Received: 15 November 2021 | Revised: 24 January 2022 | Accepted: 16 February 2022

DOI: 10.1002/ecy.3717

CONCEPTS & SYNTHESIS

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Cold-air pools as microrefugia for ecosystem functions in the face of climate change

Melissa A. Pastore[1,2] | **Aimée T. Classen**[2,3,4] | **Anthony W. D'Amato**[1] | **Jane R. Foster**[1] | **E. Carol Adair**[1,2]

[1]Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, Vermont, USA

[2]Gund Institute for Environment, University of Vermont, Burlington, Vermont, USA

[3]Ecology and Evolutionary Biology Department, University of Michigan, Ann Arbor, Michigan, USA

[4]University of Michigan Biological Station, Pellston, Michigan, USA

Correspondence
Melissa A. Pastore
Email: lispastore@gmail.com

Funding information
National Institute of Food and Agriculture, Grant/Award Number: 1020508; Office of Integrative Activities, Grant/Award Number: 1920908

Handling Editor: Samantha K. Chapman

Abstract

Cold-air pooling is a global phenomenon that frequently sustains low temperatures in sheltered, low-lying depressions and valleys and drives other key environmental conditions, such as soil temperature, soil moisture, vapor pressure deficit, frost frequency, and winter dynamics. Local climate patterns in areas prone to cold-air pooling are partly decoupled from regional climates and thus may be buffered from macroscale climate change. There is compelling evidence from studies across the globe that cold-air pooling impacts plant communities and species distributions, making these decoupled microclimate areas potentially important microrefugia for species under climate warming. Despite interest in the potential for cold-air pools to enable species persistence under warming, studies investigating the effects of cold-air pooling on ecosystem processes are scarce. Because local temperatures and vegetation composition are critical drivers of ecosystem processes like carbon cycling and storage, cold-air pooling may also act to preserve ecosystem functions. We review research exploring the ecological impacts of cold-air pooling with a focus on vegetation, and then present a new conceptual framework in which cold-air pooling creates feedbacks between species and ecosystem properties that generate unique hotspots for carbon accrual in some systems relative to areas more vulnerable to regional climate change impacts. Finally, we describe key steps to motivate future research investigating the potential for cold-air pools to serve as microrefugia for ecosystem functions under climate change.

KEYWORDS

carbon, climate change, cold-air drainage, cold-air pooling, complex terrain, ecosystem function, microclimate, microrefugia, mountains, temperature inversion

INTRODUCTION

Landscapes with complex topography are heterogeneous with local microclimates (i.e., on a scale of ≤1 km) that are often partly buffered and decoupled from regional climates (Daly et al., 2010; Lenoir et al., 2017). As a result, coarse or macroscale climate change predictions (typically >50 km) are unlikely to be realized uniformly across the landscape (Maclean et al., 2017). Indeed, complex topography (i.e., mountains, hilly terrain, concave slopes) may create local microclimates and climate change microrefugia for cold-adapted or heat-intolerant species (Dobrowski, 2011; Morelli et al., 2016). In addition to microrefugia for cold-adapted species, these locations may act as microrefugia for ecosystem processes that are depended upon for carbon sequestration, habitat provisioning, water filtration, and other functions. Across these heterogeneous landscapes, different zones of plant communities are often associated with different soil metrics and ecological functioning (Augusto et al., 2015). For instance, in the Green Mountains of the northeast USA, climatic conditions produce distinct zones of coniferous and deciduous forests, with conifers in these montane forests generating acidic soils and a thick humus layer relative to deciduous zones (Siccama, 1974). As the climate warms, the patchiness of these topographically complex regions may allow for microscale pockets of cold-adapted (e.g., boreal tree and wildlife species) and heat-intolerant organisms and associated ecosystem functions to persist. Here, we define microrefugia as areas buffered and/or decoupled from climate change over time that enable the persistence of a system's species and ecological functions. Buffering is the moderation of extreme conditions (e.g., temperatures), while decoupling occurs when microclimate does not track the regional climatic trend over time (Lenoir et al., 2017).

While it is often predicted that mountains, given their climatic gradients, will allow species and ecosystem functions to persist as the climate warms (Elsen & Tingley, 2015; Lenoir & Svenning, 2015), there are understudied but potentially important microrefugia for species and functions in low-lying areas where cold-air pooling occurs. These areas can occur in a variety of terrain types and scales, from gently to steeply sloping and shallow to deep, that generate sheltered topographic features, such as sinkholes, depressions, gullies, basins, and hill or mountain valleys. Cold-air pooling results in temperature inversions with lower temperatures at low relative to high elevations and is often seen as a layer of low-elevation fog when air temperature declines below the dewpoint (Figure 1a). This phenomenon occurs when radiative surface cooling after sunset forms dense, cold air that drains downslope and pools in sheltered, low-lying areas, forming temperature inversions that can range in depth from a few to hundreds of meters (Gudiksen et al., 1992; Mahrt et al., 2001; Whiteman et al., 2001). Temperature gradients across inversions span from a few degrees to >20°C, with the lowest temperatures at the bottom (Clements et al., 2003; Novick et al., 2016). Cold-air pooling can occur in any season and there are seasonal differences in the frequency and intensity of cold-air pool formation among locations (Bigg et al., 2014; Iijima & Shinoda, 2000; Novick et al., 2016; Pypker et al., 2007; Whiteman et al., 2001). Inversions formed by cold-air pooling typically occur on clear nights with weak winds and can be diurnal, forming in the evening and decaying after sunrise (though sometimes lasting several hours past sunrise or forming in the day), or they may persist for several days (Novick et al., 2016; Rupp et al., 2020; Whiteman et al., 2001). Due to a lack of vertical mixing, air in these inversions becomes partly decoupled from the overlying free atmosphere. Thus, low-lying areas that experience cold-air pooling may be impacted differently under a warming climate than the broader landscape, particularly where the weather patterns that promote cold-air pooling (e.g., anti-cyclonic flow) become more frequent (Daly et al., 2010). Specifically, increases in mean annual temperature and other climatic changes may occur more slowly in a cold-air pool microclimate compared to the surrounding regional climate, leading to local attenuation, but not complete escape, of climate change. However, decoupling between cold-air pools and the free atmosphere, as well as the response of this phenomenon to climate change, is still poorly understood and warrants further research.

FIGURE 1 (a) A cold-air pool destabilizing on a late October morning in Chittenden County, Vermont, USA. (b) A landscape that is influenced by cold-air pooling: the Nulhegan Basin in Vermont, USA. The uplands are dominated by deciduous species, whereas the lower elevation areas that experience cold-air pooling are dominated by evergreens

Local cold-air pooling events appear to be common in landscapes characterized by complex topography. In fact, these events have been observed in multiple countries and on all seven continents (e.g., Bigg et al., 2014; Chung et al., 2006; Daly et al., 2003; Duker et al., 2020; Dy & Payette, 2007; Grudzielanek & Cermak, 2018; Gustavsson et al., 1998; Lundquist et al., 2008; Matusick et al., 2014; Patsiou et al., 2017; Rupp et al., 2021; Speirs et al., 2009; Tenow & Nilssen, 1990). For example, cold-air pooling occurred in up to 60% of daily observations (Blandford et al., 2008) and in 25%–80% of hourly observations (Rupp et al., 2020) in high elevation mountains of the northwest United States. Also in that region, the saucer-shaped Columbia basin of eastern Washington experienced 120 persistent cold-air pool events (i.e., duration >18 h and lasting up to 103 h) during the months of October through March over a <2-year period (Whiteman et al., 2001). Similarly in the UK, over 9 months in a small lowland valley (valley depth of 100–150 m), cold-air pooling occurred on 56% of nights, with the temperature differential between the valley bottom and adjacent hilltop exceeding 4°C on 20% of nights and exceeding 6°C on 15 nights (Jemmett-Smith et al., 2018). During several weeks of intensive meteorological measurements in the pre-alpine region of southeastern France, regular temperature inversions from cold-air pooling during clear-sky nights generated temperature differentials of up to 5°C across about 100 m of elevation (Duine et al., 2017). Cold-air pooling is also characteristic of hilly grassland savanna in the Natal Drakensberg Mountains of South Africa, generating a 10°–21°C temperature differential between the warmer hilltops and frost-prone hill bases (Samways, 1990).

These localized, and not globally uncommon, examples of decoupled cold-air pool microclimates suggest that cold-air pooling may be frequent in diverse landscapes containing sheltered, low-lying areas, yet cold-air pooling studies are often limited to a single cold-air pooling event and location and rarely explore the effects of cold-air pooling in an ecological context. As such, cold-air pools are compelling, but understudied, targets for preserving organisms and associated ecosystem functions as the climate warms. Here, we review the research conducted to date on the ecological impacts of cold-air pooling with a focus on vegetation, and then discuss the potential role of cold-air pools as microrefugia for ecosystem functions, at least over the coming decades, in the face of climate change. We also describe key steps to advance research investigating the impacts of cold-air pooling on ecosystem function.

EFFECTS OF COLD-AIR POOLS ON VEGETATION AND ECOSYSTEMS

Given the importance of climatic microrefugia in the past, it is likely that networks of small but ecologically important cold-air pooling areas will buffer organisms from climatic change over time by enabling species persistence and facilitating species' range shifts (Dobrowski, 2011; Morelli et al., 2016). Climatic microrefugia are known to have enabled the survival of alpine and arctic plant species during interglacial warm periods, with the distributions of some alpine species even descending to altitudes near sea level (Birks & Willis, 2008). Similarly, in tree species on the northeastern coast of the United States, local marine microclimates decoupled from regional climate warming during the mid-Holocene provided cool, moist conditions that allowed for the persistence and subsequent expansion of spruce (*Picea* spp.; Schauffler & Jacobson, 2002). Recently, an endemic herbaceous perennial in the Maritime Alps (*Saxifraga florulenta*), showed preference for cold-air pooling sites that were buffered from contemporary climate warming (Patsiou et al., 2017), and it is probable that other species are also finding refuge in similar cold-air pooling microenvironments.

Locally, cold-air pooling can structure plant communities by selectively excluding and/or favoring species that differ from the surrounding community. The mechanisms for how or why this may happen can differ, but include reducing minimum and maximum temperatures (Daly et al., 2010), maintaining higher soil moisture and lower vapor pressure deficit (Novick et al., 2016), having a shorter frost-free season (Maclean et al., 2017), having a thicker/more persistent snowpack that may reduce soil freeze–thaw cycles and solar warming (Curtis et al., 2014; Pepin et al., 2011), and having less frequent and less severe fires (Wilkin et al., 2016). In forests, the climatic sorting of tree species may be strongest at the seedling stage when there is a strong environmental filter and trees are most vulnerable to temperature extremes, frost events, and drought. In a study of planted spruce and pine seedlings in a clear-felled area prone to cold-air pooling in the northern boreal zone of Sweden, seedling mortality risk and microscale topography were strongly correlated (Blennow & Lindkvist, 2000). Seedling mortality rates at the site ranged from 2% to 81% and minimum air temperature at seedling height, which was lowest along slopes and at the bottoms of depressions, significantly explained the observed variability. Despite the vulnerability of young vegetation to frost and low temperature extremes, over time species may be able to establish in cold-air pools if the tree canopy buffers seedlings from harsh conditions. For example, after fire in the highlands of Quebec, Canada, black spruce (*Picea mariana*) successfully established in elevated areas surrounding cold-air pools known as "frost hollows," creating an inverted tree line (Dy & Payette, 2007). Black spruce colonization then proceeded downslope, with trees colonizing the frost hollows as denser forest cover reduced frost risk. Although seedling vulnerability to frost may be greater in cold-air pools, these microclimates could alternatively protect seedlings where regional droughts and heatwaves reduce seedling survival (Calama Sainz et al., 2017; Guignabert et al., 2020). It is likely that cold-air pooling also influences competition among seedlings by shaping the abiotic environment, but more studies are needed to understand this interplay among abiotic drivers and plant competition.

Evidence from plant communities at later successional stages underscores the important role cold-air pooling plays in structuring vegetation over time. Often, vegetation found in areas subjected to cold-air pooling is more like vegetation found at disparate locations with cooler climates or higher elevations. For example, at Yosemite National Park in the Sierra Nevada Mountains of California, USA, plant communities found in cold-air pools are characteristic of the more northern Pacific Northwest region of the United States, likely because species became restricted as climate changed after the last ice age (Wilkin et al., 2016). In other instances, cold-air pools have generated unexpected vegetation distributions across slopes, resulting in observations of typical high elevation tree species at low elevations in mountains of the United States (Daubenmire, 1980; Millar et al., 2018) and "inverted tree line grasslands" in gently sloping valleys of Australia (Banks & Paton, 1993; Wearne & Morgan, 2001) and on the Angolan Plateau of Africa (Finckh et al., 2021).

In addition to structuring plant communities, cold-air pooling influences vegetation by impacting plant phenology. In a recent study in the high elevation western US Cascade Range, cold-air pooling homogenized winter microclimate and thus phenology in a year with high frequencies of anti-cyclonic weather patterns that promote cold-air pooling (Ward et al., 2018). In that region, bud break typically occurs later in spring as elevation increases; however, elevation did not predict bud break for many species, particularly herbs and shrubs, in a year with frequent cold-air pooling because plants at upper elevations (that are typically colder) were exposed to clear, sunny weather while plants in the valleys (that are typically warmer) were exposed to consistently freezing temperatures. When looking across smaller elevation differences or in low relief regions, temperature inversions impact the onset of spring phenology in slightly different ways. In long-lived perennial wildflower species of the western US Rocky Mountains, cold-air pooling resulted in substantially greater frost kill of flower buds in low-lying areas compared to slightly higher elevations (i.e., elevation differences as little as 12 m), leading to variable timing and abundance of flowering across small geographic scales (Inouye, 2008). Landsat data from an eastern deciduous forest in the low elevation region of southern New England in the northeast United States revealed that springtime cold-air pooling governs the start of leaf growth, delaying spring greenup by more than 2 weeks in forests with similar composition, age, and structure (Fisher et al., 2006). Despite low relief, spatial patterns in leaf onset dates were explained by topography rather than forest composition or structure, slope, soil type, or surface hydrology, with every 4.16 m decline in elevation delaying spring leaf onset by 1 day.

Cold-air pool areas tend to alter abiotic factors that govern leaf-level physiological processes (e.g., air temperatures, vapor pressure deficit, soil moisture), and these physiological effects may translate into positive or negative changes in plant and total ecosystem productivity. In a mixed deciduous hardwood forest in the southeastern Appalachian Mountains of the United States, cold-air pooling reduced foliar respiration by around 20% via lower air temperatures, leading to a 10% increase in net carbon uptake (i.e., net ecosystem productivity) during the growing season and a 10%–27% increase on an annual basis (Novick et al., 2016). However, in other areas, greater frost risk in cold-air pools reduces productivity, such as in the coastal lowlands of South Africa where a frost intolerant shrub exhibited lower net primary productivity (NPP) in plots that were predicted to be within the cold-air pool frost zone (Duker et al., 2020). Cold-air pooling can also impact plant water balance, as in a study in the mountains of northern Idaho, USA, where strong nocturnal temperature inversions affected nighttime stomatal opening and predawn leaf water potentials (Hubbart et al., 2007). Whether effects of cold-air pooling on plant water balance scale to influence productivity is unexplored.

COLD-AIR POOLS AS MICROREFUGIA FOR ECOSYSTEM FUNCTIONS

Cold-air pooling influences animal and plant distributions and community composition (Curtis et al., 2014; Daubenmire, 1980; Millar et al., 2018; Samways, 1990; Wearne & Morgan, 2001; Wilkin et al., 2016), which should impact ecosystem function. In addition to acting as microrefugia for organisms that are vulnerable to climate change, we propose a new conceptual framework in which cold-air pools serve as important microrefugia for ecosystem functions in regions where key functions are diminishing because of macroscale climate change. For example, low temperatures and waterlogged soils protect soil carbon from decomposition (Davidson & Janssens, 2006), and thus cooler, wetter soils found in cold-air pools could preserve soil carbon as the broader region becomes warmer and drier under climate change. More importantly, feedbacks between species sustained in these microrefugia and ecosystem properties could generate unique hotspots for carbon accrual relative to areas more vulnerable to climate change impacts.

Our conceptual framework includes short-term effects of cold-air pooling on carbon dynamics (e.g., carbon assimilation, respiration, productivity), as well as climate–plant–soil feedbacks that may govern ecosystem carbon storage over longer timescales. We focus on carbon cycling because it is an important ecosystem function involved in climate change feedbacks but note that cold-air pools could also act as microrefugia for other ecosystem functions like nutrient cycling and water retention (McLaughlin et al., 2017). We also describe contrasting scenarios where cold-air pooling could act as a stressor in some systems, constraining ecosystem functions like carbon cycling by damaging frost-intolerant species. The prevailing mechanisms of how cold-air pools affect carbon cycling and their net effect on ecosystem carbon storage likely vary among vegetation types and climates, with cold-air pooling benefitting carbon storage in some contexts and acting as a stressor in others (e.g., in forests dominated by species sensitive to cold or diurnal temperature fluctuations). Assessing the effects of cold-air pools on ecosystem function is critical to understanding their role in moderating the effects of climate change.

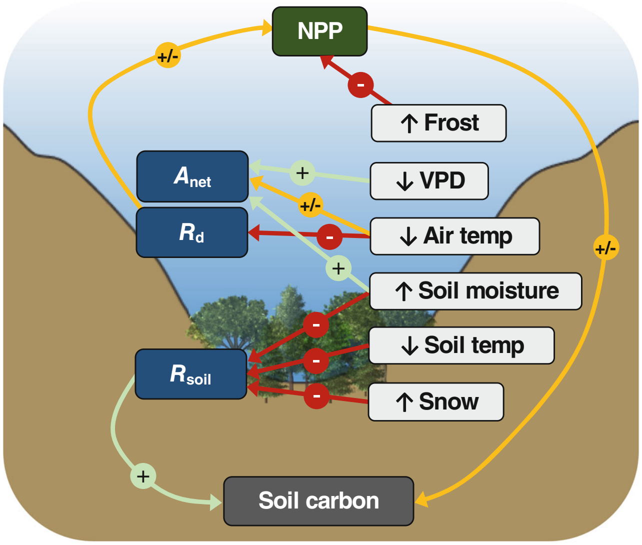


FIGURE 2 (a) Conceptual model of how cold-air pooling could influence short-term (i.e., minutes, days, months) plant and microbial processes that affect soil carbon pools. Black arrows within boxes represent conditions that are higher (↑) or lower (↓) in cold-air pools relative to the broader region. Green arrows connecting boxes represent positive (+) effects of environmental conditions, red arrows represent negative (−) effects, and orange arrows indicate effects that could be positive or negative (+/−). It is also possible that there could be no effect for certain species, systems, or times, but here we show the likely direction when there is an effect. A_{net}, leaf-level net photosynthesis; NPP, net primary productivity; R_{d}, dark respiration; R_{soil}, soil respiration; Snow, snowpack thickness/persistence; Temp, temperature; VPD, vapor pressure deficit

Short-term effects of cold-air pooling on ecosystem carbon dynamics

Cold-air pooling can have important effects on microbial and plant processes in the short term (i.e., minutes, days, months) that regulate both soil carbon losses and inputs, thereby influencing ecosystem carbon storage, a key ecosystem function (Figure 2). In addition to reducing air temperatures, cold-air pools can reduce soil temperatures, a process observed in handful of studies (Novick et al., 2016; Soler et al., 2002). In locations with persistent or strong temperature inversions, soil temperatures may decline and reach a lower minimum temperature such that soil respiration is lower compared to the broader upslope region, reducing gaseous soil carbon losses in cold-air pools (Figure 2). In support of this idea, modest reductions in soil temperature and soil respiration were associated with cold-air pooling in a southeastern US Appalachian Mountain site (Novick et al., 2016), but more observations across various regions are needed to determine the strength and frequency of cold-air pooling impacts on soil temperatures and soil respiration.

Of course, multiple factors may regulate microbial responses and soil carbon losses over the short term in areas with cold-air pooling. For example, in cold-air pooling areas, there may be smaller winter soil carbon losses because a thicker and/or more persistent layer of snowpack may reduce the frequency of soil freeze–thaw cycles and associated pulses of soil carbon losses via respiration and leaching (Wipf et al., 2015, Figure 2). Wetter soils in cold-air pools may favor lower rates of soil respiration if oxygen becomes limiting (Figure 2). The characteristics of cold-air pools will also likely interact with those of low-lying areas, such as richer soil nutrients in some valley bottoms (Tateno & Takeda, 2003) and greater organic matter and carbon accumulation in downslope positions (Rosenbloom et al., 2001), to influence carbon cycling.

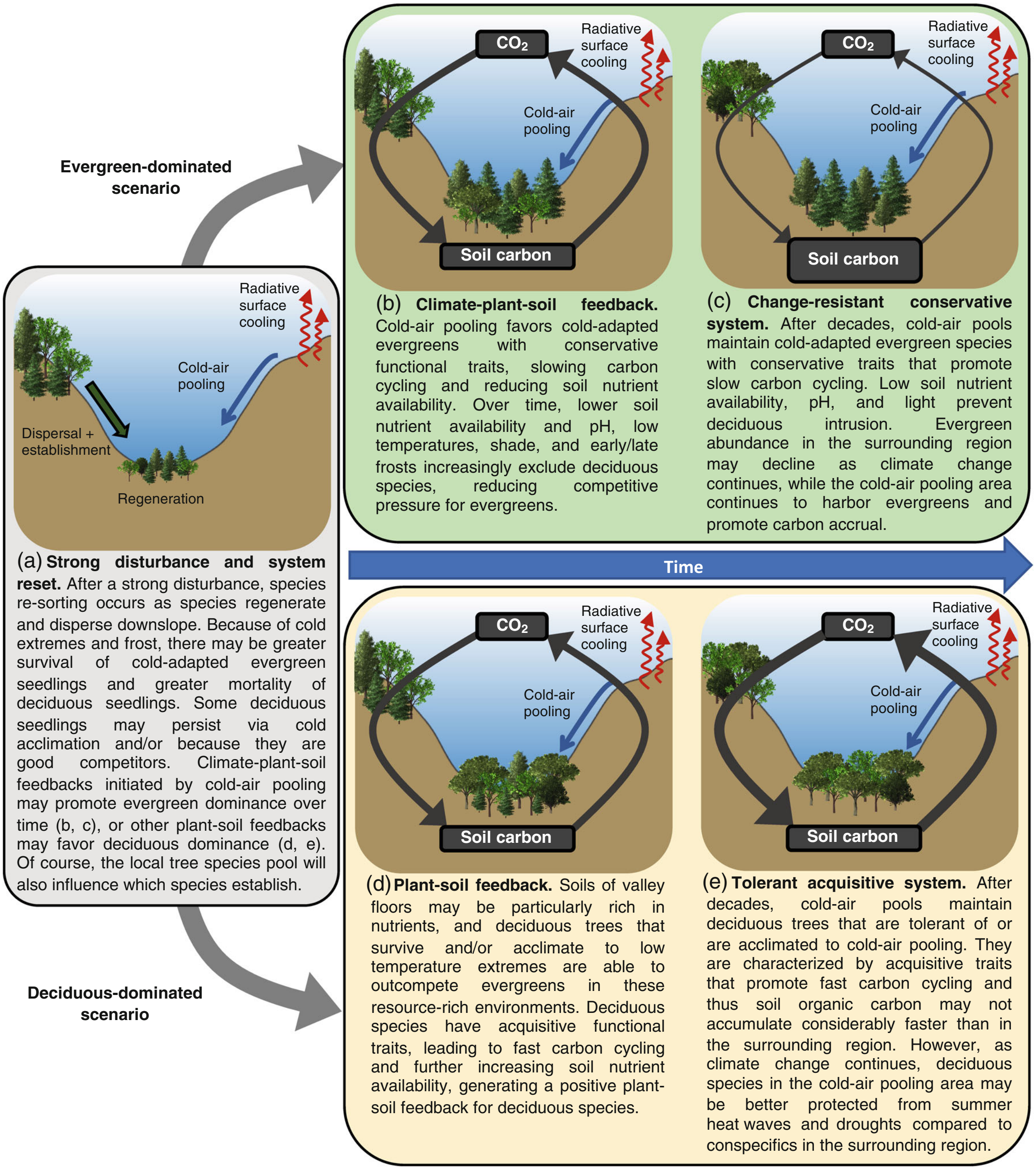
Effects of cold-air pooling on plant carbon assimilation and productivity, and thus soil carbon inputs, will depend on the composition of the plant community. For plant species that prefer cooler conditions (e.g., spruce, pine, fir, cool-season grasses and forbs), the conditions exhibited by cold-air pool areas (e.g., higher soil moisture, lower vapor pressure deficit, lower temperatures) may be favorable for maintaining rates of plant carbon assimilation and thus ecosystem productivity as the climate changes (Figure 2). This may also depend on whether species are near the warm or cold edge of their range. Species are thought to be most vulnerable to climate change near the warm edge of their distribution, where they tend to respond negatively to increases in temperature, whereas species near the cold edge of their distribution may respond positively. For instance, in a warming experiment at the temperate-boreal ecotone in Minnesota, USA, boreal tree species (e.g., *Picea glauca* and *Abies balsamea*) showed reductions in photosynthesis and growth in response to warming, while temperate species (e.g., *Acer rubrum* and *Quercus macrocarpa*) showed increases (Reich et al., 2015). Thus, as climate changes, lower temperatures, lower vapor pressure deficit, and higher soil moisture in cold-air pools could allow species at the warm edge of their range, in particular, to maintain typical rates of photosynthesis and growth while rates for stressed conspecifics in the broader region decline. In addition, cold-air pooling may positively affect plant carbon balance by suppressing foliar respiration, as observed in Novick et al. (2016) (Figure 2).

However, cold-air pooling may act as a stressor in forests dominated by species that tolerate or even benefit from climate warming, especially if they are near the cold edge of their range (e.g., temperate maple and oak species in the northern United States, Reich et al., 2015). Photosynthesis and NPP of deciduous species that are not adapted or acclimated to extreme low temperatures or large diurnal temperature fluctuations may be negatively affected by cold-air pooling because of the lower minimum temperatures reached in these areas (Figure 2). In addition, greater frost risk and a shorter frost-free period can harm buds, flowers, and emerging leaves, thereby reducing tree growth and reproduction (Augspurger, 2009, Figure 2). In a hardwood Mediterranean forest in southwest Australia, tree canopy frost damage increased with declining elevation because of cold-air pooling (Matusick et al., 2014). In temperate deciduous forests, frost damage could be especially devastating for species like sugar maple, which tends to leaf out early in the season to optimize carbon gain but is particularly vulnerable to frost damage and temperature anomalies (Hufkens et al., 2012), as well as for saplings that experience earlier budbreak than conspecific canopy trees (Augspurger, 2009; Pederson et al., 2014). In other cases, deciduous species could respond to cold stress in these areas by delaying spring phenology (e.g., later budburst and leaf emergence) and shedding leaves earlier in fall (Vitasse et al., 2014), shortening the growing season and window for carbon capture. Although lower vapor pressure deficit and greater soil moisture in cold-air pools may still benefit deciduous species, those effects may be outweighed by the negative impacts of lower temperature extremes and greater freezing stress. Thus, cold-air pooling could lead to canopy dieback and mortality events in some ecosystems, reducing plant carbon pools.

Climate–plant–soil feedbacks in cold-air pools promote carbon storage over time

Effects of cold-air pooling on plant productivity not only depend on the composition of the plant community but may also control community composition over time. Although the mechanisms described above may influence carbon cycles in various ways over timescales of minutes to months, the greatest potential benefit of cold-air pooling to soil and ecosystem carbon storage is by generating and preserving plant communities that promote slow carbon turnover. We suggest that the quasi-equilibrium stage of many cold-air pool forests is composed of species with traits that facilitate the conservation of resources, such as long leaf lifespans, low relative growth rates, low specific leaf area, low nutrient concentrations, low rates of photosynthesis and respiration, and low rhizodeposition: "conservative" traits on the leaf economics spectrum (Figure 3c, Reich et al., 1997, Diaz et al., 2004, Wright et al., 2004). For instance, the abiotic conditions characteristic of cold-air pools often favor cold-adapted evergreen species, which are characterized by conservative plant resource acquisition and processing strategies (Reich et al., 1997). Thus, cold-air pools in proximity to evergreen species, including evergreen or mixed forests, slopes with adjacent zones of trees with different thermal tolerances, and near the temperate-boreal ecotone, may promote and preserve conservative evergreen-dominated plant communities as macroscale climate changes (Figure 1b). In turn, communities of conservative species often lead to slow soil organic carbon turnover and thereby promote soil carbon accrual and preservation (Boča et al., 2014; Cornwell et al., 2008; Jevon et al., 2019).

In this way, just as cold-air pools are known to act as microrefugia for relict species associated with past climates, they may similarly act as microrefugia harboring ecosystem functions that are diminishing in the broader upslope region. Of course, cold-air pools may harbor plant communities at various stages of succession. After a disturbance event, such as fire or dieback, re-sorting of species can occur as species regenerate and disperse into cold-air pool areas from upslope positions (Figure 3a). Because of low temperature extremes and frost in cold-



(a) Strong disturbance and system reset. After a strong disturbance, species re-sorting occurs as species regenerate and disperse downslope. Because of cold extremes and frost, there may be greater survival of cold-adapted evergreen seedlings and greater mortality of deciduous seedlings. Some deciduous seedlings may persist via cold acclimation and/or because they are good competitors. Climate-plant-soil feedbacks initiated by cold-air pooling may promote evergreen dominance over time (b, c), or other plant-soil feedbacks may favor deciduous dominance (d, e). Of course, the local tree species pool will also influence which species establish.

(b) Climate-plant-soil feedback. Cold-air pooling favors cold-adapted evergreens with conservative functional traits, slowing carbon cycling and reducing soil nutrient availability. Over time, lower soil nutrient availability and pH, low temperatures, shade, and early/late frosts increasingly exclude deciduous species, reducing competitive pressure for evergreens.

(c) Change-resistant conservative system. After decades, cold-air pools maintain cold-adapted evergreen species with conservative traits that promote slow carbon cycling. Low soil nutrient availability, pH, and light prevent deciduous intrusion. Evergreen abundance in the surrounding region may decline as climate change continues, while the cold-air pooling area continues to harbor evergreens and promote carbon accrual.

(d) Plant-soil feedback. Soils of valley floors may be particularly rich in nutrients, and deciduous trees that survive and/or acclimate to low temperature extremes are able to outcompete evergreens in these resource-rich environments. Deciduous species have acquisitive functional traits, leading to fast carbon cycling and further increasing soil nutrient availability, generating a positive plant-soil feedback for deciduous species.

(e) Tolerant acquisitive system. After decades, cold-air pools maintain deciduous trees that are tolerant of or are acclimated to cold-air pooling. They are characterized by acquisitive traits that promote fast carbon cycling and thus soil organic carbon may not accumulate considerably faster than in the surrounding region. However, as climate change continues, deciduous species in the cold-air pooling area may be better protected from summer heat waves and droughts compared to conspecifics in the surrounding region.

FIGURE 3 Conceptual model of how cold-air pooling could act as an important driver of ecosystem function by governing forest vegetation composition and generating climate–plant–soil feedbacks over the long term. Multiple outcomes are possible, and here we present contrasting scenarios in which either evergreen (b, c) or deciduous (d, e) trees become dominant. After a strong disturbance (a), climate–plant–soil feedbacks generated by cold-air pooling over time (b) may produce a change-resistant conservative evergreen community that promotes carbon storage (c), or other plant–soil feedbacks may promote a tolerant/acclimated acquisitive deciduous system (d) that may not accumulate soil carbon considerably faster than in the surrounding region (e)

air pools, cold-adapted evergreen seedlings may experience greater survival than more vulnerable deciduous seedlings. Unless tree species can acclimate, early- and late-season frosts and extreme low temperatures will continue to reduce the productivity and survival of deciduous species, releasing cold-adapted evergreens from competitive pressure. In addition, the conservative traits of evergreen species will gradually modify soil properties to further favor evergreen over deciduous species, for instance, by reducing soil nitrogen availability and pH (Augusto et al., 2015; Siccama, 1974; Figure 3b). Because the litter quality of woody evergreen species is generally lower than that of woody deciduous species, and because acidification increases the strength of soil organo-mineral bonds, increasing evergreen abundance will promote slower decomposition and greater soil carbon accrual (Boča et al., 2014; Cornwell et al., 2008; Jevon et al., 2019; Moore et al., 1999; Newcomb et al., 2017). Moreover, the dense canopy cover associated with shade-tolerant evergreens may limit soil respiration via lower soil temperatures and greater snowpack duration, as well as inhibit the establishment of light-demanding deciduous species. Thus, over decades, these climate–plant–soil feedbacks may strengthen such that the evergreen community becomes more resistant to change, even as conspecifics in the surrounding region decline because of macroscale climate change, thereby preserving the slower cycling ecosystem type in cold-air pools (Figures 1b, 3c).

Other factors may be more important than temperature for plant community development; for example, the influence of local soil properties could outweigh that of cold-air pooling microclimates in some cases. Valley floor soils can be rich in nutrients (Tateno & Takeda, 2003), and deciduous seedlings may be more competitive than coniferous seedlings in these resource-rich environments (Augusto et al., 2014) if they are able to tolerate or acclimate to the low temperature extremes and frost events in cold-air pools (Figure 3d). The fast “acquisitive” traits of deciduous species (opposite of the slow conservative traits listed above; Diaz et al., 2004) will further enhance soil nutrient availability, creating a positive feedback loop for deciduous species that inhibits evergreen establishment (Figure 3d). Such traits will also lead to faster decomposition and limited carbon accrual relative to evergreen-dominated communities (Figure 3e; Boča et al., 2014, Cornwell et al., 2008). Thus, for instances in which deciduous species dominate in cold-air pools, ecosystem carbon storage may not be substantially greater relative to that of the surrounding region. As climate change continues, deciduous communities in cold-air pools may be buffered from extreme heat waves and droughts, which could benefit carbon uptake during and following these events, however we expect increases in ecosystem carbon storage mediated by cold-air pooling to be greater when evergreen communities are favored.

Currently, these climate–plant–soil feedbacks are likely ongoing in cold-air pools at various points in their successional trajectories and in regions under differing magnitudes of climate change pressure, although no studies, to our knowledge, have evaluated them. Some mature cold-air pool communities will already be resistant to change, while younger communities will be more dynamic. Plant community shifts may occur most rapidly in areas where there is greater pressure for cold-adapted species to retreat into cold-air pools. Northern temperate and boreal (i.e., cold-adapted coniferous) species were recently observed migrating downslope in response to historic land-use changes and disturbance (Foster & D’Amato, 2015); however, few studies have explored downslope migration of tree species in relation to cold-air pooling. Those that have investigated this phenomenon observed unexpected patterns in vegetation composition across elevation, such as similar plant community composition at high elevations and valley bottoms, as discussed above (Daubenmire, 1980; Millar et al., 2018; Wearne & Morgan, 2001). Whether nonlinearities in temperature and vegetation driven by cold-air pooling are linked to nonlinearities in ecosystem functions like carbon storage across slopes is unknown.

We acknowledge that differences in edaphic properties, hydrology, erosional processes, land-use history, and other factors across landscapes with complex topography could also affect current and future distributions of vegetation and soil carbon storage and determining which factors will most strongly drive patterns at local scales under climate change is an important area for future research. Additionally, in some regions, cold-tolerant deciduous tree species are characteristic at the tree line (e.g., Fajardo et al., 2013; Gansert et al., 1999), highlighting a need for studies exploring how cold-air pooling interacts with diverse vegetation patterns to generate climate–plant–soil feedbacks. Moreover, although we used forests as an example, it is probable that cold-air pools documented in other ecosystem types such as meadows (Inouye, 2008), grasslands (Samways, 1990; Wearne & Morgan, 2001), and coastal shrublands (Duker et al., 2020) promote and preserve species with trait assemblages linked to functioning, thereby acting as microrefugia for ecosystem functions in the face of climate change.

RESEARCH PRIORITIES

As we describe, cold-air pooling could have important ecological impacts on foliar transpiration, phenology, carbon cycling, hydrological processes, seedling regeneration, frost-induced tree damage, and species persistence under warming. Given the limited amount of work, to date, on this topic, we hope that our conceptual framework will motivate future research that addresses the potential for cold-air pools to serve as microrefugia for ecosystem functions. Below, we identify two key research priorities to drive future investigations into the role that cold-air pooling could play in maintaining pockets of distinct ecosystem function under climate change.

Cold-air pooling patterns across scales

First, it is critical to characterize the extent, frequency, intensity, depth, and duration of cold-air pooling events, as well as the occurrence and degree of local atmospheric buffering and decoupling, across broad temporal and spatial scales and across areas that differ in species composition, climate, and edaphic factors. Gridded temperature observations of the atmosphere or the land surface are a potential source to quantify temporal aspects of cold-air pooling events in the absence of ground-based measurements (Lembrechts et al., 2019). Land surface temperatures (LST) from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensors on the Terra and Aqua satellites have been used to characterize temperature inversions directly via reflectance differences throughout the atmospheric column in high-latitude regions (Hyvarinen & Rantamaki, 2004; Liu & Key, 2003), to model lapse rates for comparison with in-situ temperature logger networks (Lembrechts et al., 2019), and to improve agreement of interpolated gridded temperature data with station data in mountainous terrain (Oyler et al., 2016). As understanding of the relationship between remotely sensed LST and near-surface air temperatures improves (Adolph et al., 2018), MODIS LST could be used in conjunction with digital elevation models to characterize the frequency, extent, and duration of cold-air pooling events over a range of scales, from local to global.

Cold-air pooling can occur at spatial scales not captured by gridded temperature data, and thus the remote sensing techniques above should be paired with finer scale in situ environmental sensor data capable of exploring cold-air pooling dynamics at smaller scales (e.g., <1 km) below forest canopies and at the soil–air interface. Environmental sensors measuring near-surface air (e.g., ≤2 m height) and soil temperatures could be placed in plots spanning elevational transects across cold-air pooling gradients (i.e., transects on different slopes experiencing strong to no cold-air pooling, for comparison). Additionally, in situ sensors could be used to measure the indirect effects of cold-air pooling (e.g., soil moisture, vapor pressure deficit). It is likely that many existing elevational transects can be leveraged where sensor data is available or by deploying new sensors in existing plots. Likely cold-air pooling gradients could be identified using satellite imagery, digital elevation models (Lundquist et al., 2008), and local knowledge, but local, high-frequency (e.g., sub-hourly to hourly) in situ sensor data will be needed to resolve the strength and dynamics of cold-air pooling at the smaller transect scales. Vertical temperature profiles using temperature sensors spanning different heights above and below the soil surface at several locations along a slope can be paired with free-air temperature data (e.g., gridded temperature data simulated by regional and global climate models) to explore decoupling between cold-air pooling microclimates and the free atmosphere. Weather stations on hilltops and in valleys could also be leveraged for temperature and other meteorological measurements, such as wind speed and direction, that could influence cold-air pooling (Bigg et al., 2014; Daly et al., 2010).

Vegetation dynamics and ecosystem functioning

To explore how cold-air pooling influences vegetation composition and ecosystem processes, we need field studies using elevational transects, as suggested above, that span cold-air pooling gradients. Forest tree composition and demographics could be determined by identifying and measuring live overstory trees in large plots at different elevations along the transects described above, while saplings/seedlings, shrubs, and groundcover could be measured in nested subplots. Locations for which vegetation composition and dynamics (e.g., tree growth and survival) have been measured over long timescales (i.e., years, decades) could be leveraged and prioritized for transect establishment. In addition to species composition and size structure, functional traits such as foliar nitrogen concentrations and specific leaf area and other key ecosystem measurements such as soil and litter carbon and nitrogen pools could be measured in plots along transects or obtained from databases (e.g., TRY plant trait database). Ecophysiological processes linked to function that may respond to cold-air pooling in the short term, such as leaf net photosynthesis, stomatal conductance, and intrinsic water-use efficiency, could be measured in situ and at different times of the day to examine lagged effects of cold-air pooling on real-time dynamic processes that regulate productivity. The influence of cold-air pooling on forest productivity could be determined using remote-sensing approaches and retrospectively assessed by pairing dendrochronological reconstructions of past stem wood increment with historic characterizations of cold-air pooling regimes from the remote sensing techniques. To assess the likelihood of success for focal species to shift their distributions into cold-air pools, reciprocal common garden experiments along cold-air pooling slopes and plant–soil feedback greenhouse studies could be used.

CONCLUSIONS

Although the development of cold-air pools is a regular occurrence that has been locally documented, there has not been a synthetic effort exploring their extensiveness across broad spatial and temporal scales and exploring if and how these phenomena impact regional ecological patterns and processes. We propose that locations prone to frequent or persistent cold-air pooling will maintain plant communities linked to ecosystem functioning as climate changes, thereby acting as microrefugia for ecosystem functions. In many systems, cold-air pools may promote the preservation of ecosystem functions like soil carbon storage in the face of climate change, an idea that should be tested with field and remote sensing data spanning many different types of soils, vegetation, and topographic characteristics. Thus, there is a strong need for cold-air pooling research that makes connections across ecological disciplines, such as ecosystem and landscape ecology with geospatial science and remote sensing.

In summary, by inducing climatic lags at local scales, cold-air pooling may modulate species and ecosystem responses to macroclimate warming. Given that approximately a quarter of the Earth's land surface is mountainous (Sayre et al., 2018) and an additional portion of the land surface is characterized by non-mountainous yet complex topography that also generates microclimates, it is critical to determine the influence of cold-air pooling on ecosystem processes that can feed back to affect macroscale climate change.

ACKNOWLEDGMENTS

This paper was supported by NSF Award 1920908 and the USDA National Institute of Food and Agriculture, McIntire-Stennis project 1020508. We thank two anonymous reviewers and the editor for their helpful insights.

CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

AUTHOR CONTRIBUTIONS

Melissa A. Pastore conceived of the paper and wrote the first draft. All authors jointly revised the manuscript.

ORCID

Melissa A. Pastore https://orcid.org/0000-0002-7465-1418
Aimée T. Classen https://orcid.org/0000-0002-6741-3470
Anthony W. D'Amato https://orcid.org/0000-0002-2570-4376
Jane R. Foster https://orcid.org/0000-0002-5997-0269
E. Carol Adair https://orcid.org/0000-0002-8567-9045

REFERENCES

Adolph, A. C., M. R. Albert, and D. K. Hall. 2018. "Near-Surface Temperature Inversion during Summer at Summit, Greenland, and its Relation to MODIS-Derived Surface Temperatures." *The Cryosphere* 12(3): 907–20.

Augspurger, C. K. 2009. "Spring 2007 Warmth and Frost: Phenology, Damage and Refoliation in a Temperate Deciduous Forest." *Functional Ecology* 23(6): 1031–9.

Augusto, L., A. De Schrijver, L. Vesterdal, A. Smolander, C. Prescott, and J. Ranger. 2015. "Influences of Evergreen Gymnosperm and Deciduous Angiosperm Tree Species on the Functioning of Temperate and Boreal Forests." *Biological Reviews* 90(2): 444–66.

Augusto, L., T. Jonathan Davies, S. Delzon, and A. De Schrijver. 2014. "The Enigma of the Rise of Angiosperms: Can we Untie the Knot?" *Ecology Letters* 17(10): 1326–38.

Banks, J. C. G., and D. M. Paton. 1993. "Low Temperature as an Ecological Factor in the Cool-Climate Eucalypt Forests." *Studia Forestalia Suecica* 191: 25–32.

Bigg, G. R., S. M. Wise, E. Hanna, D. Mansell, R. G. Bryant, and A. Howard. 2014. "Synoptic Climatology of Cold Air Drainage in the Derwent Valley, Peak District, UK." *Meteorological Applications* 21(2): 161–70.

Birks, H. J. B., and K. J. Willis. 2008. "Alpines, Trees, and Refugia in Europe." *Plant Ecology & Diversity* 1(2): 147–60.

Blandford, T. R., K. S. Humes, B. J. Harshburger, B. C. Moore, V. P. Walden, and H. Ye. 2008. "Seasonal and Synoptic Variations in near-Surface Air Temperature Lapse Rates in a Mountainous Basin." *Journal of Applied Meteorology and Climatology* 47(1): 249–61.

Blennow, K., and L. Lindkvist. 2000. "Models of Low Temperature and High Irradiance and their Application to Explaining the Risk of Seedling Mortality." *Forest Ecology and Management* 135(1–3): 289–301.

Boča, A., H. van Miegroet, and M.-C. Gruselle. 2014. "Forest Overstory Effect on Soil Organic Carbon Storage: A Meta-Analysis." *Soil Science Society of America Journal* 78(S1): S35–47.

Calama Sainz, R., R. M. González, M. E. L. Borja, J. M. E. Morral, M. P. Nicolau, F. B. Oviedo, C. E. del Peso Taranco, and M. P. Mínguez. 2017. "Natural Regeneration in Iberian Pines: A Review of Dynamic Processes and Proposals for Management." *Forest Systems* 26(2): eR02S.

Chung, U., H. H. Seo, K. H. Hwang, B. S. Hwang, J. Choi, J. T. Lee, and J. I. Yun. 2006. "Minimum Temperature Mapping over Complex Terrain by Estimating Cold Air Accumulation Potential." *Agricultural and Forest Meteorology* 137(1–2): 15–24.

Clements, C. B., C. D. Whiteman, and J. D. Horel. 2003. "Cold-Air-Pool Structure and Evolution in a Mountain Basin: Peter Sinks, Utah." *Journal of Applied Meteorology* 42(6): 752–68.

Cornwell, W. K., J. H. C. Cornelissen, K. Amatangelo, E. Dorrepaal, V. T. Eviner, O. Godoy, S. E. Hobbie, B. Hoorens, H. Kurokawa, and N. Pérez-Harguindeguy. 2008. "Plant Species Traits Are the Predominant Control on Litter Decomposition Rates within Biomes Worldwide." *Ecology Letters* 11(10): 1065–71.

Curtis, J. A., L. E. Flint, A. L. Flint, J. D. Lundquist, B. Hudgens, E. E. Boydston, and J. K. Young. 2014. "Incorporating Cold-Air Pooling into Downscaled Climate Models Increases Potential Refugia for Snow-Dependent Species within the Sierra Nevada Ecoregion, CA." *PLoS One* 9(9): e106984.

Daly, C., D. R. Conklin, and M. H. Unsworth. 2010. "Local Atmospheric Decoupling in Complex Topography Alters Climate

Change Impacts." *International Journal of Climatology* 30(12): 1857–64.

Daly, C., E. H. Helmer, and M. Quiñones. 2003. "Mapping the Climate of Puerto Rico, Vieques and Culebra." *International Journal of Climatology: A Journal of the Royal Meteorological Society* 23(11): 1359–81.

Daubenmire, R. 1980. "Mountain Topography and Vegetation Patterns." *Northwest Science* 54(2): 146–52.

Davidson, E. A., and I. A. Janssens. 2006. "Temperature Sensitivity of Soil Carbon Decomposition and Feedbacks to Climate Change." *Nature* 440(7081): 165–73.

Diaz, S., J. G. Hodgson, K. Thompson, M. Cabido, J. H. C. Cornelissen, A. Jalili, G. Montserrat-Marti, J. P. Grime, F. Zarrinkamar, and Y. Asri. 2004. "The Plant Traits that Drive Ecosystems: Evidence from Three Continents." *Journal of Vegetation Science* 15(3): 295–304.

Dobrowski, S. Z. 2011. "A Climatic Basis for Microrefugia: The Influence of Terrain on Climate." *Global Change Biology* 17(2): 1022–35.

Duine, G.-J., T. Hedde, P. Roubin, P. Durand, M. Lothon, F. Lohou, P. Augustin, and M. Fourmentin. 2017. "Characterization of Valley Flows within Two Confluent Valleys under Stable Conditions: Observations from the KASCADE Field Experiment." *Quarterly Journal of the Royal Meteorological Society* 143(705): 1886–902.

Duker, R., R. M. Cowling, M. L. van der Vyver, and A. J. Potts. 2020. "Site Selection for Subtropical Thicket Restoration: Mapping Cold-Air Pooling in the South African Sub-Escarpment Lowlands." *PeerJ* 8: e8980.

Dy, G., and S. Payette. 2007. "Frost Hollows of the Boreal Forest as Extreme Environments for Black Spruce Tree Growth." *Canadian Journal of Forest Research* 37(2): 492–504.

Elsen, P. R., and M. W. Tingley. 2015. "Global Mountain Topography and the Fate of Montane Species under Climate Change." *Nature Climate Change* 5(8): 772–6.

Fajardo, A., F. I. Piper, and G. Hoch. 2013. "Similar Variation in Carbon Storage between Deciduous and Evergreen Treeline Species across Elevational Gradients." *Annals of Botany* 112(3): 623–31.

Finckh, M., J. Wendefeuer, and P. Meller. 2021. "Frost-Driven Lower Treelines in Angola and their Implications for Tropical Forest–Grassland Mosaics." *Journal of Vegetation Science* 32: e13084.

Fisher, J. I., J. F. Mustard, and M. A. Vadeboncoeur. 2006. "Green Leaf Phenology at Landsat Resolution: Scaling from the Field to the Satellite." *Remote Sensing of Environment* 100(2): 265–79.

Foster, J. R., and A. W. D'Amato. 2015. "Montane Forest Ecotones Moved Downslope in Northeastern USA in Spite of Warming between 1984 and 2011." *Global Change Biology* 21(12): 4497–507.

Gansert, D. K., K. Backes, and Y. Kakubari. 1999. "Altitudinal and Seasonal Variation of Frost Resistance of Fagus Crenata and Betula Ermanii along the Pacific Slope of Mt. Fuji, Japan." *Journal of Ecology* 87(3): 382–90.

Grudzielanek, A. M., and J. Cermak. 2018. "Temporal Patterns and Vertical Temperature Gradients in Micro-Scale Drainage Flow Observed Using Thermal Imaging." *Atmosphere* 9(12): 498.

Gudiksen, P. H., J. M. Leone, Jr., C. W. King, D. Ruffieux, and W. D. Neff. 1992. "Measurements and Modeling of the Effects of Ambient Meteorology on Nocturnal Drainage Flows." *Journal of Applied Meteorology* 31(9): 1023–32.

Guignabert, A., L. Augusto, F. Delerue, F. Maugard, C. Gire, C. Magnin, S. Niollet, and M. Gonzalez. 2020. "Combining Partial Cutting and Direct Seeding to Overcome Regeneration Failures in Dune Forests." *Forest Ecology and Management* 476: 118466.

Gustavsson, T., M. Karlsson, J. Bogren, and S. Lindqvist. 1998. "Development of Temperature Patterns during Clear Nights." *Journal of Applied Meteorology* 37(6): 559–71.

Hubbart, J. A., K. L. Kavanagh, R. Pangle, T. Link, and A. Schotzko. 2007. "Cold Air Drainage and Modeled Nocturnal Leaf Water Potential in Complex Forested Terrain." *Tree Physiology* 27(4): 631–9.

Hufkens, K., M. A. Friedl, T. F. Keenan, O. Sonnentag, A. Bailey, J. O'Keefe, and A. D. Richardson. 2012. "Ecological Impacts of a Widespread Frost Event Following Early Spring Leaf-Out." *Global Change Biology* 18(7): 2365–77.

Hyvarinen, O., and M. Rantamaki. 2004. "Possibilities of Operational Detection of Temperature Inversions with Satellite Remote Sensing." Proceedings of EUMETSAT Meteorological Conference, Prague, Czech Republic.

Iijima, Y., and M. Shinoda. 2000. "Seasonal Changes in the Cold-Air Pool Formation in a Subalpine Hollow, Central Japan." *International Journal of Climatology: A Journal of the Royal Meteorological Society* 20(12): 1471–83.

Inouye, D. W. 2008. "Effects of Climate Change on Phenology, Frost Damage, and Floral Abundance of Montane Wildflowers." *Ecology* 89(2): 353–62.

Jemmett-Smith, B., A. N. Ross, and P. Sheridan. 2018. "A Short Climatological Study of Cold Air Pools and Drainage Flows in Small Valleys." *Weather* 73(8): 256–62.

Jevon, F. V., A. W. D'Amato, C. W. Woodall, K. Evans, M. P. Ayres, and J. H. Matthes. 2019. "Tree Basal Area and Conifer Abundance Predict Soil Carbon Stocks and Concentrations in an Actively Managed Forest of Northern New Hampshire, USA." *Forest Ecology and Management* 451: 117534.

Lembrechts, J. J., J. Lenoir, N. Roth, T. Hattab, A. Milbau, S. Haider, L. Pellissier, A. Pauchard, A. R. Backes, and R. D. Dimarco. 2019. "Comparing Temperature Data Sources for Use in Species Distribution Models: From In-Situ Logging to Remote Sensing." *Global Ecology and Biogeography* 28(11): 1578–96.

Lenoir, J., and J.-C. Svenning. 2015. "Climate-Related Range Shifts–a Global Multidimensional Synthesis and New Research Directions." *Ecography* 38(1): 15–28.

Lenoir, J., T. Hattab, and G. Pierre. 2017. "Climatic Microrefugia under Anthropogenic Climate Change: Implications for Species Redistribution." *Ecography* 40(2): 253–66.

Liu, Y., and J. R. Key. 2003. "Detection and Analysis of Clear-Sky, Low-Level Atmospheric Temperature Inversions with MODIS." *Journal of Atmospheric and Oceanic Technology* 20(12): 1727–37.

Lundquist, J. D., N. Pepin, and C. Rochford. 2008. "Automated Algorithm for Mapping Regions of Cold-Air Pooling in Complex Terrain." *Journal of Geophysical Research: Atmospheres* 113: D22.

Maclean, I. M. D., A. J. Suggitt, R. J. Wilson, J. P. Duffy, and J. J. Bennie. 2017. "Fine-Scale Climate Change: Modelling Spatial Variation in Biologically Meaningful Rates of Warming." *Global Change Biology* 23(1): 256–68.

Mahrt, L., D. Vickers, R. Nakamura, M. R. Soler, J. Sun, S. Burns, and D. H. Lenschow. 2001. "Shallow Drainage Flows." *Boundary-Layer Meteorology* 101(2): 243–60.

Matusick, G., K. X. Ruthrof, N. C. Brouwers, and G. S. J. Hardy. 2014. "Topography Influences the Distribution of Autumn Frost Damage on Trees in a Mediterranean-Type Eucalyptus Forest." *Trees* 28(5): 1449–62.

McLaughlin, B. C., D. D. Ackerly, P. Zion Klos, J. Natali, T. E. Dawson, and S. E. Thompson. 2017. "Hydrologic Refugia, Plants, and Climate Change." *Global Change Biology* 23(8): 2941–61.

Millar, C. I., D. A. Charlet, R. D. Westfall, J. C. King, D. L. Delany, A. L. Flint, and L. E. Flint. 2018. "Do Low-Elevation Ravines Provide Climate Refugia for Subalpine Limber Pine (Pinus Flexilis) in the Great Basin, USA?" *Canadian Journal of Forest Research* 48(6): 663–71.

Moore, T. R., J. A. Trofymow, B. Taylor, C. Prescott, C. Camire, L. Duschene, J. Fyles, L. Kozak, M. Kranabetter, and I. Morrison. 1999. "Litter Decomposition Rates in Canadian Forests." *Global Change Biology* 5(1): 75–82.

Morelli, T. L., C. Daly, S. Z. Dobrowski, D. M. Dulen, J. L. Ebersole, S. T. Jackson, J. D. Lundquist, C. I. Millar, S. P. Maher, and W. B. Monahan. 2016. "Managing Climate Change Refugia for Climate Adaptation." *PLoS One* 11(8): e0159909.

Newcomb, C. J., N. P. Qafoku, J. W. Grate, V. L. Bailey, and J. J. de Yoreo. 2017. "Developing a Molecular Picture of Soil Organic Matter–Mineral Interactions by Quantifying Organo–Mineral Binding." *Nature Communications* 8(1): 1–8.

Novick, K. A., A. Christopher Oishi, and C. F. Miniat. 2016. "Cold Air Drainage Flows Subsidize Montane Valley Ecosystem Productivity." *Global Change Biology* 22(12): 4014–27.

Oyler, J. W., S. Z. Dobrowski, Z. A. Holden, and S. W. Running. 2016. "Remotely Sensed Land Skin Temperature as a Spatial Predictor of Air Temperature across the Conterminous United States." *Journal of Applied Meteorology and Climatology* 55(7): 1441–57.

Patsiou, T. S., E. Conti, S. Theodoridis, and C. F. Randin. 2017. "The Contribution of Cold Air Pooling to the Distribution of a Rare and Endemic Plant of the Alps." *Plant Ecology & Diversity* 10(1): 29–42.

Pederson, N., J. M. Dyer, R. W. McEwan, A. E. Hessl, C. J. Mock, D. A. Orwig, H. E. Rieder, and B. I. Cook. 2014. "The Legacy of Episodic Climatic Events in Shaping Temperate, Broadleaf Forests." *Ecological Monographs* 84(4): 599–620.

Pepin, N. C., C. Daly, and J. Lundquist. 2011. "The Influence of Surface Versus Free-Air Decoupling on Temperature Trend Patterns in the Western United States." *Journal of Geophysical Research: Atmospheres* 116: D10.

Pypker, T. G., M. H. Unsworth, A. C. Mix, W. Rugh, T. Ocheltree, K. Alstad, and B. J. Bond. 2007. "Using Nocturnal Cold Air Drainage Flow to Monitor Ecosystem Processes in Complex Terrain." *Ecological Applications* 17(3): 702–14.

Reich, P. B., K. M. Sendall, K. Rice, R. L. Rich, A. Stefanski, S. E. Hobbie, and R. A. Montgomery. 2015. "Geographic Range Predicts Photosynthetic and Growth Response to Warming in Co-Occurring Tree Species." *Nature Climate Change* 5(2): 148–52.

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. "From Tropics to Tundra: Global Convergence in Plant Functioning." *Proceedings of the National Academy of Sciences USA* 94(25): 13730–4.

Rosenbloom, N. A., S. C. Doney, and D. S. Schimel. 2001. "Geomorphic Evolution of Soil Texture and Organic Matter in Eroding Landscapes." *Global Biogeochemical Cycles* 15(2): 365–81.

Rupp, D. E., S. L. Shafer, C. Daly, J. A. Jones, and S. J. K. Frey. 2020. "Temperature Gradients and Inversions in a Forested Cascade Range Basin: Synoptic-to Local-Scale Controls." *Journal of Geophysical Research: Atmospheres* 125(23): e2020JD032686.

Rupp, D. E., S. L. Shafer, C. Daly, J. A. Jones, and C. W. Higgins. 2021. "Influence of Anthropogenic Greenhouse Gases on the Propensity for Nocturnal Cold-Air Drainage." *Theoretical and Applied Climatology* 146(1): 231–41.

Samways, M. J. 1990. "Land Forms and Winter Habitat Refugia in the Conservation of Montane Grasshoppers in Southern Africa." *Conservation Biology* 4(4): 375–82.

Sayre, R., C. Frye, D. Karagulle, J. Krauer, S. Breyer, P. Aniello, D. J. Wright, D. Payne, C. Adler, and H. Warner. 2018. "A New High-Resolution Map of World Mountains and an Online Tool for Visualizing and Comparing Characterizations of Global Mountain Distributions." *Mountain Research and Development* 38(3): 240–9.

Schauffler, M., and G. L. Jacobson, Jr. 2002. "Persistence of Coastal Spruce Refugia during the Holocene in Northern New England, USA, Detected by Stand-Scale Pollen Stratigraphies." *Journal of Ecology* 90(2): 235–50.

Siccama, T. G. 1974. "Vegetation, Soil, and Climate on the Green Mountains of Vermont." *Ecological Monographs* 44(3): 325–49.

Soler, M. R., C. Infante, P. Buenestado, and L. Mahrt. 2002. "Observations of Nocturnal Drainage Flow in a Shallow Gully." *Boundary-Layer Meteorology* 105(2): 253–73.

Speirs, J. C., H. A. McGowan, D. F. Steinhoff, and D. H. Bromwich. 2009. "The Polar Foehn: A Re-examination of Downslope Winds in the Mcmurdo Dry Valleys, Antarctica." 9th International Conference on Southern Hemisphere Meteorology and Oceanography, Melbourne, 9-13 February 2009. Melbourne, VIC, Australia: Bureau of Meteorology.

Tateno, R., and H. Takeda. 2003. "Forest Structure and Tree Species Distribution in Relation to Topography-Mediated Heterogeneity of Soil Nitrogen and Light at the Forest Floor." *Ecological Research* 18(5): 559–71.

Tenow, O., and A. Nilssen. 1990. "Egg Cold Hardiness and Topoclimatic Limitations to Outbreaks of Epirrita Autumnata in Northern Fennoscandia." *Journal of Applied Ecology* 27: 723–34.

Vitasse, Y., A. Lenz, and C. Körner. 2014. "The Interaction between Freezing Tolerance and Phenology in Temperate Deciduous Trees." *Frontiers in Plant Science* 5: 541.

Ward, S. E., M. Schulze, and B. Roy. 2018. "A Long-Term Perspective on Microclimate and Spring Plant Phenology in the Western Cascades." *Ecosphere* 9(10): e02451.

Wearne, L. J., and J. W. Morgan. 2001. "Floristic Composition and Variability of Subalpine Grasslands in the Mt Hotham Region, North-Eastern Victoria." *Australian Journal of Botany* 49(6): 721–34.

Whiteman, C. D., S. Zhong, W. J. Shaw, J. M. Hubbe, X. Bian, and J. Mittelstadt. 2001. "Cold Pools in the Columbia Basin." *Weather and Forecasting* 16(4): 432–47.

Wilkin, K. M., D. D. Ackerly, and S. L. Stephens. 2016. "Climate Change Refugia, Fire Ecology and Management." *Forests* 7(4): 77.

Wipf, S., M. Sommerkorn, M. I. Stutter, E. R. Jasper Wubs, and R. Van Der Wal. 2015. "Snow Cover, Freeze-Thaw, and the Retention of Nutrients in an Oceanic Mountain Ecosystem." *Ecosphere* 6(10): 1–16.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, and M. Diemer. 2004. "The Worldwide Leaf Economics Spectrum." *Nature* 428(6985): 821–7.

How to cite this article: Pastore, Melissa A., Aimée T. Classen, Anthony W. D'Amato, Jane R. Foster, and E. Carol Adair. 2022. "Cold-Air Pools as Microrefugia for Ecosystem Functions in the Face of Climate Change." *Ecology* 103(8): e3717. https://doi.org/10.1002/ecy.3717