations to estimate the stochastic growth rate. (λ_s; Caswell 2001) using the following equation:

$$\log\lambda_s = \lim_{T\to\infty}\frac{1}{T}\log\|\boldsymbol{A}_{T-1}\ldots\boldsymbol{A}_1\boldsymbol{A}_0\|. \tag{2}$$

Demographic projection under future climate change

The stochastic model describes stochastic population growth in a stationary environment characterized by specified frequencies of favorable or extreme snow years, meaning that these frequencies will not vary significantly over time. However, climate change is expected to alter the frequency of climatic extremes. Only a demographic model coupled to a projection of future snow, rain, temperature conditions in response to climate change obtained from climate models can account for this non-stationarity (Hunter et al. 2010; Jenouvrier 2009, 2012, 2013; Iles and Jenouvrier 2019). Thus, we used future climate conditions projected by the fifth phase of the Coupled Model Intercomparison Project (CMIP5) produced by the Intergovernmental Panel on Climate Change (IPCC 2013), hereafter IPCC-class models (Fig. 1, Supplementary Appendix 3).

We computed future climatic forecasts of monthly snow accumulation and temperature, and rainfall accumulation over a period of 10 days, that are the variables included in the functional relationship between vital rates and climate (Lavoie et al. 2017, step one of MUP approach Fig. 1), using IPCC-class models. Our study area covered between 1 and 8 grid points depending of the model used. We extracted daily values of maximum and minimum temperature, precipitation and snow amount for the selected simulations for the period 1982–2100. We bias-corrected the raw simulation data using the quantile mapping approach proposed by Mpelasoka and Chiew (2009). We used the NRCan ANUSPLIN gridded observation dataset (Hutchinson et al. 2009) for climatic reference for temperatures and precipitation. We spatially averaged the higher resolution reference grid points to match the lower resolution climate simulation grid points. We then applied a moving window approach to build transfer functions for each day of the year using 15 days prior to and after the day being corrected. For snow, we used a local record of snow water equivalent at Huntingdon, QC as the reference for corrections. Additive correction was used for minimum and maximum temperatures, precipitation was corrected multiplicatively. To consider uncertainties in future greenhouse gas concentration trajectories (Moss et al. 2010), we used two Representative Concentration Pathways (RCPs) adopted by the IPCC for its fifth Assessment Report: 4.5 (RCP4.5) and 8.5 (RCP8.5). These forcing correspond to two different greenhouse gas concentration trajectories until 2100 that anticipate global socio-economic evolution affecting gas emissions and climate change. Indeed, the RCP8.5 scenario assumes that greenhouse gas emissions will increase almost linearly until 2100 (Riahi et al 2011) while the RCP4.5 scenario supposes that they will be stabilized by the middle of the century (Thompson et al. 2011).

To consider uncertainties in climate projections (e.g. atmospheric and oceanic circulations, soil use and management), we used 16 global climate models (Supplementary Appendix S3). We limited our analyses to the first member (simulation) of each models to avoid overrepresentation of models with more members. Nevertheless, our approach

Table 1 Characteristics of the three study areas in southern Quebec, Canada

	Huntingdon (southernmost)	Dunham (intermediate)	Asbestos (northernmost)
Mean annual snowfall (cm)	160	283	344
Mean annual rainfall (mm)	802	998	889
Mean annual temperature (°C)	7.0	6.0	4.3
Mean winter temperature (°C)	− 2.6	− 2.9	− 4.9
Number of VHF radiotagged adult hens	33	35	15
Number of VHF radiotagged juvenile hens	18	25	35
Number of Argos/GPS radiotagged adult hens	0	0	24
Number of Argos/GPS radiotagged juvenile hens	0	0	0
Proportion of forested cover (%)	42	66	61
Proportion of crops land (%)	55	24	34

We used climate data provided by local government authorities from 1979 to 2008, covering 30 years prior to our study, to describe the historical gradient of winter harshness

accounts for stochasticity of climate related to natural variations.

For snow forecast, we account for stochasticity in climate by producing a forecast of future frequencies of favorable and extreme snow events, and then by randomly drawing the future climate state at year *t* within 3 environmental states according to these frequencies of favorable (*f*), and extreme snow (*e*) conditions. For example, to produce a forecast of extreme snow event, we classified each year as extreme or not (i.e. favorable or intermediate), by comparing the snow forecasted in that year to a specified snow cover threshold value. The result is a binary sequence of extreme snow year and normal years, produced by each climate model and each scenario, for the rest of the century. Then these sequences were translated into forecasts of the frequency of extreme snow events, using nonparametric smoothing (Jenouvrier et al. 2009).

For the projection of rain and temperature, we generated stochastic climate forecasts following the approach developed by Jenouvrier et al. (2012). Specifically, we calculated the smoothed means and variance using a Gaussian kernel smoother with smoothing parameter $h = 2$.

In summary, for each RCP and each of the GCMs, six times series are produced: two of projected values of *f* and *e* from 2006 to 2100 for snow cover, two of projected values of smooth mean for rain and temperature respectively, and two of projected values of smooth variance for rain and temperature, respectively. From these times series, we generate 100 stochastic climate forecasts, by drawing the extreme snow event with probability *f* and drawing a specific rain and temperature value from a normal distribution with mean and variance given by the smoothed mean and variance at year *t*. We used these climate time series to project the wild turkey population at their northern range.

To mimic the emigration of invaders from southern population, we project the population from time t_0 to t_{0+9}. We set t_0 as the first year of each decade of the century. At each initial time, we use an initial population vector $\mathbf{n}(0)$ given by the stable age distribution in favorable conditions. We project the population forward using Eq. 2 given the environmental state defined by stochastic climate forecasts. Specifically within each of the three snow environments the population matrix is parameterized with rain and temperature obtained from the stochastic forecast. If the value of rain and precipitation is projected beyond our observed range, we set the condition to the corresponding maxima or minima observed. Furthermore for each climate dependent simulation, we include uncertainty of parameter estimation, and

Table 2 Deterministic population growth rate of wild turkeys from three northern populations representing a gradient of climate harshness during various years and winter severity in southern Quebec, Canada

Year	Area	Winter severity	Population growth rate
2011	Southernmost	Favorable-harsh	1.08
2012	Southernmost	Favorable	0.99
2013	Southernmost	Favorable	1.12
2010	Intermediate	Favorable-mild	1.28
2011	Intermediate	Favorable	1.22
2012	Intermediate	Harsh	0.98
2013	Intermediate	Favorable	1.07
2011	Northernmost	Extremely harsh	0.40
2012	Northernmost	Harsh	1.04
2013	Northernmost	Favorable-mild	1.18
2010–2013	Overall population	1 year of extreme events	0.95
1999–2014	Overall population	11% of extreme years	1.04

We used the 15 years prior to the end of the study (1999–2014) to evaluate the recent trend other environmental factors, by drawing randomly parameters from a multi normal distribution using 100 simulations. Thus, we run a total of 100*100*16 GCMs = 160,000 simulations for the RCP 8.5 scenario and 100*100*14 GCMs = 140,000 simulations for the RCP 4.5 scenario. We performed all analyses using Matlab (Mathworks, Natick, Massachusetts, USA).

Models of complex biological systems are never true but are meant to provide a useful approximation to reality (Edwards 2013). Consequently, as with all models, our projections are dependent on the assumption that our sample is representative of turkey dynamics under a wide variety of conditions. Specifically, we hypothesize that future snow depth, temperature and rain will be similar to those projected by our selected IPCC-class models, that extreme climate events will affect the demographic rates as the only ECE recorded did during our study, and that wild turkey demographic rates collected from 3 marked population over 4 years are representative of other northern populations. Indeed, we expect snow cover restriction on food access to operate globally at the northern limit of the wild turkey's range even if local population will respond differently to climate-change considering access to artificial food sources or immigration rates. However, as we employed a state-of-the-art approach that consider uncertainties in parameters estimation, environmental factors, future greenhouse gas concentration and climate projections, our results are robust. To improve this study, more data are needed to assess the variability and uncertainty in demographic rates under extreme climate events as well as the role of ongoing immigration in helping the northern population to persist (Niedzielski and Bowman 2014).

We acknowledge that hindcasting is a useful approach for evaluating model performance. It would consist to force a demographic model with past climate variables, like we do in the climate-dependent population model section, and evaluate how well the wild turkey population trends match with known observations. Unfortunately, there are no observation of past population dynamics to compare our projected population growth using past snow, rain and temperature data. However, the slightly positive growth rate estimated for the whole period from 1999 to 2014 using historical weather data is compatible with the observed trend in hunting success and support our model.

Results

Deterministic demographic analysis

The deterministic population growth rate varied across years and areas (range of $\lambda = 0.40–1.28$) and was at its lowest level under extremely snowy conditions (Table 2). Under favorable winters, the southern population did not increase as much as populations in the northernmost and intermediate areas. Furthermore, inter-annual variability in the growth rate followed the gradient of climate harshness and increased from south to north. During the 4 years of the study (2010–2013), we experienced a year of extreme events and the overall population declined (Table 2).

The prospective analysis shows the differences between the three areas in their sensitivity of the growth rate to changes in the transitions of the life cycle (i.e. matrix entries; Supplementary Appendix S4, Fig. 5). The stage with the highest impact on the growth rate was adults attempting two nest staying in the same stage in the southernmost area and the production of new offspring in the intermediate and northernmost areas. For the three populations, the sensitivities of the growth rate λ with respect to winter survival had the highest impact (supplementary Table S5). However, the population growth rate was more sensitive to winter adult survival in the southernmost area while it was more sensitive to winter yearling survival in both the intermediate and northernmost areas (supplementary Table S5).

The retrospective analysis revealed differences in the contribution of each life stage to the growth rate variations between the three populations. Indeed, the largest contributions occurred from adults attempting two nest staying in the same stage in the southernmost area, the transition from yearling to adults attempting one nest in the intermediate area, and the production of offspring by yearling in the northernmost area (Supplementary Appendix S4, Fig. 5). Among demographic parameters, in the southernmost population, population growth rate variations are most influenced by nest success of the yearlings, while in the northernmost and intermediate populations, variations are most influenced by winter survival of the yearlings (Supplementary Appendix S5).

The life expectancy at birth was higher in the southernmost area (3.6 years), intermediate in the middle are (3.1 years), and lower in the northernmost area (2.0 years), following the gradient of winter harshness. Accordingly, there was a lower proportion of yearling within the population at equilibrium in the southernmost area compared to the other two areas (Table 3).

For both populations, the deterministic population growth rate of wild turkeys remained relatively constant at 1.15 under 30 cm of snow cover. However, above this threshold, the growth rate decreased dramatically and at a faster rate as temperature decreased and rain increased (Fig. 6). The effect of temperature and rain was insignificant when snow was less than 30 cm because turkeys have more ease finding food under that threshold (Lavoie et al. 2017).

Table 3 Stable age distribution obtained from the right eigenvector of the population matrix **A** for four reproductive status stages and three northern populations of wild turkeys along a gradient of winter harshness in southern Quebec, Canada

Stages	Southernmost	Intermediate	Northernmost
Y_f	0.33	0.41	0.45
F_0	0.04	0.06	0.03
F_1	0.27	0.35	0.25
F_2	0.36	0.18	0.27

The four stages are yearlings (Y_f), non-nesting adults (F_0), adults attempting one nest (F_1), and adults attempting two nest (F_2)

Stochastic demographic analysis

The stochastic analysis revealed that when the frequency of extreme winter events and/or the frequency of harsh environments increases, the population growth rate decreases. Figure 7 shows that the population declines when extreme weather events exceed a frequency of 10%, despite favourable temperature and rain conditions. If the frequency of favourable snow conditions is null, the population is predicted to decrease for a frequency of 8% of extreme winter events. However, if temperature and rain vary randomly in the observed range of values, the population is predicted to decline even in the absence of ECE. The population is predicted to increase only if the frequency of harsh event remain below 9%. Consequently, temperature and rainfall greatly impact wild turkey population persistence as the population is not viable even when snow extreme events never occurs.

Demographic projection under future climate change

The probability of extreme snow accumulation is projected to decrease during the next 100 years in southern Quebec (Fig. 8, Supplementary Appendix S6). However, depending on the month, the probability of extreme snow accumulation remains as high as 8% by the end of the century. On the contrary, projected winter temperature and, to a lesser extent, rainfalls are expected to increase (Fig. 9, Supplementary Appendix S6).

Wild turkey populations at the northern limit of their range are projected to decrease within the next century (Fig. 10). Because a population at the northernmost limit is predicted to decline rapidly, we project an immigrant population every ten years between 2010 and 2090 to mimic a source and sink dynamic. Under the RCP 8.5 scenario, an immigrant population is very likely to decline below 10% of their initial size over 10 years, except if individuals migrate in 2080. This exception illustrates that it is difficult to predict the persistence of an immigrating population because future climate change are non-stationary, and coupling demographic models to IPCC-class climate models is necessary. Under the scenario RCP 4.5, population trajectories are also projected to decline, but a population of immigrants is less likely to be extinct after 10 years following the expansion. For example, if individuals migrate in 2060, the median population size is projected to slowly decline by about 33% after 10 years relative to initial population size. Furthermore, the projected median decline is smaller when the population is projected from an initial timing after 2050.

Discussion

The population growth and structure of wild turkey, as well as the mechanism underlying the population dynamics, are contrasted among three populations along a latitudinal gradient of climate conditions. While the functional response of the three populations to climate conditions is the same, they experience different snow, rain and temperature conditions that influence population dynamics. Snow cover is the main driver limiting the population growth rate. However, it is a combination of rain, temperature and extreme snow events that preclude the persistence of the population without immigration at the northern species range. Linking projection projections of snow cover, rain and temperature from General Circulation Models (GCM) of Earth's climate included in the most recent Intergovernmental Panel on Climate Change (IPCC) assessment report, we show that the northernmost population of wild turkey is unlikely to be self-sustainable, hence without immigration, their permanent range will probably not move poleward by 2100.

Populations differ in their growth and structure along a latitudinal gradient of climate conditions

Animals inhabiting the edge of the species distribution may display higher reproductive parameters and population growth especially while establishing (Baker 1974; Sol et al. 2012). This is especially true for short-lived species where the risk of dying before the next breeding season is high (Ricklefs and Wikelski 2002). In the southernmost area of our study, wild turkeys have first been observed in 1976, while the other two areas were colonized more recently (1992 and 1997, respectively). Our analysis suggests that the southernmost population is likely increasing but close to saturation, while the two other populations are still at the demographic expansion front. Indeed, the inter-annual variation of the population growth rate λ were lower in the southernmost area and population increased on average at a rate of 6% per year, while λ showed larger inter-annual variations in the northernmost areas with high positive (18% increase per year) and extremely low negative values (60% decline per year). Furthermore, the age structure of the population changed from a higher proportion of younger individuals in the north to older birds in the south. The life expectancy of individuals breeding in the north is indeed shorter than the ones breeding in the south.

The classical theory of biological invasion predicts that species should prioritize reproductive effort over survival during the phase of establishment (Lodge 1993; Sol et al. 2012). This should increase population growth rate and reduce the vulnerable period when demographic stochasticity is high. As expected, different mechanisms control population dynamics in the three populations related to a southern–northern continuum between high survival and high reproduction life history strategies (Sandercock et al. 2005). Indeed, recruitment and adult survival were, respectively, 1.33 poults per female and 0.62 for the southernmost population, 1.43 poults per female and 0.63 for the intermediate population and 2.16 poults per female and 0.52 for the northernmost population. Furthermore, in the south the transition to remain a nesting adult from one year to another had the largest sensitivity and contribution while in the north it is the fecundity of yearlings, revealing a fast-paced life history strategies at the northern population compared to a relatively slow-paced life history at the southern population.

Winter conditions drive population dynamics

The functional relationships between climate and vital rates are the same for the three populations. Therefore, the local climate conditions experienced by these populations may set whether or not wild turkey can persist at the limit of their species range and move poleward. In the north, the annual average snowfall is least two times higher than in the south, while air temperature is at least two times colder. These two weather variables are crucial for survival of wild turkey at the northern range of their distribution. Indeed, survival drastically decreases when snow depth remains above 30 cm for more than 10 days and when temperature is colder (Lavoie et al. 2017). This highlights the contrasted effect of various seasons through different phase of the life cycle and the need to account for these various effects when projecting population responses to climate change as rate and intensities of change vary across season (Jenouvrier 2013).

By integrating the effect of rain, temperature and snow cover in a population model, our deterministic analysis reveals that snow depth is the main factor affecting the population growth rate through its effect on winter adult survival. Temperature has only an effect when monthly snowfall is higher than 30 cm. However, it has important consequence for population dynamics as the population decline, caused by snow depth, is reduced when temperature increases. Heavier daily rain reduced the population growth, but did not result in negative population growth rate over the historical range when snow cover is below than 30 cm. Thus, the biogeographic limit of wild turkeys is defined by snow accumulation that restrains food access (Wright et al. 1996) and to a lesser extent winter temperatures (Lavoie et al. 2017) that yields increased metabolism and energy requirement (Haroldson et al. 1998).

Population growth depends on extreme snow depth

A population at the cold edge of the species distribution usually stays at low numbers and vary according to environmental factors (Zimmermann et al. 2009; Aikio et al. 2010). ECE have more severe impacts on population at the limit of species distribution, because the population may experience climatic conditions at the edge of the climatic niche (Hijmans and Graham 2006; Williams et al. 2008; Princé and Zuckerberg 2015). For example, during warm episodes of El Niño Southern Oscillation some populations experience rapid expansion in their distribution with setbacks during cool periods (Holmgren et al. 2001; Walther et al. 2002). During the last 15 years, direct field observations and locations of harvested wild turkeys showed that wild turkey abundance has been increasing northward. Our demographic model is consistent with that trend. However, an opposite tendency may have occurred during the last 4 years of the study because the northern population experienced a persistent and large snowfall during three consecutive months. This extreme snow event resulted in the loss of 70% of tracked birds and, as a consequence, an extremely low population growth. Likewise, long-term viability of an isolated population of black grouse (*Tetrao tetrix*) in England was jeopardized by an historic severe winter with prolonged snow (Warren et al. 2013).

Our stochastic analysis shows that if harsh or extreme snowfall occurs with variable temperature and rainfall similar to those observed over our historical period, the population at the northern species range will decline to extinction. The stochastic population growth rate is slightly positive only if the frequency of harsh environment is very low and extreme events is null. However, if the winter temperature and rainfall are the most favorable, they will dampen the effect of harsh conditions and extreme snow events. Indeed, if ECE occurs with a frequency lower than 8%, the stochastic population growth rate is positive for any frequency of harsh conditions. Thus, a combination of limited snowfall and rainfall with warmer temperatures are the keys to predict the successful establishment of a viable northern populations of wild turkeys.

The northernmost population may experience a source and sink dynamic typical of population at the edge of their range (Järviven and Väisänen 1984; Sagarin et al. 2006) and its current occurrence is set by dispersers from nearby sources populations. To predict whether or not an immigrant population will persist at the northern species range under future climate change, it is necessary to couple a climate-dependent demographic stochastic model to climate projections from IPCC-class models (Jenouvrier 2013).

Future population projection at the northern species range

Linking population models to IPCC projects that integrate both radiative forcing and natural variability in climate (Jenouvrier 2013) is critically important when extreme events drive population dynamics. Indeed, extreme events may have a larger impact on populations than mean climate (Zscheischler et al. 2014; Pardo et al. 2017) and demographic models need to incorporate their frequency to project population responses to future climate change (Jenouvrier et al. 2015; De Pol et al. 2017).

Using the projection projections of snow cover, rain and temperature from GCM of Earth's climate included in the most recent IPCC assessment report, we found that, at the north of the wild turkey species range, the frequency of extreme snow events is extremely variable, with some climate models projecting a decline, while other projecting that it stay stable (Fig. 8, Supplementary Appendix S6). Climate change should also lead to milder winter conditions that may allow the successful establishment of northern populations of wild turkeys.

The northernmost population is projected to decline by 2100. Our population projections show that each time an event of immigration occur throughout the next century, the population will decline dramatically, being almost extinct after 10 years in most cases. Interestingly the projected median population size decline is smaller when the population is projected from an initial timing after 2050, especially for the RCP scenario 4.5. In most cases, even if the frequency of harsh winter snow events and long spell of cold temperature is projected to decrease, it will remain above the threshold preventing the persistence of wild turkey populations.

By integrating the non-linear effect of climate on the seasonal life history of the wild turkey in a demographic model, we showed that ECE and harsh snowfall may prevent the persistence of wild turkey at the northern part of their range. Noteworthy, warmer temperatures and lower rainfall can buffer the effect of snowfall, and play a key role for potential subtle conditions for the population to persist. Despite that more infrequent snowfall and mild cold spell will arise in the future, our population projections suggest that wild turkey are unlikely to establish further north without immigration. Whether southern populations will be able to sustain a flow of emigrants is an open question. Answering this question require developing the MUP approach as illustrated here for the northern populations.

These results stressed the importance of integrating several climate variables and their effects on species life cycle to improve our understanding and projecting of the ecological response to climate change and ECE. In a recent review on birds, Iles and Jenouvrier (2019) highlighted that there are surprisingly few studies that have developed climate-dependent population models, and even fewer studies linking these population models to climate forecasts from IPCC-class models (17 studies by 2019), especially studies accounting for extreme events (1 study). Those studies are critically needed to inform legal frameworks for implementing conservation and management strategies in face of climate change (Jenouvrier et al. 2021).

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Author contribution statement ML, SJ, PB, SL, and JPT conceived and designed the experiments. ML, SJ and PB performed the experiments. ML and SJ analyzed the data. ML and SJ wrote the manuscript and all authors contributed substantially to the interpretation of the results and edited the manuscript.

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Availability of data and material The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Capture and handling of turkey was approved by the Animal Welfare Committee of Laval University No. 2010018-2.

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