

Primary Drivers of Reptile Overwintering Habitat Suitability: Integrating Wetland Ecohydrology and Spatial Complexity

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Identifying ecosystems resilient to climate and land-use changes is recognized as essential for conservation strategies. However, wetland ecosystems may respond differently to stressors depending on their successional state and the strength of ecohydrological feedbacks resulting in fluctuations in habitat availability and suitability. Long-term habitat suitability is necessary for the persistence of wetland-dependent species and a key characteristic of climatic refugia. In the present article, we review and synthesize biogeochemical, thermal, ecological, and hydrological feedbacks and interactions that operate within wetlands and, consequently, regulate overwintering suitability for many freshwater turtles and snakes. We propose that understanding the breadth and interconnected nature of processes controlling temperature, dissolved oxygen, and water table position are vital for the conservation of northern reptile populations that depend on wetlands to survive winter conditions. Finally, we suggest that our integrated framework can guide future research and the management of wetland ecosystems in an era of unprecedented change.

Keywords: climate change, habitat management, resilience zone, species at risk, wetland conservation

Climate and land-use changes among other anthropogenic stressors have resulted in almost one in five reptilian species at risk of extinction worldwide (Gibbons et al. 2000, Todd et al. 2010, Böhm et al. 2013). The significant reduction in reptile biomass could have cascading ecosystem effects given the importance of reptiles in predator–prey dynamics and energy flow within and between ecosystems (see Todd et al. 2010, Böhm et al. 2013, Lovich et al. 2018) with the potential for further habitat degradation. Although habitat loss and degradation continue to be primary drivers of widespread reptile losses, it is becoming clear that the cumulative impacts of land-use changes and accelerated rates of climate change will require conservation and management strategies that cut across traditional disciplinary boundaries (e.g., Frusher et al. 2014, McDonald et al. 2018). A focus on ecosystem conservation is in line with the paradigm shift toward understanding ecosystem function through an interdisciplinary, landscape-scale research approach (see Murray 2019). However, the development of an integrated, mechanistic framework to inform conservation approaches and to identify and predict responses to perturbations remains a challenge (e.g., Williams et al. 2015).

A key facet of an integrated conservation framework is understanding the processes and characteristics that make wetland ecosystems resilient to climate and land-use changes. Understanding these processes and characteristics can enhance our ability to identify resilient wetlands or refugia over large spatial scales. From a reptile conservation perspective, a resilient wetland continues to act as a refugium despite changing climatic conditions and provides the habitat stability and suitability required for species to carry out necessary life activities. For instance, approximately 108 reptile species found north of 35–40 degrees north (°N) are associated with freshwater wetland habitats (IUCN 2020), and we estimate that about 43 of these species (approximately 29 turtle, 13 snake, and 1 lizard species) use wetlands for thermal refugia during winter (figure 1). Therefore, the long-term suitability of wetland habitat directly influences individual survival and population persistence for many reptile species globally. In particular, identifying thermal refugia in regions between 40° and 50°N is of critical importance because the duration of exposure to low temperatures in subterranean environments as a result of decreased snow cover is predicted to

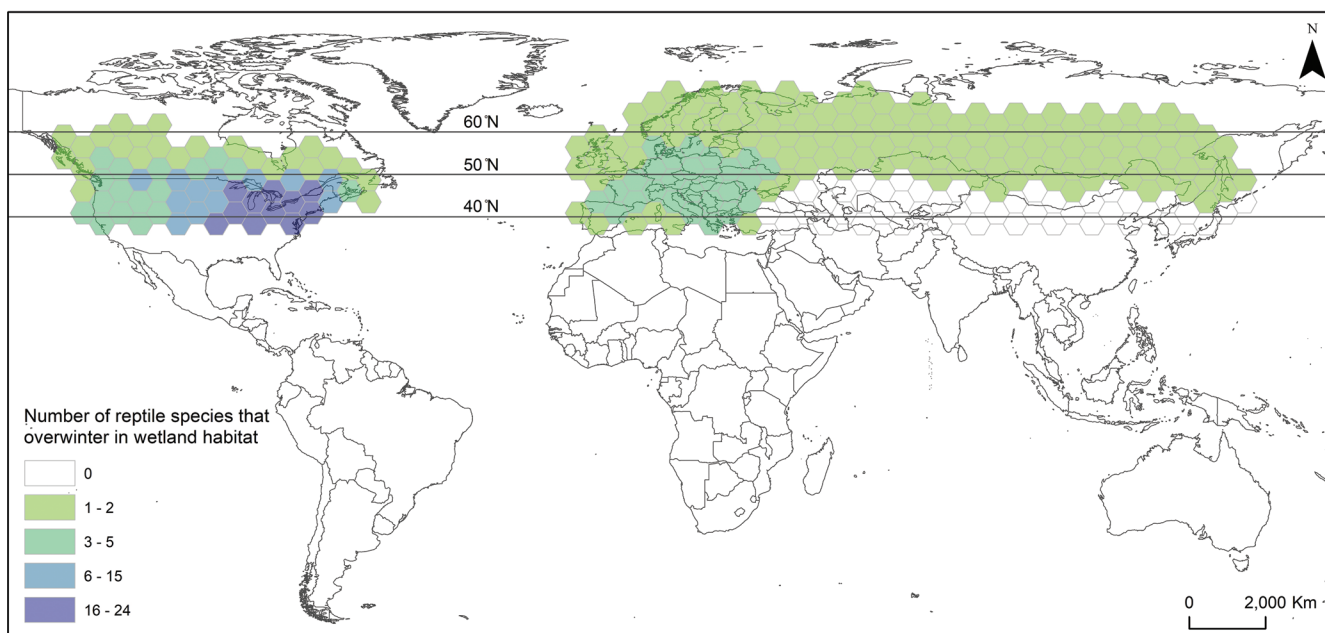


Figure 1. Approximate distribution of reptile species north of 35°–40°N that can use freshwater wetland microhabitats for overwintering. Estimated ranges for reptile species were obtained from the IUCN (2020) and supplemented with data from the US Geological Survey (2018) and Sillero and colleagues (2014). Additional range estimates for Canadian species were digitized from the Canadian Herpetological Society (2017). As a result of spatial data availability, mapping was conducted at the species level except for the four subspecies of painted turtle (*Chrysemys picta*).

increase (Zhu et al. 2019). Furthermore, the majority of reptile species that use wetland habitat for overwintering occur within the 40°–50°N latitudinal band and are centered on the Great Lakes in North America (figure 1). It is imperative to determine wetland ecosystem feedbacks and interactions that directly and indirectly contribute to habitat suitability because the strength of such feedbacks are expected to vary across time scales, across wetland types, and in their response to multiscale stressors (Waddington et al. 2015). Altered feedback strengths are suggested to contribute to variability in wetland dynamics such as water table position and thermal conditions (Waddington et al. 2015). As a result of such variability, wetlands may also experience greater fluctuations in habitat availability and suitability increasing the vulnerability of reptile overwintering habitat.

Given that the threats to wetland-dependent reptiles vary in magnitude and occur across multiple spatial scales, conservation strategies and restoration techniques should strive to integrate multiple research disciplines including terrestrial and wetland ecology, ecohydrology, and biogeochemistry. As a first step toward developing an integrated conservation framework for wetland-dependent reptiles, we review and synthesize a conceptual link between wetland ecological succession, wetland ecohydrological feedbacks, and suitability of wetland habitat for overwintering turtles and snakes. We suggest that this step will aid in the recovery of species at risk and help ensure persistence

of more common species because reptiles at northern latitudes can spend almost half their lives overwintering in wetlands or wetland microhabitats. We begin by discussing the characteristics of suitable wetland overwintering habitat for freshwater turtles and snakes, with a primary focus on North American species that occur in the region supporting the highest density of reptile species using wetlands for overwintering (figure 1). We outline the primary physical drivers of suitability (e.g., oxygen availability, temperature, water table position) and integrate these drivers within the context of wetland spatial complexity through the lens of wetland ecological development to demonstrate that wetland successional state plays a significant role in habitat availability. A discussion of the role of ecohydrological feedbacks and interactions in regulating overwintering site suitability is then presented in order to gain a better understanding of both the breadth and interconnected nature of such feedbacks. We present an integrated framework that aims to advance our understanding of how climate and land-use changes can alter feedback strengths that ultimately affect the resilience and vulnerability of overwintering habitats. Finally, we discuss gaps in knowledge and highlight priorities for future research.

Reptiles and overwintering suitability

Reptiles are ectotherms, which means the tight coupling between environmental temperature and metabolic regulation requires individuals to select habitats to control body

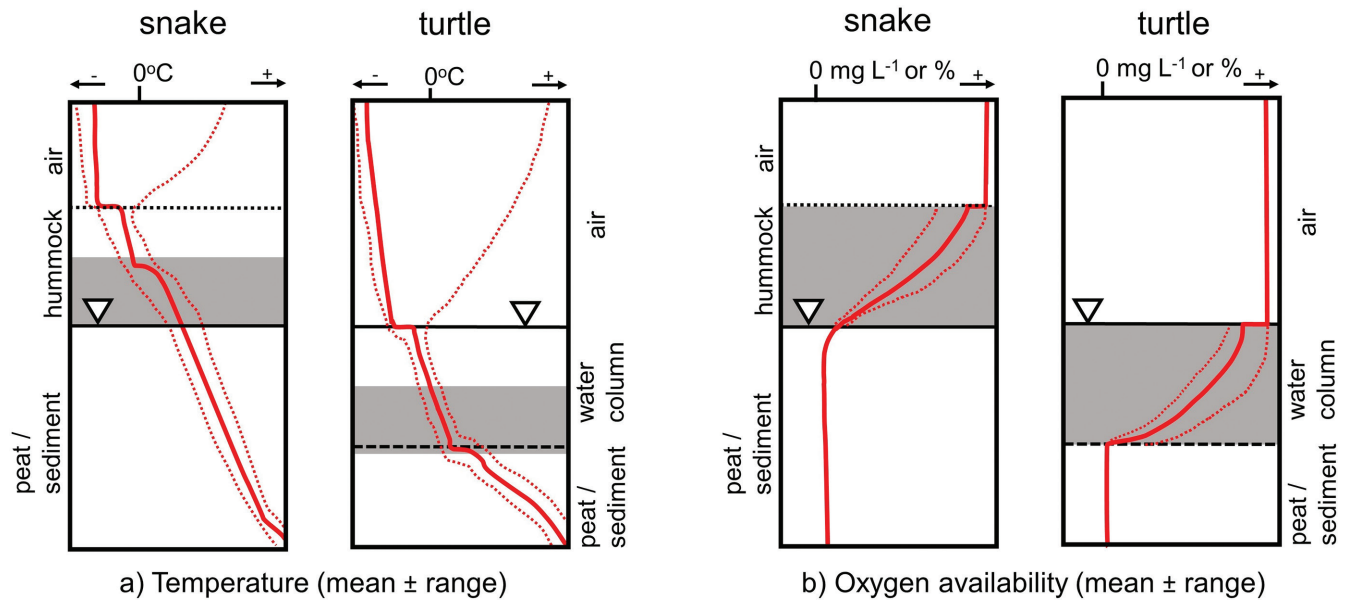


Figure 2. Delineation of the resilience zone is illustrated for freshwater turtles and snakes (hummock overwintering sites) where temperature (a) and oxygen (b) are considered important environmental conditions for overwintering in aquatic ecosystems. (a) Change in mean temperature in a snake (supplement A) and turtle (supplement B) wetland overwintering profile; the dotted lines indicate the range. (b) Change in mean oxygen availability in a snake (peatland data from Estop-Aragonés et al. 2012) and turtle (lake data from Jackson and Lasenby 1982) overwintering profile; the dotted lines indicate the range here as well. The overlap between (a) temperature, (b) oxygen availability, and overwintering position in regards to the mean water table position (▽) represents the area providing suitable overwintering conditions (the gray shaded area).

temperature (Huey 1991). At northern latitudes, in which cold temperatures and the chance of snow can last up to half the year, reptiles retreat underground or underwater and reduce their metabolic activity to survive the winter (Ultsch 1989). Northern freshwater aquatic turtle species primarily overwinter underwater in aquatic ecosystems such as rivers, lakes, and several wetland types (shallow open water, marshes, bogs, and fens; e.g., see Ultsch 2006). Although overwintering in terrestrial habitat is most common among snakes and lizards (Gregory 1982, Ultsch 1989), species including the massasauga (Johnson 2000, Rouse and Willson 2002), the European adder (*Vipera berus*; Viitanen 1967), the northern watersnake (*Nerodia sipedon*; Carpenter 1953), the common gartersnake (*Thamnophis sirtalis*; Carpenter 1953), and the European common lizard (*Zootoca vivipara*; Grenot et al. 1998) have been found to overwinter in microhabitats (e.g., hummocks, muskrat lodges, peat along wetland edge) within wetland ecosystems. Although macrohabitat use varies among and within reptile species, overlap in winter refugia between some species of turtle and snake can occur in wetland ecosystems presumably because the microenvironment meets certain physical, biogeochemical, and thermal conditions to permit winter survival.

Overwintering underwater provides shelter from freezing temperatures (assuming the water column does not freeze) and prevents desiccation (figure 2a; Ultsch 2006). However, during periods of ice cover, restricted access to

aerial oxygen requires species to rely on extrapulmonary uptake of dissolved oxygen or the ability to tolerate anoxic (less than 1 milligrams [mg] per liter [L]) or hypoxic (less than 2–3 mg per L) conditions (figure 2b; Ultsch 2006). Many species of northern freshwater turtle use stable, cool water temperatures (e.g., Litzgus et al. 1999, Novotný et al. 2004, Thienpont et al. 2004, Greaves and Litzgus 2007, 2008, Rollinson et al. 2008, Edge et al. 2009, Markle and Chow-Fraser 2017), which can help maintain a relatively constant, low body temperature and lower metabolic rate (Herbert and Jackson 1985). Maintaining a lower metabolic rate would be advantageous when access to aerial oxygen is limited because it reduces the risk of metabolic acidosis (Herbert and Jackson 1985) but can increase vulnerability to predation (e.g., otters; Brooks et al. 1991, Kotenko 2000). Therefore, the presence of sufficient substrate depth can provide important temporary refugia if the water column freezes and shelter from predation (Brown and Brooks 1994, Thienpont et al. 2004). It has been hypothesized that site fidelity (returning to the same overwintering site annually) and communal overwintering (multiple individuals overwintering together) are indicators of limited availability of suitable overwintering sites (Gregory 1984), and this behavior has been documented for multiple turtle species (e.g., Brown and Brooks 1994, Litzgus et al. 1999, Thienpont et al. 2004, Markle and Chow-Fraser 2017). Although communal overwintering

does provide other opportunities including easier access to mates, individuals overwintering together can put populations at risk of mass mortality events because a change in environmental conditions would affect multiple individuals. The possible increased risk of mass overwintering mortality events as a result of climate and land-use changes is especially concerning because turtle population size can be severely affected by adult mortality because of their slow life histories (Congdon et al. 1993, Keevil et al. 2018, Piczak et al. 2019).

Taken together, a suitable vertical overwintering profile incorporates the basic physical and biogeochemical microhabitat characteristics contributing to site suitability (see figure 2). We use the term resilience zone to define the space that optimizes suitability (Smolarz et al. 2018). Therefore, the turtle resilience zone is the space that provides stable, cool water temperatures near 0 degrees Celsius ($^{\circ}\text{C}$; figure 2a), sufficient dissolved oxygen (figure 2b), and availability of substrate for burying. The resilience zone is related to the concept of a niche, notably described by Grinnell (1917), Elton (1927), and Hutchinson (1957) but reconceptualized and quantified in different ways over the years (e.g., Chase and Leibold 2003, Peterson et al. 2015). The resilience zone is not unlike a fundamental niche in that it quantifies environmental conditions that affect certain species, further described as physiological tolerances (Peterson et al. 2011), but excludes biotic interactions (e.g., competition, Hutchinson 1957). The resilience zone is rooted in a mechanistic understanding of the fundamental niche linking winter environmental conditions and habitat use or selection with survival based on reptile behavior and physiology (functional traits, Kearney 2006, Kearney and Porter 2009). However, the resilience zone is similar to a habitat suitability model in its application such that it quantifies a space that optimizes suitable winter conditions for certain reptiles (Kearney and Porter 2009) and, we suggest, that changes in the resilience zone size can be used as a metric to identify vulnerable overwintering habitat. Although we argue that the presence of a resilience zone contributes to winter survival and that its complete absence would not permit winter survival, additional data would be required before attempting to predict survival probability (i.e., a fitness component; Kearney 2006, Kearney and Porter 2009).

Both aquatic and terrestrial snakes generally overwinter above the water table, although some species are more tolerant to flooding (see Ultsch 1989). Although overwintering above the water table increases accessibility to aerial oxygen (figure 2b), snakes are at risk of desiccation (Gregory 1982). Consequently, most snakes require a subterranean microenvironment that protects against desiccation but is unflooded and above 0°C (figure 2; Carpenter 1953, Costanzo 1989). Snake mortality during winter could suggest that suitable overwintering sites are limited (e.g., Shine and Mason 2004, Podloucky et al. 2005, Yagi et al. 2020), which is supported by multiple snakes overwintering together (e.g., Viitanen

1967, McInerny 2014) and snakes returning to the same area (Johnson 2000, Harvey and Weatherhead 2006) or site (Shine and Mason 2004) each year. Although these general microenvironmental conditions apply to many species of overwintering snakes, we focus on the snake species that overwinter in wetland hummocks such as the massasauga (e.g., Johnson 2000) and adder (e.g., Viitanen 1967). In the context of landscape-scale wetland ecosystem conservation, the potential for the massasauga and North American turtle species to overwinter in the same wetland is of particular interest, especially considering the density of overwintering reptile species using wetlands in this region (figure 1). Peat wetland hummocks provide an optimal overwintering site because they tend to be raised above the water table and provide a moist, insulated subterranean space (Smolarz et al. 2018, Markle et al. 2020). Therefore, the vertical overwintering profiles (figure 2) allows us to delineate the location of the snake resilience zone: the space that buffers against an advancing 0°C isotherm and a fluctuating water table to minimize the risk of drowning or freezing (Smolarz et al. 2018).

Wetland succession, spatial complexity, and states

Based on the delineated vertical overwintering profiles, we can begin to identify aquatic habitats that provide the unique combination of physical and biogeochemical conditions. For example, the potential overlap between overwintering habitat of the massasauga and freshwater turtles (e.g., painted turtle, *Chrysemys picta*; snapping turtle, *Chelydra serpentina*; Blanding's turtle, *Emydoidea blandingii*; spotted turtle, *Clemmys guttata*) highlights a unique ecosystem with the potential to support species not commonly found overwintering together. This overlap, or co-occurrence, points to the importance of wetlands with a stable water table and sufficient accumulation of substrate and development of peat microtopography. We propose that co-occurrence may be observed at the wetland scale or even in the same profile (vertical co-occurrence) depending on the complexity and diversity of microhabitats (figure 3). The stability of suitable overwintering conditions each year is necessary for the persistence of long-lived species (Armstrong and Brooks 2014), especially given the observations of site fidelity (e.g., Brown and Brooks 1994, Litzgus et al. 1999, Markle and Chow-Fraser 2017). Therefore, long-term changes in overwintering suitability should be placed within the context of wetland succession and spatial complexity of wetland habitat. Through this approach we aim to identify the wetland state or states (stage along wetland succession described by vegetation and peat structural characteristics) that are most likely to provide optimal overwintering sites for different species of turtles, the massasauga, and the potential for species co-occurrence.

To ascertain why certain wetland states provide optimal overwintering sites and how these conditions persist, it is valuable to understand how these wetlands form and the

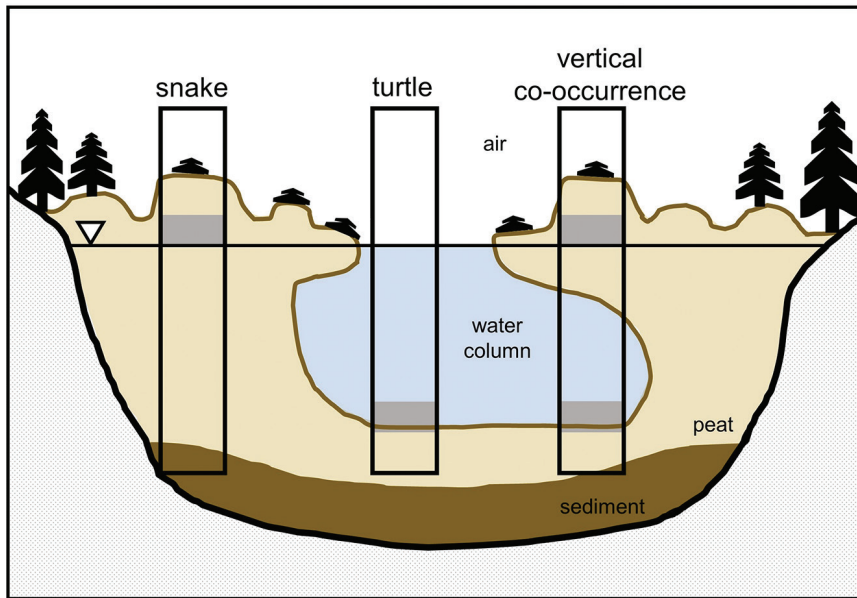


Figure 3. An illustration of a wetland that provides overwintering sites for both snakes and turtles (individual vertical profiles) resulting in co-occurrence at the macrohabitat scale (wetland). This wetland also provides a vertical profile that provides overwintering sites for both snakes and turtles (vertical co-occurrence). The gray shaded area represents the area suitable for overwintering, also referred to as the zone of resilience.

processes that drive succession. Because the vertical overwintering profile for turtles requires a deep water column to minimize the likelihood of freezing, we recognize the importance of wetlands that develop through infilling (terrestrialization; Rydin and Jeglum 2013) as meeting this requirement. Indeed most of the wetlands in basins of various depths and areal extent are formed by the infilling developmental pathway (National Wetlands Working Group 1997) whereby a small body of water (e.g., pond or lake) is filled in by the accumulation of peat and sediment and is typically characterized by a floating mat of vegetation and peat at the infilling edge (Whittaker 1975). As such, we focus our discussion in the present article on the succession, spatial complexity, and states of wetlands that form via infilling from a basin pond (figure 4a).

In general, the process of wetland succession through infilling progresses through numerous wetland classes from shallow open water, to marsh, then fen and bog (National Wetlands Working Group 1997). Infilling begins as a ring of floating vegetation (hereafter referred to as a *mat*) that forms around the perimeter of a pond or shallow open water wetland with an aquatic sediment bottom (state A to state B in figure 4; Kratz and DeWitt 1986). Turtle species found overwintering in lakes or ponds (state A and B wetlands) include the northern map turtle (*Graptemys geographica*), painted turtle, and snapping turtle (Brown and Brooks 1994, Ernst and Lovich 2009, Rollinson et al. 2008). Vegetation (e.g., *Chamaedaphne calyculata*, *Equisetum* spp., and *Carex* spp.) continues to

grow into the open water, developing into a marsh and providing overwintering habitat for species including the European pond turtle (Thienpont et al. 2004), the snapping turtle, and the bog turtle (*Glyptemys muhlenbergii*, Ultsch 2006). The vegetation provides structure and habitat on which *Sphagnum* moss and other sedges colonize leading to the accumulation of peat (organic material) that also thickens the mat vertically (Kratz and DeWitt 1986). This mat is slightly buoyant and floats in deeper water allowing it to expand both vertically and horizontally toward the middle of the water body. As the mat develops, the surface and vertical spatial complexity of the wetland increases. As the wetland undergoes succession from state B (figure 4b) to state C (figure 4c) species including the Blanding's turtle (Edge et al. 2009, Markle and Chow-Fraser 2017), spotted turtle (Litzgus et al. 1999), and the massasauga may use a state C wetland for overwintering. It is worth noting that, although it is not represented in

figure 4, floating peat may also develop when areas with preexisting organic deposits break away from the substrate and float to the surface (Tallis 1983). Nevertheless, during state C (figure 4c) the initial floating mat in state B has accumulated enough peat that it becomes grounded to aquatic sediments at the bottom of the basin providing a mosaic of open water, floating peat and grounded peat. The floating edge of a wetland mat is exposed to different conditions than the grounded peat portion near the wetland perimeter. Unlike the anoxic water, which is in contact with the same depth of peat in the grounded portion of the wetland system (e.g., Estop-Aragonés et al. 2012), the water near the mat edge is well mixed with the pond water, which is open to the atmosphere (when not covered in ice) and readily exchanged.

As wetland development and succession progress to a relatively more terrestrial state (i.e., states C–E in figure 4), the spatial variation in vegetation species and peat properties (e.g., density) leads to different rates of peat accumulation. In turn, spatial variability in peat accumulation leads to the development of surface microtopography composed of hummocks and hollows (Rydin and Jeglum 2013). Hummocks are raised mounds above the water table and hollows are the surrounding flat, low areas (Rydin and Jeglum 2013, Nungesser 2003). Hummocks are important microhabitats for snake overwintering because of their unique ability to retain moisture. *Sphagnum* moss species that characterize hummocks tend to stay relatively moist under dry conditions (McCarter and Price 2012) because of their ability

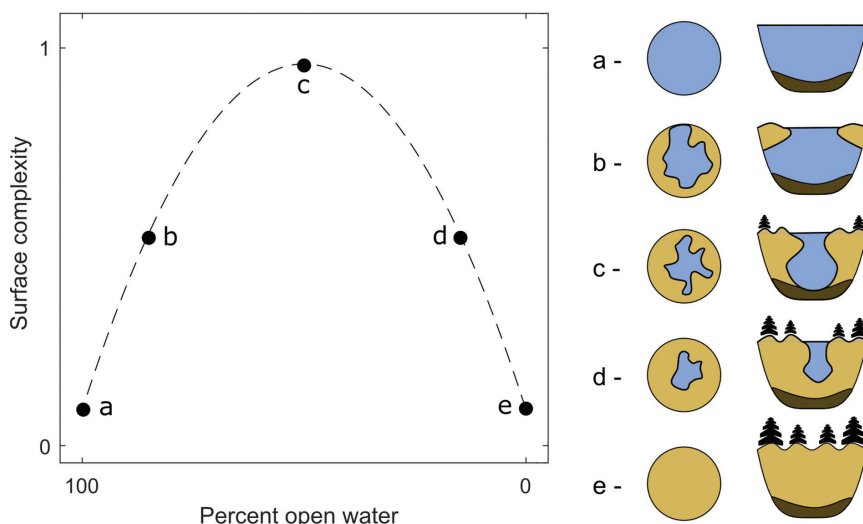


Figure 4. Conceptual diagram showing open water versus surface spatial complexity with five different states for wetlands formed by infilling state A (a), state B (b), state C (c), state D (d), and state E (e). State C is highlighted because the mosaic of grounded peat, floating peat and open water likely optimizes the probability of turtle and snake co-occurrence for overwintering. State C also likely has the highest long-term resilience to external drivers that contribute to the resistance of wetland state C to succession or retrogression in a way that allows the microhabitat diversity (and availability of overwintering sites) to persist into the future. Although we have not considered wetlands that continue to grow vertically once state E has occurred, see Belyea and Baird (2006) for an extensive review.

to draw water upward from a low water table (Titus and Wagner 1984). Therefore, even when the water table is below the wetland surface (along the edge in state C), the unique dynamics of hummocks provide snakes with a moist overwintering site to avoid desiccation (Costanzo 1989).

Although our discussion, so far, has presented wetland succession from aquatic shallow open water and marsh wetlands to fen and bog wetlands through the process of peat accumulation as the normal pathway (progressive succession; Rydin and Jeglum 2013), retrogressive succession to an earlier state also occurs (e.g., Harris et al. 1996). Short-term (Strack and Waddington 2007) and long-term (Chimner et al. 2017) experimental evidence demonstrates that a wetland state with a mix of open water (pools, hollows) and peat (mats, hummocks), such as that observed in state C, enhances resilience to external drivers such as drought and flooding (see peat feedbacks below). Long-term resilience to external drivers contributes to the resistance of wetland state C to succession or retrogression in a way that allows the microhabitat diversity to persist into the future. In this case, the result is a wetland that contains a suite of microhabitats characteristic of multiple wetland classes (shallow open water, open pools; marsh, emergent vegetation; fen and bog, accumulation of peat; see figure 4c) that continually provides suitable overwintering sites and is critical for long-lived reptile species that also tend to overwinter in the same habitat year after year

(e.g., Brown and Brooks 1994, Litzgus et al. 1999, Markle and Chow-Fraser 2017). Wetland state C also provides an opportunity for North American turtle species and the massasauga to overwinter in the same wetland (co-occurrence) because the wetland provides microhabitats suitable for both groups (figure 3). Accordingly, state C provides turtle overwintering sites with the opportunity for access to aerial oxygen (during ice-off conditions) or some availability of dissolved oxygen, vegetation cover (floating mat) for protection from predation, and sediment for burying. Likewise, it provides massasaugas overwintering sites because *Sphagnum* on floating mats leads to the development of an insulated space safe from desiccation and flooding (hummocks). In addition to providing habitat for multiple co-occurring species, a state C wetland is spatially diverse and resilient to degradation. That being said, even if the combination of feedbacks and external pressures results in a state C wetland succeeding to state D or E or retrogressing to state A or B either resulting state could permit overwintering of either massasaugas or turtles, respectively.

Cross-scale feedbacks and interactions in wetland habitat

Belyea and Baird (2006) identified the importance of cross-scale feedbacks in the development, succession, and resilience of many wetland types. Specifically, they determined that wetland resilience is controlled by the cross-scale interaction of both small-scale peat accumulation processes and larger-scale watershed conditions where strong memory effects are present across scales. Some of these memory effects are manifested through moss traits and a suite of ecohydrological feedbacks that generally dampen external drivers (Waddington et al. 2015). The findings of these two studies guided our review and synthesis of the feedbacks that drive the function of suitable overwintering habitat and, therefore, the presence and size of the resilience zone. In particular, we integrate the seasonal and multiannual feedbacks and interactions that regulate the physical, chemical, and thermal properties of basin wetland ecosystems whose strengths are likely to be affected by climate and land-use changes. We review the following five feedbacks that are directly or indirectly linked to wetland water table position, peat thickness, oxygen availability (either aerial or dissolved oxygen), or ice cover and frost table position: (a) biogeochemical feedbacks and interactions, (b) thermal interactions, (c) peat

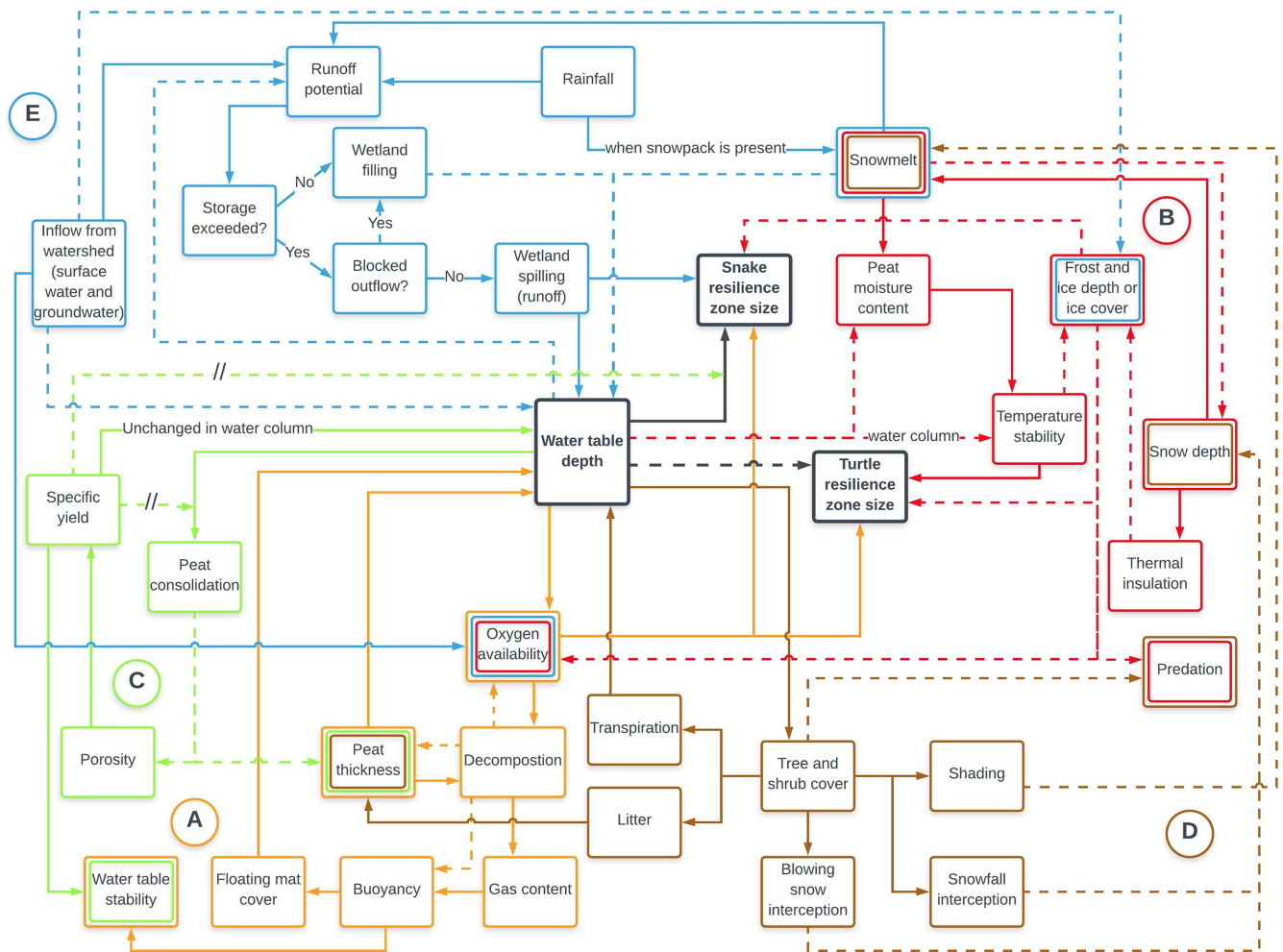


Figure 5. The primary feedbacks and interactions that influence turtle and snake resilience zone size include (a) biogeochemical, (b) thermal, (c) peat, (d) vegetation, and (e) water storage and runoff. Solid and dashed lines represent positive and negative relationships, respectively. The amplifier term (//) can increase or decrease the strength of the interaction. For a comprehensive review of wetland biogeochemistry and interactions see Rezanezhad and colleagues (2016) and Strack and colleagues (2005), and for wetland hydrological feedbacks see Waddington and colleagues (2015).

feedbacks and interactions, (d) vegetation feedbacks and interactions, and (e) water storage and runoff feedbacks and interactions (see figure 5).

Biogeochemical feedbacks and interactions. Physiological adaptations such as the ability to tolerate anoxia permit species to overwinter underwater or endure flooded conditions (Ultsch 1989, Storey 1996). Therefore, overwintering reptiles can be generally classified into relatively tolerant or intolerant of anoxic conditions. Turtle species that are considered anoxia intolerant (e.g., map turtles, *Graptemys* spp.; eastern musk turtle, *Sternotherus odoratus*; wood turtle, *Glyptemys insculpta*) require more well-oxygenated microenvironments, such as lakes and rivers, or access to aerial oxygen (Ultsch 2006). Species considered anoxia tolerant (e.g., bog turtle, painted turtle, snapping turtle, spotted turtle, Blanding's

turtle; Ultsch 2006) are found to overwinter in more-developed wetlands including fens and bogs (e.g., Meeks and Ultsch 1990, Litzgus et al. 1999, Rollinson et al. 2008, Markle and Chow-Fraser 2017). Although massasaugas and adders are likely able to tolerate short-term inundation (Viitanen 1967, Smith 2009, Markle et al. 2020), long term flooding and water level fluctuations may be detrimental (Viitanen 1967, Smith 2009, Yagi et al. 2020) supporting the requirement for aerial oxygen availability. Overall, overwintering in a microenvironment with access to sufficient oxygen is less physiologically stressful than in anoxic conditions, and therefore, the resilience zone for both turtles and snakes is maximized under conditions that increase oxygen availability (figures 2, 3, 5a).

Turtle and snake resilience zone size is directly related to groundwater inflow into wetlands and changes in the

position of the water table (figure 5e). Groundwater can be oxic or anoxic and the spatiotemporally heterogeneous nature of this inflow can create complex hydrological microrefugia (McLaughlin et al. 2017). Nevertheless, a greater water table depth increases oxygen availability in the near-surface peat and as a result directly increases the size of snake resilience zone (figure 5a). Although greater water table depth increases oxygen availability because of increased potential for mixing with air, it also reduces the depth of the water column having mixed effects on the size of the turtle resilience zone (figure 5a). Moreover, a lower water table position also enhances peat decomposition rates (figure 5a). Peat decomposition (manifested through peat density) is central not only to the long-term ecohydrology of these systems but also to a number of peat feedbacks described below. Decomposition results in the collapse of large pores (and increasingly smaller pores with time), an increase in peat density and may result in a decrease in peat thickness or reduce the potential for floating mat buoyancy. As such, decomposition can lead to a decrease in snake resilience zone size by reducing available overwintering space or increasing flooding potential (see figure 5c, peat feedbacks); however, the continued production of new (and low density) moss or leaf litterfall counteracts losses through decomposition (see figure 5d, vegetation feedbacks).

Anoxic decomposition of deeper peat in the wetland can lead to the production of methane, which can get entrapped in the wetland below a confining layer (e.g., woody peat strata, roots, dense peat, bottom of floating mats; Strack et al. 2005, Coulthard et al. 2009). In many situations the trapped gas can reduce the peat density to below that of water, resulting in the potential for increased floating mat cover (Strack et al. 2005). As such, the floating mat surface moves up and down with fluctuations in the water table thereby reducing fluctuations in water table depth relative to the peat surface. The stabilization of water table depth would help to maintain a relatively constant size of the snake resilience zone by reducing the probability of hummock flooding events.

Thermal feedbacks. By selecting for low temperatures without freezing, reptiles can suppress metabolic rates and reduce the physiological stress of acidosis (Jackson 2002). For freshwater turtles that are relatively anoxia tolerant, field data suggest that snapping turtles (Paterson et al. 2012), Blanding's turtles (Edge et al. 2009), and painted turtles (Rollinson et al. 2008) select overwintering sites based on temperature as opposed to dissolved oxygen concentration. Species including the spotted turtle (Litzgus et al. 1999), snapping turtle (Brown and Brooks 1994, Paterson et al. 2012), and Blanding's turtle (Markle and Chow-Fraser 2017) were observed to overwinter in mean water temperatures ranging from 0.3°C to 2.6°C and turtles often maintained a stable, lower mean body temperature just above 0°C to 1.3°C (Edge et al. 2009, Paterson et al. 2012). To maintain a stable, cool shell temperature, turtles may move vertically in the

water column or select sites near inflows where unfrozen, oxygenated water is entering (figure 5b, 5e).

Observing turtles burying in sediment during winter is variable among species and locations (e.g., Taylor and Nol 1989, Rowe and Moll 1991, Brown and Brooks 1994, Rollinson et al. 2008) and could indicate a trade-off between seeking shelter or using cooler water with a higher probability of access to dissolved oxygen. That being said, burying just below the substrate–water interface could permit turtles to have their head in the water column to access dissolved oxygen. For example, snapping turtles within the same northern population were found to bury in deep mud, not bury at all, or only remain covered by a thin layer of silt (Brown and Brooks 1994). On the other hand, painted turtles were found to avoid spending much of the winter deep within the warm, anoxic sediment, instead using microhabitats to maintain a cool body temperature (Rollinson et al. 2008, but see Taylor and Nol 1989).

Analogous to turtles, snakes must seek shelter from cold air temperatures to avoid freezing (Gregory 1982). Snakes remain at a reduced metabolic state by overwintering below the frost line, where temperatures are stable and cool (Macartney et al. 1989, Ultsch 1989). An important component influencing temperature stability, and therefore, suitability is the presence and depth of snow cover because it acts as an insulator, reducing heat loss and controlling the extent of frost penetration (figure 5b; Zhang 2005). For example, a decline in the European adder was possibly because of a warm, wet winter that exposed snakes to cold temperatures because a higher water table position would have required snakes to overwinter at a shallower depth (Podloucky et al. 2005). Similarly, fewer massasauga sightings were associated with flooded winter conditions, suggesting a population decline (Yagi et al. 2020). Although snow cover buffers against fluctuating air temperatures, a rapid mid-winter or spring snowpack melt can increase wetland water levels substantially or drastically (Ketcheson et al. 2012) and potentially flood snake overwintering habitat (figure 5b, 5e; Markle et al. 2020).

The maintenance of peat temperatures above 0°C during the winter is manifested by the interaction of the peat–water–groundwater and snow–insulation thermal feedbacks (figure 5b). Groundwater inflow can buffer peat temperature decline in the winter and create complex zones of thermal refugia (Kaandorp et al. 2019) especially if the residence time of this upwelling water is long. Moreover, because the heat capacity of water is several times greater than that of air, the presence of a high water table or open water in the wetland means that the wetland is somewhat buffered against cooling, the development of ice cover, and a frost table early in the winter. Moreover, temperatures are also moderated at depth by a thick peat layer or a deep water column resulting in low temperature variability at depth (figures 2a and 5b). When ice cover does form on the wetland surface, it restricts access to aerial oxygen and prohibits oxygenation of the water column.

The development of anoxic conditions reduces the turtle resilience zone, but ice cover can provide protection from predation (figure 5b; Greaves and Litzgus 2008, but see Brooks et al. 1991).

When the water table is high the moisture retention traits of *Sphagnum* moss and peat (McCarter and Price 2012) maintain a relatively high moisture content in the unsaturated zone that results in greater temperature stability and a greater snake resilience zone size (figure 5b). In contrast, because a drop in water table results in a decrease in bulk peat water content (figure 5b), there is also a concomitant decline in bulk peat heat capacity and a higher likelihood of deeper frost penetration in the peat. Greater penetration of temperatures below 0°C decreases the size of the snake resilience zone. Given that prior to winter the water table position is lower below the surface of hummocks than hollows, the need for additional insulation from snow is especially important for hummock snake overwintering sites (Smolarz et al. 2018).

Peat feedbacks. For turtles that depend on aquatic hibernation sites, low water levels or large temporal variability of water table position can negatively affect the amount of available high-quality overwintering sites (figure 5c). For example, across a range of turtle species, low water levels have been linked to winter mortality (Christiansen and Bickham 1989, Bodie and Semlitsch 2000, Gasbarrini 2017) possibly from anoxia, freezing, or increased predation pressure. Overwintering success is also linked to water table dynamics for snake overwintering sites (Viitanen 1967, Yagi et al. 2020). A trade-off exists in optimal overwintering habitat because snakes must balance the risk of desiccation (Costanzo 1989) and long-term flooding (Viitanen 1967, Smith 2009, Markle et al. 2020, Yagi et al. 2020). In particular, suitable sites are those that are not vulnerable to flooding and have a stable water table that is close to the surface (figures 2, 3, 5c). However, a near-surface water table isn't necessarily required in peatland hummock hibernacula because the high moisture retention traits of *Sphagnum* hummock species (McCarter and Price 2012) could provide snakes with a moist overwintering space.

Moss traits and autogenic feedbacks also operate together to dampen water table fluctuations in response to both dry and wet conditions in many wetlands (Waddington et al. 2015), increasing turtle and snake resilience zone size (figure 5c). Similar to the buoyancy feedback discussed earlier (figure 5a), the deformable nature of highly porous peat often leads to peat subsidence during a drop in the water table and an expansion of the peat matrix as the water table rises (figure 5c; Price 2003). As such, the peat surface relative to the water table position tends to be buffered against change that is critical for maintaining snake resilience zone size stability. Peat with low bulk density and few large tree roots, such as that found on low density floating mats (e.g., Roulet et al. 1992, Waddington et al. 2010), has a greater water table dampening strength than the denser grounded

peat that also contains a higher proportion of trees and woody roots. Therefore, the stability of the snake resilience zone size may be lower near the edges of the wetland (e.g., figure 4c, 4d).

Denser peat (e.g., wetland edges, mined peatlands) also has a much flashier water table response to wetting and drying (figure 5c; see Waddington et al. 2015 for details) as manifested through a peat property referred to as specific yield. Briefly, specific yield (ranges from 0 to 1) determines the rate of water table change per unit volume addition (removal) of water to (from) the saturated zone with low (high) values having relatively more flashy (stable) water tables. For example, deeper and older peat (typically more decomposed with higher peat densities) generally has flashier water tables. As such the older peat at the wetland edge will likely contribute more to a flashy water table than the younger floating mat peat in the middle of the wetland (figure 4c). Moreover, given that the specific yield of open water is 1, turtle overwintering sites in the water column have a more stable water table for a given water surplus or deficit (figure 5c), thus positively contributing to overwintering site suitability. All else being equal, the development of the wetland from state A to state E (figure 4) suggests that the wetland develops to an increasingly less stable water table and less stable resilience zone for a given water surplus or deficit. This process further highlights that the overwintering conditions available in state C are optimal for turtle and snake co-occurrence, whereas turtle overwintering sites are also available in state A and B and snake overwintering sites in state D and E.

Vegetation feedbacks. In response to the decrease in wetland water storage that occurs as a wetland develops from state A to state E (i.e., peat replaces open water; figure 4), there is also a general increase in tree or shrub cover along this successional pathway (figure 5d). Afforestation or shrubification has the potential to cause a strong positive drying feedback whereby an increase in tree or shrub cover leads to an increase in transpiration, a further lowering of the water table that then further promotes tree or shrub growth (Liefers and MacDonald 1990). However, many northern wetlands wet up in the fall and spring, which limits the ability of roots to respire, leading to relatively shallow rooting depth and low annual productivity. Although snake resilience zone size increases with a lower water table position, a near-surface water table is still important for reducing snake desiccation risk, so optimal overwintering sites would likely exist in wetland state C through state E (figure 4). The presence of trees and shrubs is suspected to be important for providing structure to moss hummocks, where snakes have been observed to overwinter in peatland hummocks with a network of shrub roots (e.g., Johnson 1995). The balance between tree and shrub density is also important for springtime emergence because access to open canopy areas for thermoregulation is vital following overwintering (e.g., Johnson 1995).

For state C, the presence of trees along the wetland edge and shrubs on the hummock microtopography likely

provides additional important benefits for reptile overwintering habitat. First, trees and shrubs provide shelter, thereby potentially reducing predation pressure on overwintering turtles (figure 5d). Second, the greater shrub biomass acts to trap blowing snow (Sturm et al. 2001), which can increase hummock insulation (see section on thermal feedbacks above; figure 5b). At the same time, the snowpack under tree cover may be lower because of increased snow interception (Woo and Giesbrecht 2006). Trees can both reduce and enhance snowmelt during mid-winter thaws through reduced shortwave radiation (shading) and enhanced long-wave radiation, respectively (Woo and Giesbrecht 2006). The influence these feedbacks have on turtle and snake resilience zone size then becomes a trade-off of thermal insulation (figure 5b) and water storage and runoff dynamics during snowmelt (see water storage and runoff feedback below, Markle et al. 2020). Third, as shrub and tree cover increase, there is also an increase in litterfall, which supplies organic material to both surface peat and to the bottom of the water column, the latter of which provides the opportunity for turtles to bury during winter.

Water storage and runoff feedbacks. Wetland water table stability can also be manifested through the fill and spill wetland water storage and runoff concept (figure 5e; Spence 2010). When wetland water levels or peat moisture conditions are dry, new water inputs from rainfall, snowmelt or watershed surface water and groundwater are primarily partitioned into filling the storage capacity of the wetland's basin (figure 5e; Oswald et al. 2011). As the water level in the wetland increases the runoff potential also increases because the ease at which water flows through (hydraulic conductivity) near-surface peat is higher than the deeper and denser peat (see peat feedbacks, figure 5c; cf., Waddington et al. 2015). However, runoff cannot occur until the water storage threshold is surpassed, after which additional water input generates outflow (figure 5e; e.g., Spence 2010). The rate at which the wetland fills and spills is partially controlled by the volume, area, and depth of the basin as this determines the potential water storage capacity of the wetland (e.g., Brooks and Hayashi 2002), and these wetland characteristics influence the dynamics and stability of the resilience zone (figure 5e) in addition to biogeochemical (figure 5a) and thermal feedbacks previously discussed (figure 5b). For a comprehensive review of watershed hydrology and water storage thresholds, see Spence (2010).

In the situation in which the outflow is temporarily (days to weeks) blocked (e.g., sediment, ice, snow) the snake resilience zone becomes vulnerable as water levels in the wetland can rise greatly especially when water supply from rain-on-snow events (rainfall on an existing snowpack) from the watershed dominate (see figure 5e; Markle et al. 2020). This is especially important for wetlands that have a high ratio of watershed area to basin area (Spence 2010), which have the potential for a high volume of water to enter the wetland during a single weather event (rainfall, rain on snow). Under

these scenarios, the increase in oxygen availability from the supply of dissolved oxygen to the wetland from watershed inflow (figure 5e) would increase turtle resilience zone size, but a rapidly rising water table compressing or even flooding snake resilience zone for days or even weeks at a time would severely reduce snake resilience zone size (Markle et al. 2020). In situations in which beaver dams block the outflow the increase in the depth, extent, and duration of wetland water storage can be altered for months to decades (Westbrook et al. 2006, Woo and Waddington 1990) affecting wetland development and biogeochemistry (figure 5a). Beaver dams are known to affect habitat availability and use throughout the turtle active season (e.g., Yagi and Litzgus 2012). A stable, higher winter water table position would likely increase the availability of turtle overwintering habitat but reduce the availability of snake overwintering habitat. However, in the event the beaver dam collapses, a sudden drop in winter water table position could have negative consequences for both turtles (reduction in habitat) and snakes (reduced moisture and access to water table).

A framework to guide management, restoration, and research

Many northern reptiles depend on wetlands for refugia to survive winter conditions. Understanding the ecohydrological feedbacks and interactions that regulate wetland habitat suitability during winter is an important step toward identifying resilient ecosystems and managing and restoring habitat for reptiles in the face of unprecedented landscape change. Predicting changes in winter refugia is critical because warmer and wetter winters are expected to result in increased exposure to low air temperatures because of increased freeze-thaw cycles (Zhu et al. 2019). Based on these projected changes, we demonstrate below how the framework (figure 5) can be used to predict changes in the strengths of the ecohydrological feedbacks and interactions and the resulting effect on habitat suitability, proactively direct management strategies, and highlight areas for potential restoration activities (supplemental figure S1).

The first step is to identify the starting points on the feedbacks and interactions diagram based on the primary physical changes resulting from the stressors. In the case of the predictions made by Zhu and colleagues (2019), the short-term responses (within a single overwintering season) are increased rainfall (figure S1a), increased inflow from watershed via surface runoff (figure S1b), and decreased snow depth (figure S1c). The second step is to follow each arrow to predict changes in environmental conditions and how these influence size of the resilience zone (direct measure of habitat suitability). Increased rainfall can result in changes in habitat suitability through increased runoff potential (figure S1i) and increased snowmelt (figure S1ii) when snowpack exists. The increased potential for runoff can reduce snake resilience zone size (reduce suitability) if the wetland outflow is blocked and the water table continues to rise, putting snake overwintering sites at risk of flooding

(figure S1iii). This risk of flooding is further exacerbated from increased inflow from the watershed (figure S1iv) and snowmelt (figure S1v), which can directly decrease water table depth and snake resilience zone. However, the increased inflow from the watershed (surface runoff) brings oxygenated water into the system (figure S1vi) and water movement can reduce the probability of ice cover formation (figure S1vii), both increasing turtle resilience zone size. Although areas without ice cover can also increase dissolved oxygen availability through mixing with air (figure S1viii), they can expose turtles to predators (figure S1ix). The combination of warmer temperatures and increased melt events result in shallower snow depths, which reduces thermal insulation (figure S1x) and increases frost depth (figure S1xi), thereby reducing snake resilience zone size. Overall, an increase in water entering the ecosystem and reduced snow depth on the wetland surface results in an increase in water table position and compromises hummock thermal insulation. Therefore, we would predict a general decrease in snake resilience zone size and increase in turtle resilience zone size. Although turtle resilience zone size isn't necessarily negatively affected, changes in freeze–thaw cycles could have energetic consequences (Williams et al. 2015) and a mechanistic model would provide an opportunity to examine the cumulative impact on turtles.

We also encourage the use of the feedback diagram as a starting point to guide management and research on how the potential impacts of other climate-mediated disturbances (e.g., drought, wildfire), land-use changes (e.g., road construction, resource extraction), and restoration actions may affect the size of the resilience zone. In our example, management strategies for the massasauga could involve monitoring outflows (figure S1d) to prevent temporary blockages and potential restoration actions could include altering hummock height to limit frost penetration (figure S1e) and increase snake resilience zone size.

Although our framework can be used as a starting point, multidisciplinary research is needed to address knowledge gaps including watershed–wetland interactions following disturbance and reptile tolerance to changes in microhabitat conditions. This will further our understanding of the fitness consequences of anthropogenic stressors and enable large-scale identification of overwintering habitats that support diverse reptile assemblages. Where wetland surface complexity is a suitable indicator of reptile assemblages, remote sensing could be used to map wetlands onto our wetland successional states (figure 4) and predict habitat suitability for, or even occurrences of, species at risk. We believe this would allow for better estimates of the regional distribution of species at risk habitat and would likely be a useful tool for conservation planning. Finally, we hope that our framework will encourage the development of mechanistic models (e.g., Mitchell et al. 2008, Fitzpatrick et al. 2019) that explicitly incorporate reptile physiology and habitat ecohydrological feedbacks to predict the effects of climate and land-use changes on the physico-chemical conditions of the overwintering environment and

reptile species' survival and distribution patterns. Through an interdisciplinary and more mechanistic approach, ecosystem response to disturbances can be more readily quantified and predicted, and conservation strategies can be implemented to effectively protect species at risk and ensure our common species remain common.

Supplemental material

Supplemental data are available at *BIOSCI* online.

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