Warming-induced upslope advance of subalpine forest is severely limited by geomorphic processes

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Edited by Monica G. Turner, University of Wisconsin, Madison, WI, and approved March 7, 2013 (received for review December 7, 2012)

Forests are expected to expand into alpine areas because of climate warming, causing land-cover change and fragmentation of alpine habitats. However, this expansion will only occur if the present upper treeline is limited by low-growing season temperatures that reduce plant growth. This temperature limitation has not been quantified at a landscape scale. Here, we show that temperature alone cannot realistically explain high-elevation tree cover over a >100-km^2 area in the Canadian Rockies and that geologic/geomorphic processes are fundamental to understanding the heterogeneous landscape distribution of trees. Furthermore, upslope tree advance in a warmer scenario will be severely limited by availability of sites with adequate geomorphic/topographic characteristics. Our results imply that landscape-to-regional scale projections of warming-induced, high-elevation forest advance into alpine areas should not be based solely on temperature-sensitive, site-specific upper-treeline studies but also on geomorphic processes that control tree occurrence at long (centuries/millennia) timescales.

biogeoscience | forest ecology | climate change | niche modeling | remote sensing

In line with observations of significant temperature-related upward shifts in plant and animal species optimum elevation during the 20th century (1), future climate warming in mountain ecosystems is expected to cause an upward movement of tree cover. This upward forest expansion would effectively shrink the extent of alpine tundra, possibly causing species loss and ecosystem degradation through greater fragmentation (2–4), as well as a minor feedback on climate through increased carbon sequestration in subalpine forests (2). These predictions stem from upper treeline studies (5–8), which dominate research on tree cover in the alpine/subalpine region of mountain landscapes and overwhelmingly focus on the physiological temperature (T) limitation of tree growth (6, 9, 10) on specific kinds of sites. Although seldom described, typical site-based upper treeline studies have been performed away from cliffs, talus slopes, avalanche paths, incisive features, and bedrock and on gentle to moderately steep colluvium-mantled slopes with regolith where fieldwork is feasible and the climate signal maximized.

Tree presence depends on successful recruitment, establishment, and growth (11, 12), and these demographic processes are largely controlled by the availability and stability of substrate and the local energy and hydrological budgets. Changes in high-elevation tree cover will, thus, result from modifications on any of these controlling processes. Although topography and geomorphology have been identified as important in setting the observed heterogeneity of high-elevation mountain tree cover (13–19), the effect of geomorphology on present and future high-elevation tree cover remains unquantified, and site-based studies overwhelmingly treat terrain physiognomy as a uniform neutral background. To address these questions, we conducted a statistical modeling exercise of tree presence at high spatial resolution (10 m) over a ~100-km^2 area comprising the geologic and geomorphic diversity found in the Front Ranges of the Canadian Rocky Mountains of Alberta (Fig. 1 and *Text S1* and *Text S2*) and incorporating covariates chosen to represent climatic and geomorphic processes. The resulting model was further used to forecast tree cover under a late-21st century moderate warming scenario.

Results

Model runs showed excellent performance (Fig. 1 and *Text S2*) and a strong contribution of geomorphic and topographic variables to the observed tree-cover variability (geomorphic unit and growing season temperature were consistently selected as the two most important model variables; Fig. S1). Moreover, response curves for the top-contributing model variables showed realistic patterns (Fig. 2), allowing possible causal relationships to be inferred from them. These were a decrease in probability of tree presence with colder summer temperatures (modeled temperature threshold was on the range of 8.5–9.5 °C), steep slopes, as well as on incisive, but especially bedrock geomorphic units. Colluvium- and alluvium-covered terrains were strongly associated with higher probabilities of tree presence (Fig. 2). Optimal ranges of summer moisture availability, which combines both climate and topography, and exposure to solar radiation (linked to energy input and spring snowmelt) were also suggested. Finally, the low explanatory power of aspect highlights the importance for tree cover of factors other than temperature alone, because the potential effect of colder north- and east- vs. warmer south- and west-facing slopes is masked by the high geomorphic and geologic heterogeneity of the landscape.

A very small proportion of the temperature-based, tree-growth limit zone was found to be currently tree-covered, regardless of this zone being defined according to literature (5.5–7.5 °C) (8, 9) or empirically as a 2 °C interval with its lowest temperature at the highest treed 10-m cell in the landscape (5.81–18.98%; Fig. 3, Fig. S2, and Tables S1 and S2). This small proportion indicates that current tree cover in the area is already limited to a great extent by factors other than temperature. Furthermore, only 5.98% of the terrain within and above this area was found to be colluvium-covered (Fig. 4*A*), whereas the modeled current temperature threshold for tree growth (~8.5–9.5 °C; Fig. 2*A*) fairly coincided with the transition from colluvium to bedrock-dominated landscape (Fig. 4*A*), as well as with steeper slope angles and, thus, more exposed terrain (Fig. S3). These results agree with tree-cover values of 83.91% and 10.72% on colluvium-covered and bedrock-dominated terrain, respectively (Fig. 4*B*).

Projections of future (2041–2070) tree cover under a ~2.5 °C warmer scenario [A2 Special Report on Emissions Scenarios (SRES) scenario: moderate to high warming] (20) strongly suggest that future upslope tree-cover advance might be severely limited by geologic and geomorphic processes, which might become even more prevalent than at present in determining the distribution of trees on the landscape (Fig. 1 *C* and *D*). Predicted advance is not homogeneous and concentrates in gentle to moderately steep colluvium-mantled slopes, mostly in the shale-dominated southwest range. Tree loss is also predicted, mostly in steep

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Author contributions: M.M.-F. and E.A.J. designed research; M.M.-F. and E.A.J. performed research; M.M.-F. analyzed data; and M.M.-F. and E.A.J. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

See Commentary on page 7971.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1221278110/-/DCSupplemental.

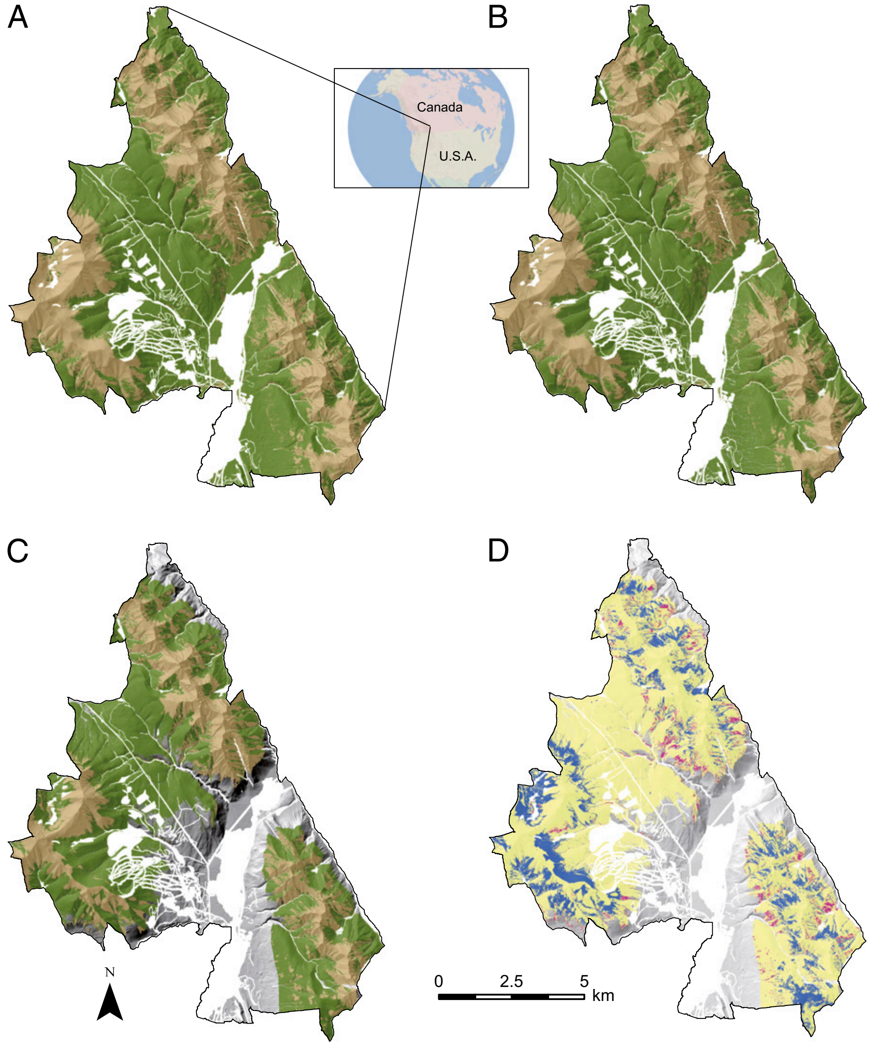

Fig. 1. (*A*) Observed tree cover (green) over the study area, filtered into binary form from a 2008 RGB orthophoto (*Materials and Methods* and *Text S2*). (*B*) Predicted current tree cover (median of 11 runs; green) from Breiman and Cutler's RF model, each calibrated using a different random subset of 50% of the full study area and verified over the remaining 50%. Covariates include geomorphic features and bioclimatic normals for the period 1971–2000. (*C*) Projected tree cover (median of 11 runs; green) using Breiman and Cutler's RF model. Covariates include geomorphic features and bioclimatic normals for the period 2041–2070 [Canadian Regional Climate Model (CRCM) nested within Third Generation Coupled Global Climate Model of the Canadian Centre for Climate Modeling and Analysis (CGCM3), A2 SRES scenario; *Materials and Methods* and *Text S2*]. (*D*) Predicted changes between present and projected tree cover in 2041–2070. Blue, tree gain; yellow, no change; magenta, tree loss. (*C* and *D*) Areas in gray show the area for which 2041–2070 climatic data falls outside the range of variability of the model training data (1971–2000 climate) and have, thus, not been used in the projection. Resolution of the maps: 10 m. *Inset* between *A* and *B* shows the location of the study area within a North American geographic context. Centroid coordinates of the study area: $x = 630133.4$; $y = 5647355$ (Universal Transverse Mercator zone 11N).

and exposed sites in the limestone northeast range. Model projections suggest that the curve relating tree cover and temperature will shift toward warmer values: that is, despite occurring in the landscape, late 21st century temperatures at which trees currently occur will be unsuitable for trees (Fig. 4*B*). Projected late 21st century tree cover in the temperature-based, tree-limit zone may reach negligible values (0–2.34%; Fig. 3, Fig. S2, and Tables S1 and S2). Furthermore, the 8.5–9.5 °C zone (modeled present temperature threshold for tree growth) will move upwards, occurring in places dominated by bedrock, steeper, and more exposed (Fig. 4*A* and Fig. S3). That is, as temperatures increase, the upward-moving tree cover will encounter harsher geomorphic environments not colonizable by trees, and an increased landscape-scale control of high-elevation tree cover by geological/geomorphic processes is predicted. Forecast tree cover on colluvium of 91.5% (Fig. 4*B*) suggests little room for tree advance, further reinforcing this view.

Discussion

Our data show that tree presence over a rugged, mountainous landscape is controlled by an interaction of atmospheric (climate) and lithologic (geologic and geomorphic) processes that directly influence substrate properties and the local energy budget, affecting tree recruitment, establishment and growth. Although summer temperature plays a large role in explaining tree presence in the region, it cannot explain the enormous spatial heterogeneity of tree distribution. More likely, any given tree growing on these slopes experiences a suite of processes of which temperature is but one important factor. These processes result in a heterogeneous distribution of trees on the landscape that realistically represents actual subalpine tree-cover patterns (Fig. 1). Such spatial diversity in tree-cover patterns further highlights the challenges and potential biases resulting from studies carried on spatially limited study sites.

Predicted tree cover in a warmer late 21st century scenario suggests an increasing limitation by geologic/geomorphic factors (Fig. 4 and Fig. S3). As the region warms up, climatic suitability

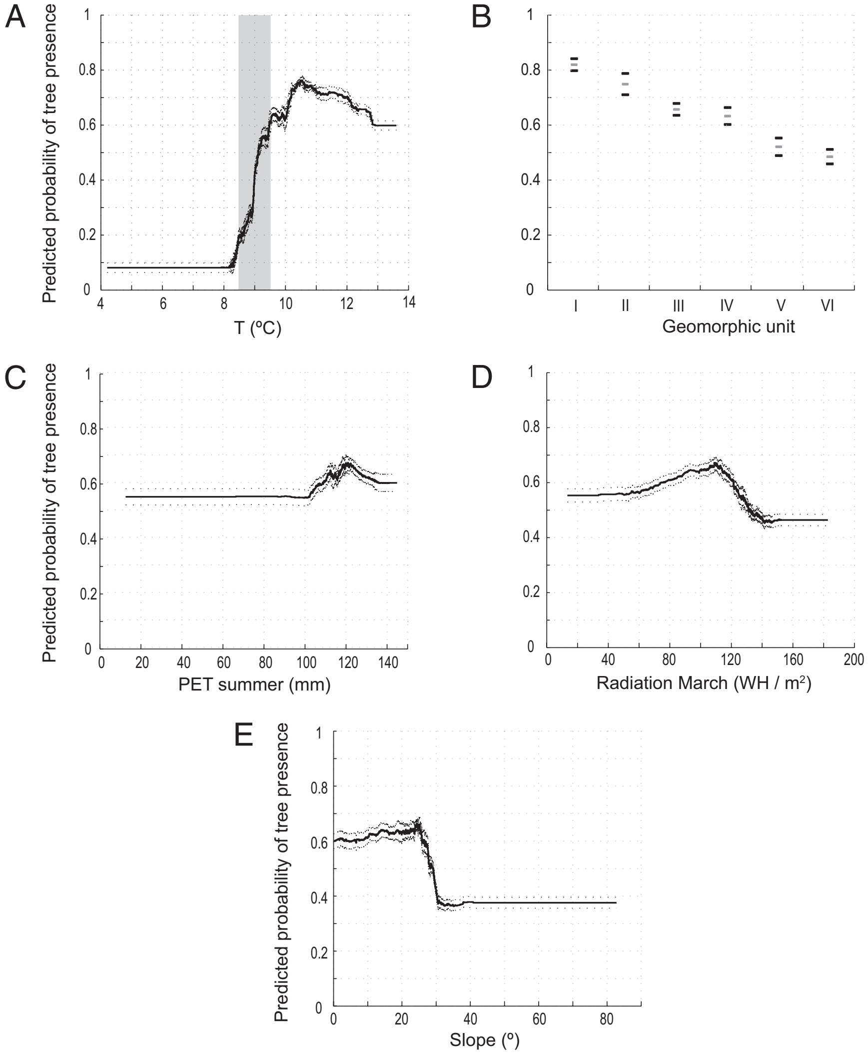

Fig. 2. Response curves of the five main variables for the 11 model runs performed with Breiman and Cutler's RF model. (*A*) average summer (June to August) temperature [°C ; modeled temperature (T) threshold (8.5–9.5 °C range) is highlighted in gray]. (*B*) geomorphic unit (I, colluvium; II, alluvium; III, fan; IV, landslide; V, incision; VI, bedrock). (*C*) summer (June to August) potential evapotranspiration (mm). (*D*) March solar radiation (WH/m^2; exposure). (*E*) Slope angle, °. (*A* and *C*–*E*) Continuous line depicts the median of the 11 runs, and discontinuous lines represent the 1 SD envelope. (*B*) Gray dash depicts the median of the 11 runs, and black dashes represent the 1 SD envelope. Note the overall physically sound relationships.

increasingly occurs on geologic/geomorphic unsuitable areas. The presence of trees in these areas depends on the existence of suitable habitat with appropriate substrate and energy balance. Only slopes with very specific characteristics (i.e., colluvium- or alluvium-covered, low to moderate angle, not too exposed; Fig. 2) contain suitable habitats above the current tree-covered area susceptible of being colonized by trees in a scenario of climate warming. Such features are the result of geomorphic processes acting on a framework set by the structural geology of the region, and thus the appearance of new sites suitable for tree growth does not depend on short (yearly to decadal) timescales but rather on longer ones (centuries to millennia), in stark contrast to predicted upper-treeline response times for reaching new equilibrium conditions on the order of 100 y or more, based solely on biological assumptions (2). Such lithologic constraints might enhance the reported climate warming-caused range contraction of subnival to nival plants (21).

Sustained warming in the Canadian Rockies might cause a tree-cover advance in some suitable areas followed by a stabilization in which temperature may not be a reliable predictor of upper tree cover (Figs. 3 and 4). We can speculate that such a geologic/geomorphic limitation of vegetation might have occurred in the early Holocene, after the retreat of the large valley glaciers left much of the slopes denudated. Only the slow buildup of colluvium over valley slopes might have allowed tree cover to advance upslope and keep up with temperature changes (a limited number of favorable places might have allowed pockets of trees to track climate change, but not a whole landscape-scale response). In our study area, climate can, thus, affect upslope tree advance at centennial to millennial time scales by, for example, modifying the rates of erosion, periglacial processes, and/or regolith formation (22). The distribution of slope characteristics relevant to tree presence will surely change as a function of the geological and climatic history of the area under study: young, glaciated, or recently deglaciated mountain systems will most probably offer little room for upslope tree advance; old, eroded, gentler mountain systems might offer more. The methodology presented in here provides a way to test this hypothesis elsewhere in the globe.

Upper-treeline studies generally focus on the effect of temperature on tree growth and survival and treat geomorphic/geologic processes as either exceptions or as a uniform background within a temperature-controlled environment (2, 5–7, 9). The few exceptions to this (13, 14, 19) have not yet quantified their

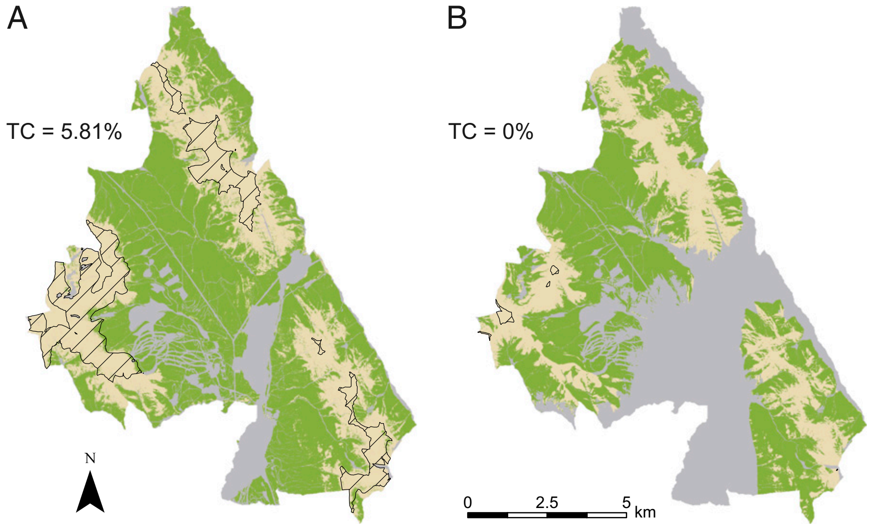

Fig. 3. Hatched area indicates area with summer (June to August) average temperature ranging from 5.5 °C to 7.5 °C, typically reported in the literature to be the temperature-based, tree-growth limit zone (9): based on temperature normals for the period 1971–2000 (*A*); based on predicted temperature normals for the period 2041–2070 (climate model CRCM nested within CGCM3, A2 SRES scenario; *Materials and Methods* and *Text S2*) (*B*). Green, observed (*A*) and projected (*B*) treed area; beige, nontreed area; gray, area not used in the study, corresponding to human infrastructures, channels, and lower valley alluvial floodplains (in *A*) plus the area for which 2041–2070 climatic data falls outside the range of variability of the model training data (1971–2000 climate) and, thus, not used in the projection (in *B*). TC, percentage of tree-covered area in the temperature-based, tree-growth limit zone. Note the low overall tree cover within the temperature-based, tree-growth limit zone, being lowest in the future scenario. (Resolution of the maps: 10 m.)

effect on the landscape. The use of site-based upper-treeline results and methodology to infer regional subalpine tree dynamics hinders in our view significant advances in the study of tree presence on high-elevation slopes (and slopes in general), because this framework does not take into account that noise might be as important (or more) as signal. Whereas the study of temperature limitation of physiological pathways in woody vegetation is fundamental, it is insufficient to explain the complex reality of landscape-scale (ecologically relevant) high-elevation tree cover, because it overlooks the fact that climatic limitation can prevail only on a small proportion of the landscape. Together with temperature, trees tend to experience other controlling mechanisms, such as those related to the physical characteristics of the lithosphere on which they grow (14–17). Although some of our model variables are linked to avalanches or landmass movements, the present study did not directly address disturbance processes [e.g., wildfires, insect outbreaks (23)], which would add even more complexity to the dynamics of subalpine tree-cover change under warmer climate scenarios. Upscaling from site-based upper-treeline studies to regional scale has often been done without accountancy of the spatial representativity of these sites on the landscape. The effect of this practice has been quantified in this study for the Front Ranges of the Canadian Rocky Mountains, and found to be very large. The presented approach should foster new studies in this line, providing a landscape perspective to the potential response of high-elevation tree cover in the face of climate change.

Materials and Methods

Study Area. The study area comprises ~100 km^2 of mountainous terrain in the Front Ranges of the Canadian Rocky Mountains of Alberta (Canada), characterized by a Continental Subarctic climate (*Text S1*). It consists of a thrusted sedimentary terrain, heavily glaciated during the Quaternary, ranging from 1,300 to 2,830 m above sea level, with two main southeast–northwest–oriented ranges, one dominated by shale and the other by limestone, and a diversity of aspects, slopes, and substrate types (Fig. S4).

Mapping of Tree Presence/Absence. Mapping of trees was limited to coniferous trees and aspen groves. Deciduous shrubs were not mapped. A binary map (tree vs. no tree) was produced (Fig. 1*A* and Fig. S5) from a 1-m composite orthophoto [red, green, blue (RGB)] of the study area taken in September 2008 and intensive ground-truthing done in the summers of 2009–2011. Discrimination between treed and nontreed 1-m pixels was performed in a supervised and recursive semiautomatic manner, based on the selection of threshold RGB-band values within slope facets of homogeneous illumination (*Text S2*). Human infrastructures, lower valley alluvial floodplains, and channels were excluded from the study. The final map was resampled from 1 to 10 m and accounted for all trees large enough to be detected. That is, seedlings were not mapped, and no distinction was made between upright and krummholz tree forms. Tree-covered areas dominated the lower terrain, whereas treeless areas dominated the higher elevations.

Modeling Approach. Presence or absence of trees at a 10-m spatial resolution (860,925 observations) was modeled over the study area using Breiman and Cutler's random forest for classification and regression (RF) model (24), which associates a set of covariates with occurrence records and relies on assumptions fully described in *Text S2*. The nine covariates used to parameterize the model were chosen to represent climatic (1971–2000 normals) and geologic/geomorphic processes: average summer (June to August) air temperature, geomorphic unit, summer potential evapotranspiration, March solar radiation, slope angle, substrate type, aspect, slope type, and contributing area (*Text S2*). The model was run 11 times, each time being calibrated with a different random subsample comprising 50% of the observations and validated with the remaining 50%. The role of the most important model variables was assessed. Tree cover was projected into late 21st century using climatic normals for the period 2041–2070 from a downscaled CRCM driven by the CGCM3 (25), A2 SRES scenario (moderate to high warming) (20), and assuming no significant geological/geomorphic changes. A2 scenario is adequate from an impact and adaptation point of view (25), because projected tree cover under this scenario will be at the higher end of possible forecast change. The statistical nature of the RF model makes it unable to predict beyond the ranges of variability of the training data: thus, all areas forecast to experience climatic conditions unobserved in the study area during model calibration (nonanalog) were removed from future tree-cover projections. Because of the large temperature and precipitation elevational gradients present in the area, subalpine areas were not affected by forecast nonanalog climates, which were concentrated at low elevations (Fig. 1). All models were run at the Oxford Supercomputing Centre using the BIOdiversity MODelling (BIOMOD) package (26).

Definition of the Temperature-Based Tree-Growth Limit Zone. A conservative literature-based (9) growing-season temperature threshold zone for tree growth in the Canadian Rocky Mountains of Alberta was defined as 5.5–7.5 °C (Fig. 3). Additionally, and to account for potential lags in tree response to warming and/or underestimations of the temperature lapse rate, an empirical temperature

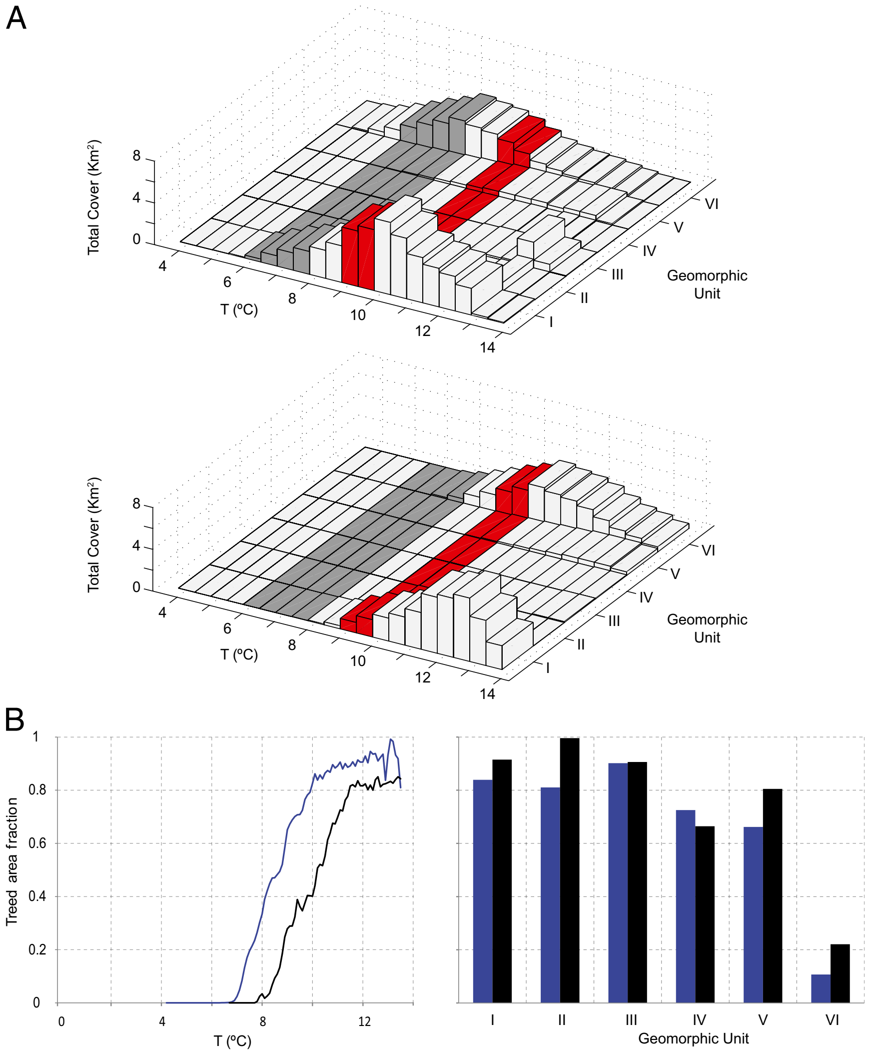

Fig. 4. (*A*) Bivariate histogram depicting the proportion of terrain within the study area according to the temperature (T) gradient and the geomorphic unit for present (1971–2000) (*Upper*) and future (2041–2070) (*Lower*). Gray-shaded area highlights the literature (9) temperature-based, tree-growth limit zone (i.e., June to August average temperature within 5.5–7.5 °C). Red-shaded area highlights the modeled present T threshold for tree growth (~8.5–9.5 °C; Fig. 2). Geomorphic units: I, colluvium; II, alluvium; III, fan; IV, landslide; V, incision; VI, bedrock. Note the very low available colluvium at the temperature-based, tree-growth limit zone, even lower for the 2041–2070 projection. Note that the alluvium dominating the main river floodplain was not accounted for in the analyses because these areas were not used in modeling. (*B*, *Left*) Fraction of land covered by forest vs. T (°C) based on modeled present tree cover (RF; blue line) and on projected tree cover in 2041–2070 (black line). Note that the relationship of tree cover with summer temperature markedly changes toward higher values in the future projection. (*B*, *Right*) Fraction of land covered by trees vs. geomorphic unit (legend as above) for present (blue) and future (black) scenarios. Note that most of the areas with suitable substrate are occupied by trees, even more in the future projection.

tree-growth limit was defined as a 2 °C range, with a minimum temperature corresponding to the 10-m treed pixel occurring at maximum elevation (Fig. S2). The latter measure is very conservative, tuned to the observed patterns. Future literature-based, temperature-limited tree-growth zone was kept at 5.5–7.5 °C, whereas the empirical one was defined as the range between the temperature at the highest forecast treed pixel and the highest temperature in present empirical temperature tree-growth limit. Definition of these areas allowed quantifying tree cover within each temperature-based, tree-growth limit area. These should not be interpreted as absolute values but as measures of divergence from isotherms (and thus from the thermal elevation gradient) of the upper limit of tree cover.

ACKNOWLEDGMENTS. We acknowledge the helpful comments of W. Thuiller on the software package BIOMOD and the help of Thomas Hoffmann in the production of the geomorphic map. M.M.-F. was funded by a Marie Curie Research Fellowship (Grant 254206, Project "ECOCHANGE: Creating conditions for persistence of biodiversity in the face of climate change") and by a GEOmatics for Informed DEcisions postdoctoral grant during the completion of this study.

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