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Article

Predicting Effects of Climate Change on Habitat Suitability of Red Spruce (*Picea rubens* Sarg.) in the Southern Appalachian Mountains of the USA: Understanding Complex Systems Mechanisms through Modeling

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Abstract: Alpine, subalpine and boreal tree species, of low genetic diversity and adapted to low optimal temperatures, are vulnerable to the warming effects of global climate change. The accurate prediction of these species' distributions in response to climate change is critical for effective planning and management. The goal of this research is to predict climate change effects on the distribution of red spruce (*Picea rubens* Sarg.) in the Great Smoky Mountains National Park (GSMNP), eastern USA. Climate change is, however, conflated with other environmental factors, making its assessment a complex systems problem in which indirect effects are significant in causality. Predictions were made by linking a tree growth simulation model, red spruce growth model (ARIM.SIM), to a GIS spatial model, red spruce habitat model (ARIM.HAB). ARIM.SIM quantifies direct and indirect interactions between red spruce and its growth factors, revealing the latter to be dominant. ARIM.HAB spatially distributes the ARIM.SIM simulations under the assumption that greater growth reflects higher probabilities of presence. ARIM.HAB predicts the future habitat suitability of red spruce based on growth predictions of ARIM.SIM under climate change and three air pollution scenarios: 10% increase, no change and 10% decrease. Results show that suitable habitats shrink most when air pollution increases. Higher temperatures cause losses of most low-elevation habitats. Increased precipitation and air pollution produce acid rain, which causes loss of both low- and high-elevation habitats. The general prediction is that climate change will cause contraction of red spruce habitats at both lower and higher elevations in GSMNP, and the effects will be exacerbated by increased air pollution. These predictions provide valuable information for understanding potential impacts of global climate change on the spatiotemporal distribution of red spruce habitats in GSMNP.

Keywords: climate change; physiological mechanisms; red spruce (*Picea rubens* Sarg.); habitat model (ARIM.HAB); simulation model (ARIM.SIM)

1. Introduction

With increasing evidence of global climate change during recent decades, changing distributions of important forest tree species have become of concern [1,2]. Long-term records indicate that earlier phenological development [3,4], range shifts [5,6] and shrinking habitats [7] are all in progress now.

Red spruce (*Picea rubens* Sarg.) is a commercially important boreal species in the eastern United States and Canada. This species has sustained widespread growth decline and high mortality for a half century [8,9]. Alpine, subalpine and boreal trees are generally more susceptible to climate change than other species due to low genetic diversity and migration limitations [10,11]. Red-spruce in the Great Smoky Mountains National Park (GSMNP), its southern distribution limit, is threatened with losses of suitable habitat. Impacts on this and other species in this park have not to date been fully assessed. Responding to the need, this study makes a modeling-based assessment for red spruce by coupling a non-spatial growth simulation model (ARIM.SIM) to a spatial habitat model (ARIM.HAB). These models are described in Koo *et al.* [12–14].

Species distribution models (SDMs) have been used to map plant distributions and predict spatiotemporal variations and range shifts under climate change [15–17]. Correlative SDMs depend on direct correlations between environmental factors and the presence/absence of species. Mechanistic SDMs count on knowledge of biophysical processes [18–21], species' fitness relationships with the environment [22–25] and estimates of many phenotypic parameters [21,26]. In both model types, ecosystem complexity has not been adequately taken into account. This limits predictive power, particularly at local scales, where relationships are fine-tuned. Ecosystems are complex, and this complexity is manifested more by indirect than direct effects [27]. For example, indirect factors influence habitat development [27] when interactions between substrate, precipitation and soil biota produce a nitrogen-enriched patch favoring certain species in a grassland ecosystem [28].

Indirect effects contribute to both within- and across-scale complex ecosystem functioning [29]. Interactions across scales frequently explain nonlinearity, heterogeneity and emergent properties of ecological processes that cannot be predicted based on lumping and extrapolating data and simple up- and down-scaling of observations to a single scale [30]. Failing to explain interactions across scales results in misunderstanding of controlling factors, which can lead to ineffective or erroneous management decisions [31]. Hierarchical models, such as Bayesian statistical models, have been used to quantify interactions across scales [31–33], but still, only a few studies have quantified such interactions [34].

ARIM.HAB, with ARIM.SIM its pixel basis, accounts for a full range of ecological processes defining within- and across-scale red spruce habitat suitability in GSMNP [12]. The dual approach of a non-spatial simulation model providing the basis for a GIS spatial model represents a true complex systems framework for better depicting and predicting spatiotemporal distributions of tree species across landscapes.

2. Materials and Methods

2.1. Study System

GSMNP includes approximately 2070 km^2 of forest ecosystems located in the southern Appalachian Mountains of the southeastern USA (Figure 1). The red spruce-Fraser fir forest complex follows an elevation gradient [35]. Red spruce dominates lower down (1370–1675 m) and Fraser fir (*Abies fraseri* (Pursh) Poir) higher up (>1890 m). Both species co-dominate at mid elevations (1675–1890 m). GSMNP has a temperate rainforest climate; its mean annual temperature and precipitation are 8.5 °C and 222 cm [36,37]. The cool climatic conditions cause short growing seasons, 100–150 days, and frequent cloud immersion [38]. Relief ranges from about 250 m in the valleys to 2025 m at the highest peak, Clingman's Dome [39]. Soils are Inceptisols with abundant surface organic matter [36,40]. Diverse habitats support more than 1570 species of flowering plants and over 4000 nonflowering species [41].

2.2. Environmental Data and Model Scenarios

Regional temperature and precipitation from the years 1939 to 1999 were measured at the airport meteorological recording station in Knoxville, Tennessee. Air pollution (nitrogen oxides (NO_x), sulfur oxides (SO_x) and ozone (O_3)) was estimated from data obtained from the U.S. Environmental Protection Agency [42]. Annual mean temperature was determined by averaging daily temperatures and total annual precipitation by summing daily precipitations for each year. Extreme winter cold temperatures were estimated by averaging the lowest daily temperatures from November to February. Air pollution data for 1998 were used for both 1998 and 1999 due to a lack of 1999 data.

Future regional projections of temperature and precipitation for 2080 through 2099 were extrapolated from the 1980 to 1999 period based on the Intergovernmental Panel on Climate Change (IPCC) regional projections for the eastern USA [43]. IPCC predicted a 3.6 °C increase in annual mean temperature, a 3.8 °C increase in winter temperature and a 7% increase of annual precipitation for the 2080–2099 period compared to values for 1980 through 1999. These projections were median values taken from a set of 21 global models in the multi-model data for IPCC's A1B scenario [43]. Climate change effects on red spruce distribution were also investigated in interactions with three different air pollution emission scenarios for 2080 through 2099: 10% increase, 0% change and 10% decrease.

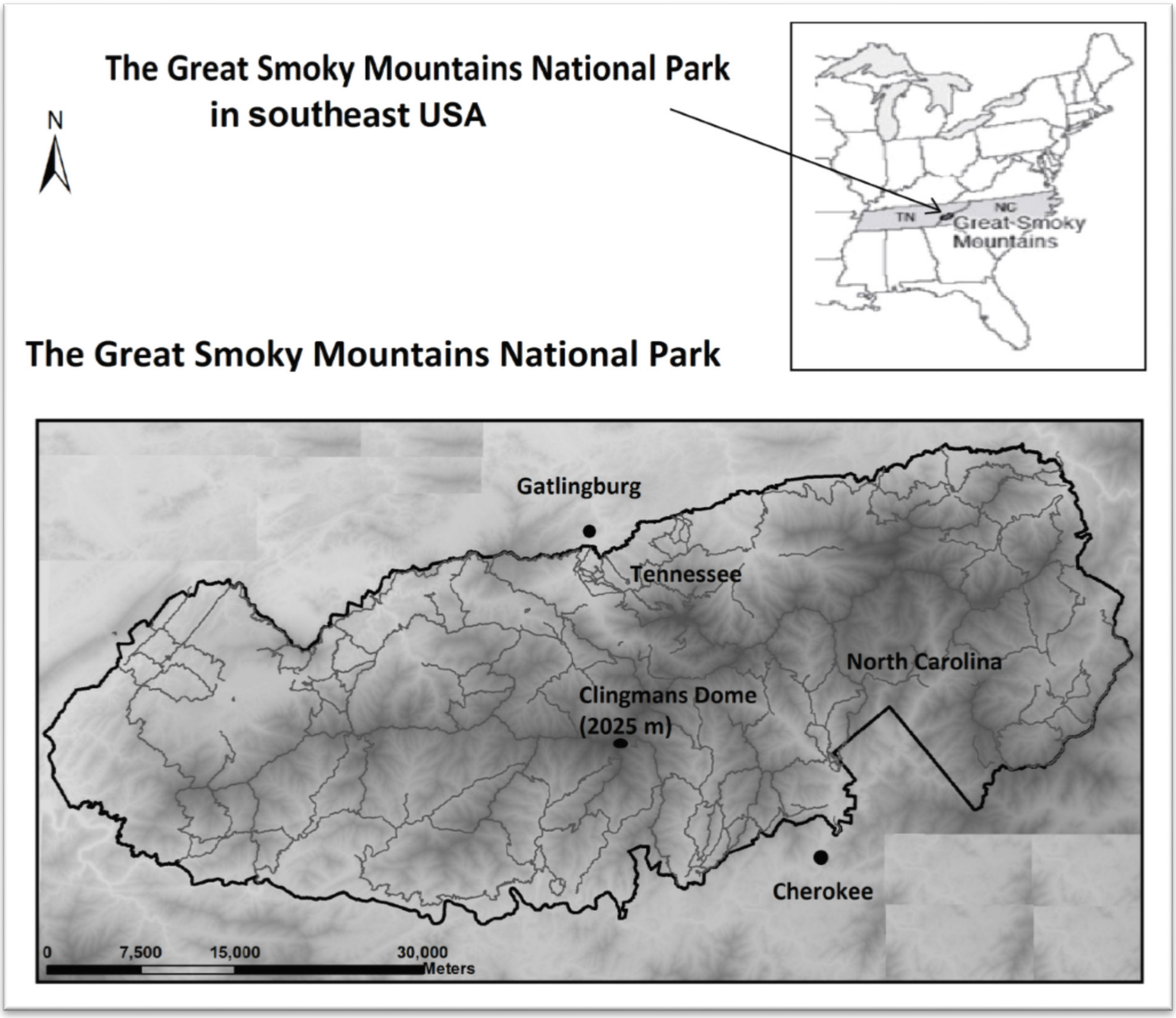


Figure 1. Location of Great Smoky Mountains National Park (GSMNP) in the southeastern United States. Source: Koo *et al.* [12].

2.3. Red Spruce Habitat Model: ARIM.HAB

A spatially-distributed red spruce habitat model (ARIM.HAB) was formulated for GSMNP [12] based on a previously developed non-spatial, dynamic, tree-growth simulation model, ARIM.SIM [13]. ARIM.HAB estimates habitat suitability as the percentage of the presence generated from ARIM.SIM growth predictions [12]. Assuming greater growth reflects higher probabilities of presence, ARIM.SIM simulates red spruce growth for each cell (pixel) in ARIM.HAB to predict spatial climate change impacts on habitat suitability. ARIM.HAB has been described in detail by Koo *et al.* [12].

ARIM.SIM computes annual radial growth as mean standardized ring widths of trees. Red spruce growth differs at high- *vs.* low-elevation sites [37,44]; therefore, separate models were developed for elevations ≥1700 m (ARIM.SIM$_{\mathrm{high}}$) and <1700 m (ARIM.SIM$_{\mathrm{low}}$). The simulated period for ARIM.SIM runs was 1940–1998. Annual growth in these models is mediated by many environmental factors [13,14]; therefore, interannual biomass changes generated by corresponding ARIM.SIM$_{\mathrm{high}}$ and ARIM.SIM$_{\mathrm{low}}$ models are controlled by multiple environmental factors.

$ARIM.SIM_{high}$ simulates air pollution (AP) directly affecting biomass changes of red spruce at high elevations. Air pollution values were not collected in the field, but estimated from simulations with the air pollution submodel (Table 1). $ARIM.SIM_{low}$ is a function of radiation (RA), water availability (WA) and air pollution, which directly influence biomass change at low elevations. The variables *RA*, *WA* and *AP* (Table 1) were obtained from simulations of their corresponding submodels applied to the following equations:

$$ARIM.SIM_{high} = -0.68AP + 1.56 \tag{1}$$

$$ARIM.SIM_{low} = 5.34RA + 11.32WA - 0.27AP - 11.40 \tag{2}$$

Annual values of temperature, precipitation and air pollution were divided by the corresponding long-term mean of the values in order to estimate non-dimensional indices (NDI) [13]. The long-term averages were estimated using data from the 1940 to 2099 period. These non-dimensional index values were then applied to corresponding parameters in the submodels of $ARIM.SIM_{high}$ and $ARIM.SIM_{low}$ to simulate red spruce growth for the periods of 1940 to 1998 and 2080 to 2099.

As explained below, these equations give the annual radial growth of red spruce at high and low elevations expressed in terms of tree-ring index values (mean standardized ring widths, range 0–2). The tree-ring index value is defined by an annual tree-ring width divided by the expected growth predicted by a negative exponential growth function [45].

Table 1. Model equations used for the submodels: air pollution (a), radiation (b) and water (c). This table is from Koo *et al.* [12]. Detailed explanations for the equations are provided in Koo *et al.* [12].

(a) Air pollution submodel.

AP (air pollution) = $(NO_x + SO_x) \times (0.083 + 0.25\boldsymbol{CI} + 0.17\boldsymbol{P}) + O_3 \times (0.17 + 0.33\boldsymbol{AC})$

P (precipitation)

If elevation < 1700 m, then $P = 0.33$ precipitation (measured at the station)

If elevation ≥ 1700 m, then $P = 0.67$ precipitation (measured at the station)

CI (cloud immersion)

If elevation < 1400 m, then $CI = 0$

If 1400 ≤ elevation < 1800 m, then $CI = 0.5$

If elevation ≥ 1800 m, then $CI = 1$

AC (acidic rains and cloud)

$AC = (NO_x + SO_x) \times (0.083 + 0.25CI_{AC} + 0.17P_{AC})$

$\boldsymbol{P_{AC}}$ (precipitation for acidic rains and cloud)

If elevation < 1700 m, then $P_{AC} = 0.33$ precipitation (measured at the station)

If elevation ≥ 1700 m then $P_{AC} = 0.67$ precipitation (measured at the station)

CI (cloud immersion for acidic rains and cloud)

If elevation < 1400 m, then $CI_{AC} = 0$

If 1400 ≤ elevation < 1800 m, then $CI_{AC} = 0.5$

If elevation ≥ 1800 m, then $CI_{AC} = 1$

Table 1. ***Cont.***

(b) Radiation submodel.

$\boldsymbol{RA}$ (radiation) = $0.167\boldsymbol{A} + 0.167\boldsymbol{S} + 0.167\boldsymbol{FM} - 0.167\ \boldsymbol{CI} - 0.167\boldsymbol{P} + 0.167\boldsymbol{T} \times (1.317 - \boldsymbol{T})$

$\boldsymbol{A}$ (aspect)

If aspect = north (315°–45°), then $A = 1$; if aspect = east (45°–135°), then $A = 2$;

if aspect = south (135°–225°), then $A = 3$; if aspect = west (225°–315°), then $A = 2.5$

$\boldsymbol{S}$ (slope)

If slope = 33.2°–62.3°, then $S = 1$; if slope = 26.6°–33.1°, then $S = 2$;

if slope = 19.6°–26.5°, then $S = 3$; if slope = 11.7°–19.5°, then $S = 4$;

if slope = 0°–11.6°, then $S = 5$

$\boldsymbol{FM}$ (fir mortality)

If elevation < 1700, then $FM = 0.33 \times$ mean winter cold temperature (measured at the station)

If elevation ≥ 1700, then $FM = 0.67 \times$ mean winter cold temperature (measured at the station)

$\boldsymbol{CI}$ (cloud immersion)

If elevation <1,400, then $CI = 0$

If 400 ≤ elevation < 1800, then $CI = 0.5$

If elevation ≥ 1800, then $CI = 1$

$\boldsymbol{P}$ (precipitation)

If elevation < 1700 then $P = 0.33$ precipitation (measured at the station)

If elevation ≥ 1700 then $P = 0.67$ precipitation (measured at the station)

$\boldsymbol{T}$ (temperature)

$T = AT \times (0.4 + 0.2A_T + 0.2\ E_T + 0.2S_T)$

AT is annual mean temperature measured at the station

A_T (aspect for temperature parameter)

If aspect = north (315°–45°), then $A_T = 0.3$; if aspect = east (45°–135°), then $A_T = 0.5$;

If aspect = south (135°–225°), then $A_T = 1$; if aspect = west (225°–315°), then $A_T = 0.65$

S_T (slope for temperature parameter)

If slope = 33.2°–62.3°, then $S_T = 0.2$; if slope = 26.6°–33.1°, then $S_T = 0.4$;

If slope = 19.6°–26.5°, then $S_T = 0.6$;

If slope = 11.7°–19.5°, then $S_T = 0.8$; if slope = 0°–11.6°, then $S_T = 1$

E_T (elevation for temperature parameter)

If elevation = 1000 m, then $E_T = 1$; if elevation = 1100 m, then $E_T = 0.9$;

if elevation = 1200 m, then $E_T = 0.8$; if elevation = 1300 m, then $E_T = 0.7$;

if elevation = 1400 m, then $E_T = 0.6$; if elevation = 1500 m, then $E_T = 0.5$;

if elevation = 1600 m, then $E_T = 0.4$; if elevation = 1700 m, then $E_T = 0.3$;

if elevation = 1800 m, then $E_T = 0.2$; if elevation > 1800, then $E_T = 0.1$

Table 1. ***Cont.***

(c) Water submodel.

WA (water) = $0.3\boldsymbol{P} + 0.1\boldsymbol{DS} + 0.1\boldsymbol{A} + 0.1\boldsymbol{S} + 0.1*(1.317\text{-}\boldsymbol{T})\boldsymbol{T} + 0.1\boldsymbol{RA} - 0.1\boldsymbol{T} - 0.1\boldsymbol{FM}$

P (precipitation)
If elevation < 1700 m, then $P = 0.22\mathrm{CP} + 0.11\mathrm{PP}$
If elevation ≥ 1700 m, then $P = 0.44\mathrm{CP} + 0.22\mathrm{PP}$

where CP is current year precipitation and PP the previous year precipitation (measured at the station)

DS (distance from stream)
If distance from stream = 0 −149.3 m, then $DS = 3$;
If distance from stream = 149.4−482.3 m, then $DS = 2$;

if distance from stream = 482.4−980 m, then $DS = 1$

A (aspect)
If aspect = north (315°–45°), then $A = 3$;
if aspect = east (45°–135°), then $A = 2.5$;
if aspect = south (135°–225°), then $A = 1$;

if aspect= west (225°–315°), then $A = 2$

S (slope)

If slope = 33.2°–62.3°, then $S = 5$; if slope = 26.6°–33.1°, then $S = 4$;
if slope = 19.6°–26.5°, then $S = 3$; if slope = 11.7°–19.5°, then $S = 2$;

if slope = 0°–11.6°, then $S = 1$

T (temperature)

$T = AT \times (0.4 + 0.2A_T + 0.2\,E_T + 0.2S_T)$

AT is annual mean temperature measured at the station

A_T (aspect for temperature parameter)

If aspect = north (315°–45°), then $A_T = 0.3$; if aspect = east (45°–135°), then $A_T = 0.5$;
if aspect = south (135°–225°), then $A_T = 1$; if aspect= west (225°–315°), then $A_T = 0.65$

S_T (slope for temperature parameter)

RA (radiation)

Values calculated in the radiation submodel were applied for the *RA* parameter here

FM (Fir mortality)

If elevation < 1700, then $FM = 0.33 \times$ mean winter cold temperature (measured at the station)

If elevation ≥ 1700, then $FM = 0.67 \times$ mean winter cold temperature (measured at the station)

For two-dimensional GIS projections, growth was simulated during a 59-year period (1940–1998) and averaged for each 30-m grid cell in ArcGIS 9.3 (Environmental Systems Research Institute (ESRI), Inc., Redlands, California, USA) using Equation (3) and the submodels in Table 1:

$$\begin{aligned}
&ARIM.HAB_i;\\
&\text{if elevation} > 1800\text{ m, then } ARIM.HAB_i = ARIM.SIM_{high}\\
&\text{if elevation} \leq 1600\text{ m, then } ARIM.HAB_i = ARIM.SIM_{low}\\
&\text{if } 1600\text{ m} < \text{elevation} \leq 1800\text{ m, then: } ARIM.HAB_i = (ARIM.SIM_{high(1800)} +\\
&ARIM.SIM_{high(1700)} + ARIM.SIM_{low(1700)})/3
\end{aligned} \tag{3}$$

The $\text{ARIM.SIM}_{\text{high}}$ and $\text{ARIM.SIM}_{\text{low}}$ models as used in this study represent elevations above and below 1700 m and reflect two distinct mechanisms controlling growth at high (1800 to 2025 m) *vs.* low (1400 to 1600 m) elevations. These mechanisms are inherent in submodel simulations fitted to published tree-ring data [37] representing two different elevation ranges: high (1800 to 2025 m) and low (1400 to 1600 m). The intermediate range 1600–1800 m was determined by averaging the growth obtained by $\text{ARIM.SIM}_{\text{high}}$ and $\text{ARIM.SIM}_{\text{low}}$ (Equation (3)). For spatial projection, ARIM.HAB computes the habitat suitability distribution of red spruce as growth indices that range 0–2, the scale generated in ARIM.SIM simulation runs. The 59 years of growth indices were rescaled to 0–1 to give probabilities of occurrence and then converted to 0–100 percentage scales for presentation. Finally, habitat suitability (0%–100% scale) was classified into five 20% classes, indexed by the upper number in each class (for example, 40%–60% suitability has the index value of 60).

2.4. Prediction of Red Spruce Habitat Suitability under Climate Change

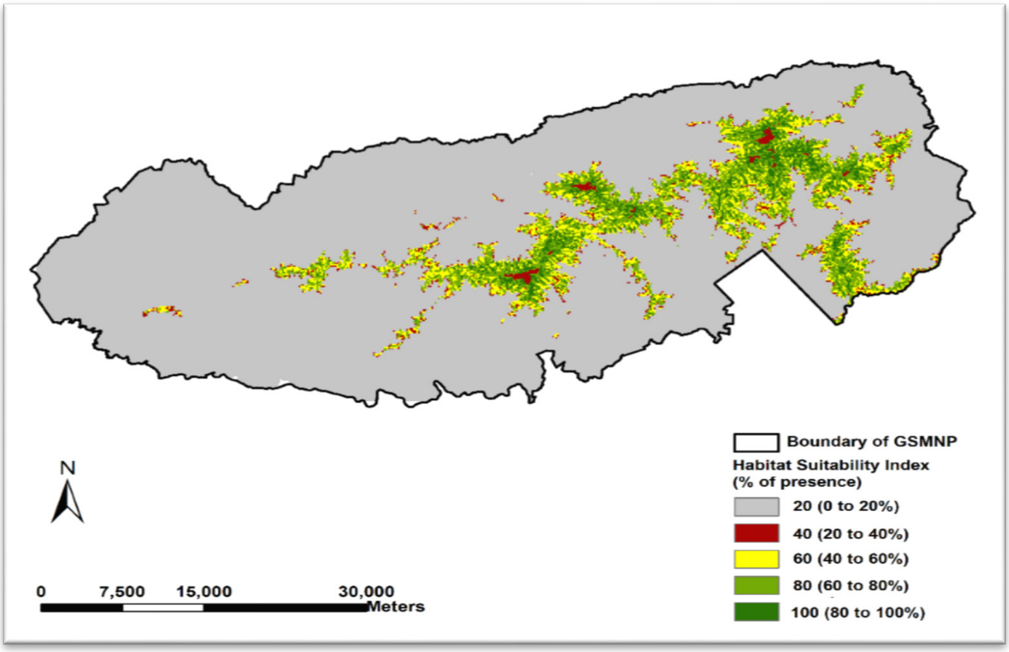
ARIM.SIM simulated red spruce growth from 2080 to 2099 for each cell in ARIM.HAB under climate change and the three previously indicated air pollution scenarios: 10% increase, 0% change and 10% decrease [46]. Then, the 20-year simulated growth was averaged for spatial projection. Of the five 20% classes, the index of 20 (0%–20%) was not used, because it applied to low elevation areas in GSMNP (<1400 m) where red spruce showed zero growth due to its absence and unfavorable habitat conditions for reoccupation (high temperature and water stress due to low precipitation and high evapotranspiration [9]). ARIM.SIM simulates growth above 1400 m based on previous studies [37] and observations [40]. The simulations showed that variations in suitable habitat were related to climate change in interaction with air pollution. The total area of suitable habitats was quantified by multiplying the number of pixels by 900 m^2, the area of a pixel with 30-m spatial resolution.

3. Results

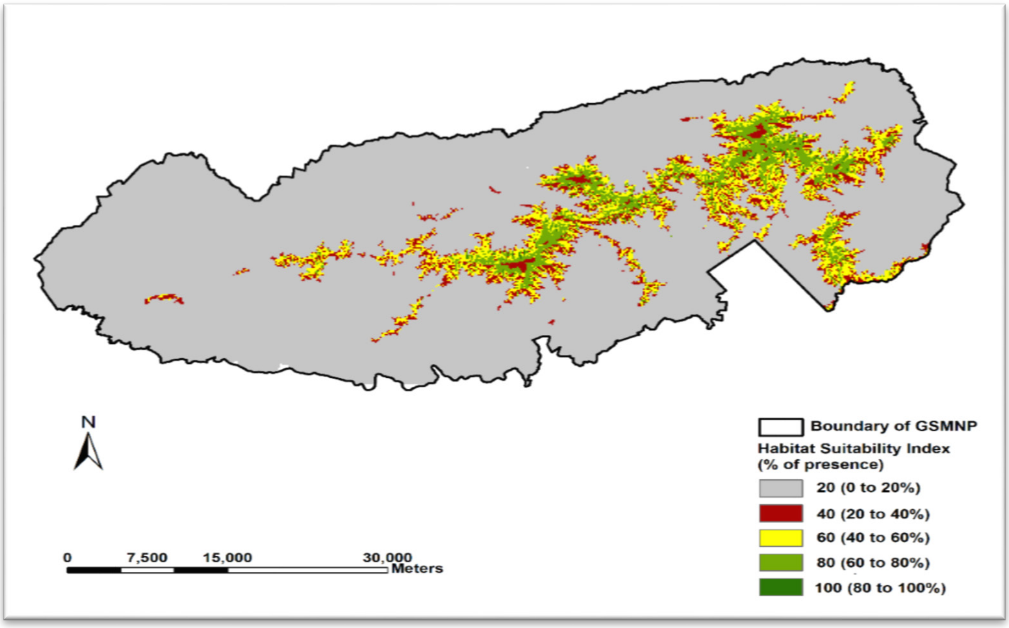
Figure 2a shows the current projection by ARIM.HAB of red spruce habitat suitability in GSMNP [12]. This serves as the nominal reference for results generated by ARIM.HAB simulations of air pollution perturbation scenarios and climate change.

ARIM.HAB projected low habitat suitability (index of 40) at higher elevations (1800–2028 m) and also at lower elevations down to 1400 m. As stated above, very low index values of 20 signify unsuitable habitat conditions for red spruce due to zero growth of red spruce in areas <1400 m estimated from the absence of red spruce. ARIM.SIM predicted growth only for elevations ≥1400 m based on growth estimations. Medium suitability, with indices of 60 and 80, occurred at 1400–1600 m and on south-facing and gentle slopes at intermediate elevations (1600–1800 m). The highest suitability index of 100 was exhibited at intermediate elevations (1600–1800 m). The predicted range at the threshold value of the habitat suitability (34) was verified by an existing geospatial database and showed excellent consistency with the current distribution (Area Under the Curve (AUC) = 0.99, kappa = 0.87, True Skill Statistic (TSS) = 0.88).

ARIM.HAB simulations (Figure 2b–d *vs.* 2a) predicted that increased temperature and precipitation with increased air pollution would cause degradation of habitat suitability at all elevation ranges in GSMNP (Figure 2b, Figure 3a,b). Increased air pollution with increased precipitation, causing acidic rains and clouds, will cause serious loss of suitable habitats. This is shown by more red and less green areas in Figure 2b compared to Figure 2a. Figure 3b quantifies how much low suitability areas would increase and high suitability areas decrease. Simulated low suitability indices of 40 and 60 increased 189% and 34%, respectively, while the high indices of 80 and 100 decreased 40% and 86%. Climate change without air pollution change alter habitat suitability less compared to increased pollution, but both cause habitat degradation (Figure 2c and Figure 3a,b). The simulated low suitability indices of 40 and 60 increased 154% and 15%, respectively, mostly at low elevations (1400–1600 m) (Figure 2c). The high indices of 80 and 100 decreased 34% and 40%.

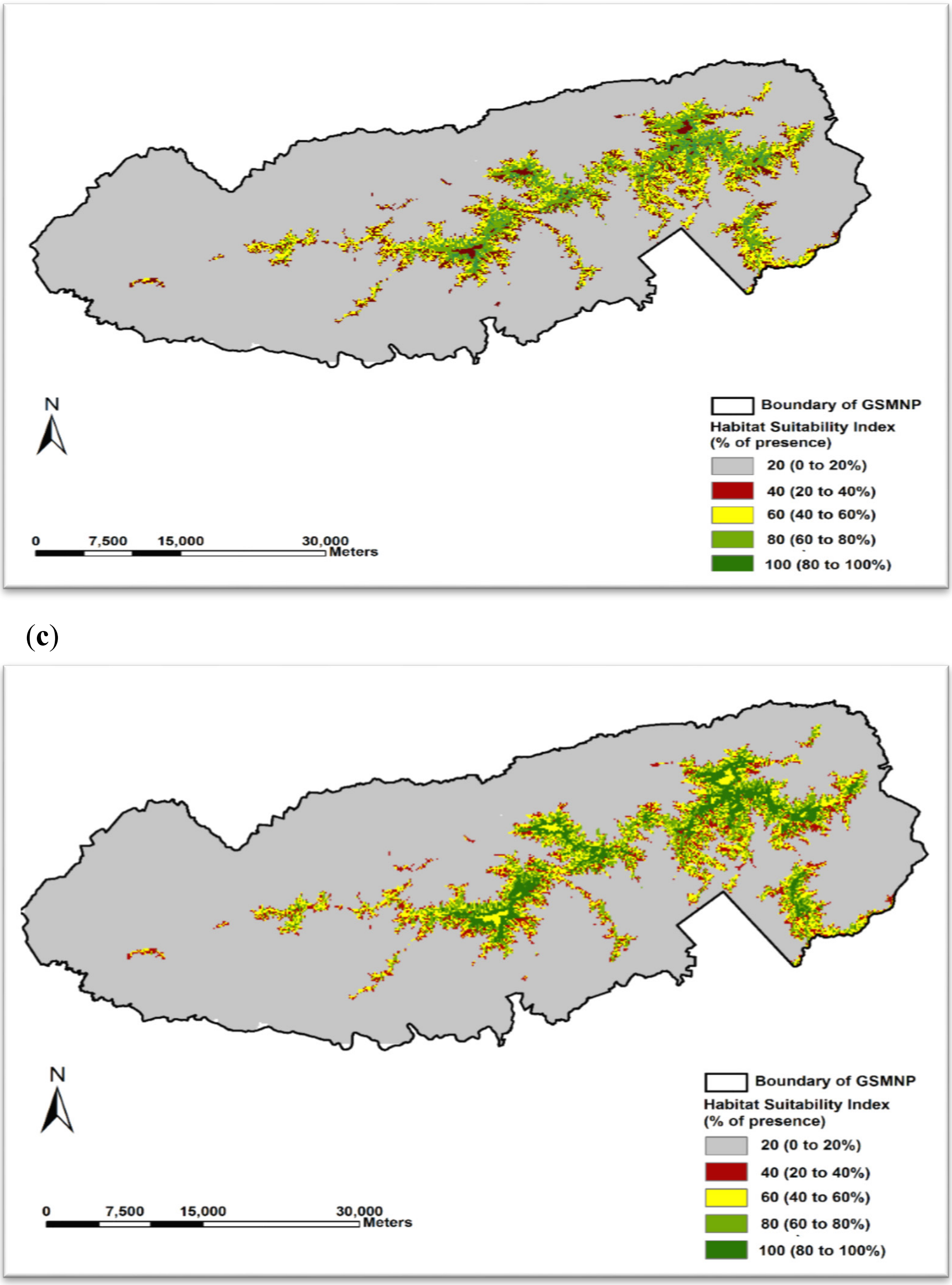


(a)



(b)

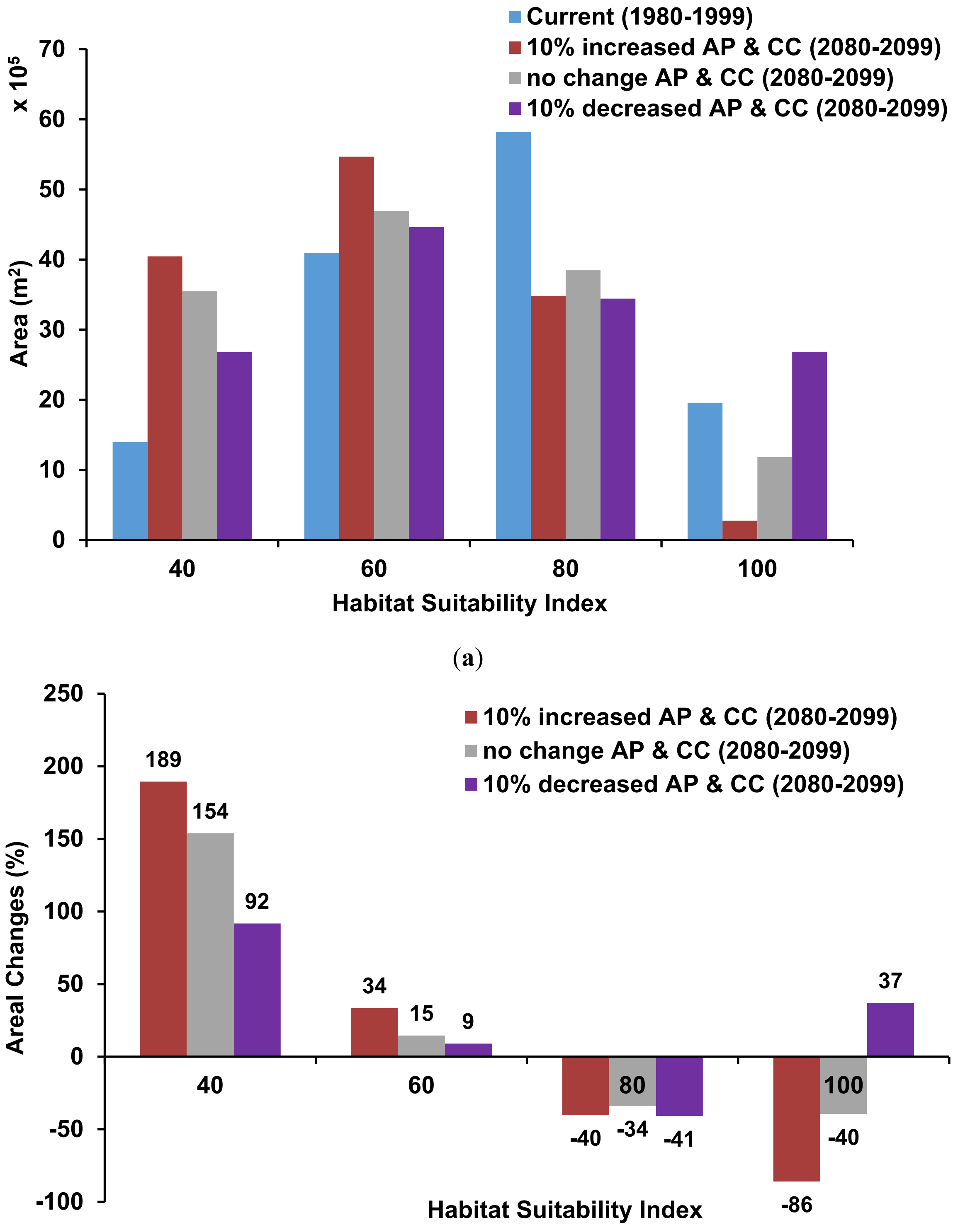
Figure 2. *Cont.*



(**c**)

(**d**)

Figure 2. Changes in red spruce habitat suitability (zero to 100 scale) in the Great Smoky Mountains National Park under climate change and three air pollution changes: (**a**) current habitat suitability distribution (source: Koo *et al.* [12]); (**b**) habitat suitability under climate change with 10% increased air pollution; (**c**) habitat suitability under climate change with no increase of air pollution; and (**d**) habitat suitability under climate change with 10% decreased air pollution.



(**a**)

(**b**)

Figure 3. Changes in each habitat suitability of red spruce under climate change and three air pollution scenarios: (**a**) areal changes in habitat suitability; and (**b**) percent changes in habitat suitability. The habitat suitability of 20 showed the absence of red spruce in red spruce habitat model (ARIM.HAB) in Great Smoky Mountains National Park (GSMNP), because red spruce growth model (ARIM.SIM) predicted red spruce growth for the elevations above 1400 m. Abbreviations: CC = climate change, AP = air pollution.

Climate change with decreased air pollution reduced habitat degradation in most areas and increased habitat suitability at high elevations. This is shown by yellow colors at the high elevations (1800 to 2028 m) in Figure 2d. Figure 3a,b shows reduced increases of the suitability indices of 40 (92%) and 60 (9%). The greatest increase in the index of 40 was found at low elevations (Figure 2d). The area of the index of 100 increased, but that of 80 did not (Figure 3a).

Overall, the ARIM.HAB results indicate that climate change by itself will result in range contraction of red spruce in GSMNP, and its effects will be increased by interaction with air pollution, causing habitats to shrink in both directions: upslope from low to high elevations and downslope from high to low elevations.

4. Discussion and Conclusions

Three issues of complex systems modeling at landscape scales are: (1) multifactorial interrelationships; (2) within- and across-scale interactions; and (3) mediation of both of these by indirect effects. In this and our other studies of red spruce in GSMNP [12–14,46], GIS treatment of many within- and across-scale interactions in ARIM.HAB, through ARIM.SIM operating at the pixel level, has served to clarify the many mechanisms involved in translating global-scale climate change effects into local-scale habitat suitability. ARIM.HAB consists of spatially-distributed GIS cells implemented by a non-spatial simulation model, ARIM.SIM. The latter incorporates multiple biotic and abiotic factors (Figure 4) in its treatment of red spruce growth in GSMNP. Its simulations provide insights into the multiple mechanisms and indirect effects involved in defining habitat suitability across elevation zones.

For example, in the air pollution submodel (Table 1a), effects are mediated by several indirect factors acting together: reduced air pollution coupled with increased stress from elevated temperatures accompanying lowered precipitation cause habitat suitability to rise to medium levels from low values at lower elevations. Air pollution and precipitation are general variables expressed at large (national and regional) scales, but at local scales, they must be formulated as functions of specific local parameters, such as (in Table 1a and Figure 4) elevation.

Although much prior research has focused on interactions within multiple independent scales [47–50]—local, regional, continental, *etc.*—a need exists for studies that incorporate scale interdependency. This has not yet been well achieved in previous studies [51–55]. Across-scale interactions may explain features of ecological patterns and processes, such as non-linearity, heterogeneity, scale dependency and emergent properties [30,51,55,56]. Failure to elaborate across-scale interactions limits the ability to account for local environmental issues based on regional and global studies [52,53,57,58]. Therefore, understanding of within- and across-scale relationships is necessary to predict global climate change effects on habitat suitability of local species [30,53,55,58].

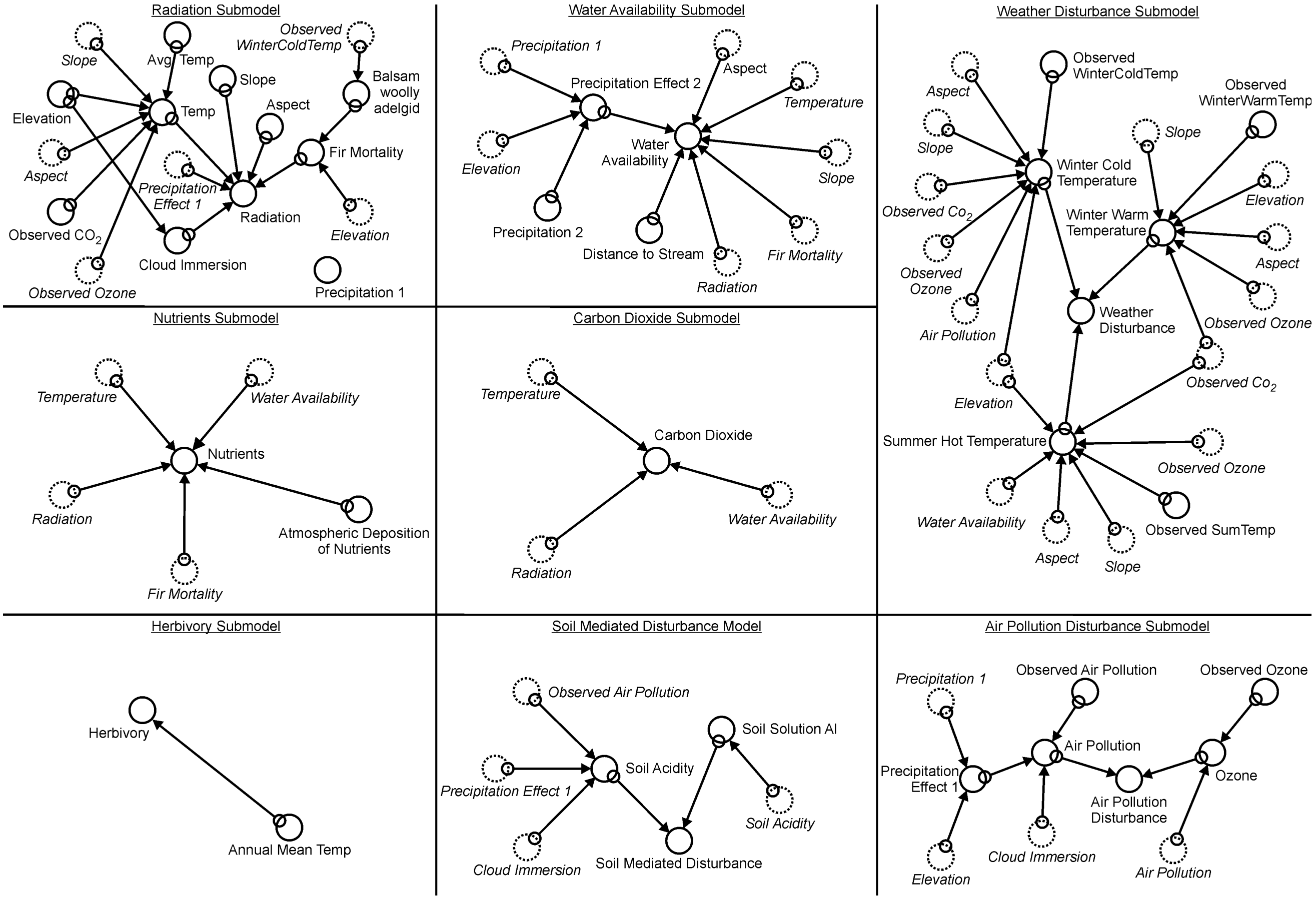


Figure 4. Overview of variables and how they interact, directly and indirectly, within and across scales, in the eight submodels that make up red spruce growth model (ARIM.SIM) (Source: Koo *et al.* [13]).

ARIM.HAB, with its pixel basis in the growth simulation model ARIM.SIM, takes account of multiple indirect interactions expressed within- and across-scales by complicated habitat conditions. For example, at low elevations, radiation in $\text{ARIM.SIM}_{\text{low}}$ (Equation (2)) was indirectly estimated from the output of a quite complex radiation submodel (Table 1b, Figure 4). The radiation variable represents insolation absorbed by red spruce after being acted upon by many intermediary variables (Table 1b, Figure 4)—topographic, climatic, meteorological and biotic. These factors, expressed over multiple indirect pathways, exert influence on actual radiation conditions in the field. Taking them into account enables more refined and accurate description and understanding of the contributing habitat conditions than even empirically measuring insolation directly in the field, without any consideration of its complex array of causes [13].

Multiple indirect interactions modeled at local to continental scales in ARIM.HAB reflect both within- and across-scale relationships. As examples, at local scales, interspecific interactions (biotic variables) between red spruce and Fraser fir may be the most important determinants of growth and distribution (Table 1b). At regional scales, where Fraser fir may not always co-dominate with red spruce, significant variables in growth and distribution are elevation and cloud immersion (topographic and meteorological variables) (Table 1a). At the continental scale, biotic and topographic/climatic variables still operate, but the more important determinants of growth and range over longer time scales are precipitation and air pollution (climatic and anthropogenic variables) (Table 1a). The latter also operate and provide ecological context at lesser scales, but they are overridden in the shorter time frames of these by the more important topographic/meteorological (regional) and biotic (local) variables. Between scales, clouds, air pollution and acidic rain, which are climatic/anthropogenic factors expressed at continental scales, interact with elevation and precipitation, which are topographic/meteorological variables expressed at regional scales. These and many other within- and across-scale relationships pose challenges for modeling and also for understanding the full range of influences that operate in determining the growth and distribution of any species in interactions with others and also a multitude of abiotic ecological factors.

In this and our other studies of red spruce in GSMNP [12–14,46], GIS treatment of many within- and across-scale interactions in ARIM.HAB, through non-spatial ARIM.SIM simulations at the pixel level, has clarified many mechanisms involved in translating global-scale climate change effects into local-scale habitat suitability. For example, consideration of air pollution shows how one environmental factor can cut across many others. Key elements in increased acid rain production at higher elevations are the following: (1) increased precipitation × air pollution, regional factors [38]; (2) increased precipitation and air pollution, regional factors, × elevation, a local factor [57]; (3) interaction between increased air pollution, regional factor, × elevation, a local factor, causing more acidic clouds [59–61]; and (4) interaction between acidic rain × clouds × ozone at the local scale [62] (Table 1). The first and fourth interactions are within-scale, and the second and third are expressed across scales.

Mechanisms are more complicated at low elevations, because there are more factors, and they are less decisive in their effects. These include interactions between: (1) temperature × precipitation, which are regional climatic factors, × elevation × slope and aspect, local topographic factors [63]; (2) regional climatic factors and local topographic factors × Fraser fir mortality, a local biotic factor [64,65] (Table 1b,c); and (3) increased winter temperature × the balsam woolly adelgid insect pest, the first a regional climatic factor and the second a local biotic factor in Fraser fir mortality [66] (Table 1b). With many variations on their direct and indirect expression, these factors operate within, and their interaction sets both within and across, spatiotemporal scales.

The ability of ARIM.HAB to account for indirect effects allows climate change on a global scale to be translated into spatial and temporal changes in red spruce habitat suitability at the regional and local scales of GSMNP. The projections of ARIM.HAB in Figure 2 show spatial differences in global climate change effects in relation to topographic factors and air pollution levels. Especially at high elevations, red spruce ecosystems are very vulnerable to air pollution × climate change. Reduced air pollution leads to increased habitat suitability at all elevations, shown in Figure 2d as increases in dark green areas (high suitability) and decreases in red areas (low suitability). At the highest elevations (1800 to 2028 m), no red areas remain. However, Figure 2d shows that many areas are still red at low elevations, as they are also in Figure 2b under increased air pollution. This indicates that low elevation red spruce habitat suitability is less impacted by air pollution change than by climate change. ARIM.HAB clearly predicts that climate change will degrade habitat suitability of red spruce in GSMNP (Figure 2b–d, Figure 3) and could result in range reduction. However, its specific effects will vary with air pollution. Climate change with increased air pollution will cause red spruce to lose more high suitability habitats (indices of 80 and 100; Figure 2b, Figure 3). The most suitable habitats (index of 100) can be expected to expand at higher elevations with decreased air pollution, but shrink at lower elevations (Figure 2d and Figure 3). These highly nuanced relationships are manifestations of a complex assortment of factors inherent in the concepts of both "global change" and "air pollution", and ARIM.HAB and ARIM.SIM both make it clear that it is the indirect relationships that are the most telling in the final determination of causalities.

Other factors also figure into the habitat suitability equation. These include dispersal limitation [67,68], interactions with coexisting species and the ability of plants to adapt and acclimate [1]. Theoretical and field studies have supported dispersal-limited distribution patterns of plant populations [69,70]. Numerous population genetics studies have revealed genetic differentiation along environmental gradients and concluded that extant populations are adapted to the climatic conditions of their present habitats [1,71,72]. In particular, tree species with various dispersal mechanisms might contain adequate genetic diversity through high gene flow among populations to respond to changed climatic conditions [1]. However, boreal species, such as red spruce, geographically isolated from other populations, may have low genetic diversity and, thus, lower acclimation and adaptation potentials to respond to climate warming [9,10]. High mortality and growth decline of red spruce in GSMNP strongly support the conclusion that this species at its range limits cannot fully adapt and tolerate environmental stresses related to air pollution and climatic change. In spite of the limitations, predictions from ARIM.HAB represent a step forward in providing information to help understand the complexities involved in the expression of climate change effects on the spatiotemporal distribution of habitats and populations of red spruce in GSMNP. Furthermore, the complex systems modeling principles and methods embodied in ARIM.SIM and ARIM.HAB carry over to interests in other species and geographic areas.

Author Contributions

Koo, K. and Madden, M. conceived the ideas and collected the data; Koo, K., Madden, M. and Patten, B.C. analyzed the data; and Koo, K., Madden, M. and Patten, B.C. led the writing.

Conflicts of Interest

The authors declare no conflict of interest.

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