



# Modelled incubation conditions indicate wider potential distributions based on thermal requirements for an oviparous lizard

Vaughn Stenhouse<sup>1</sup> | Anna L. Carter<sup>1</sup>  | David G. Chapple<sup>2</sup>  | Kelly M. Hare<sup>1</sup>  |  
Stephen Hartley<sup>1</sup>  | Nicola J. Nelson<sup>1</sup> 

<sup>1</sup>Centre for Biodiversity and Restoration Ecology, School of Biological Sciences, Victoria University of Wellington, Wellington, New Zealand

<sup>2</sup>School of Biological Sciences, Monash University, Clayton, Victoria, Australia

## Correspondence

Nicola J. Nelson, School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand.  
Email: nicola.nelson@vuw.ac.nz

## Present addresses

Anna L. Carter, Department of Ecology, Evolution & Organismal Biology, Iowa State University, 2200 Osborne Dr., Bessey 251, Ames, IA, 50011.

Kelly M. Hare, School of Graduate Research, University of Waikato, Private Bag 3105, Hamilton, 3240, New Zealand.

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## Abstract

**Aim:** Predicting the distribution of species relies increasingly on understanding the spatially explicit constraints of environmental conditions on an organism's physiological traits. We combined an empirical model of temperature-dependent embryonic development with a mechanistic model of soil temperatures to examine potential thermal limitations on the distribution of a nocturnal, oviparous skink, *Oligosoma suteri*, a range-restricted endemic.

**Location:** New Zealand.

**Methods:** We estimated a thermal requirement for successful embryonic development as 616 degree-days above a threshold of 13.8°C. We then modelled soil temperatures at representative sites across New Zealand and predicted duration of incubation to map the distribution of potentially viable oviposition sites, given variation in the timing of egg-laying under even temperature increases.

**Results:** Successful development of *O. suteri* embryos is possible in locations outside their current distribution. Increasing temperatures increased the species' potential range, reducing incubation duration and lengthening the oviposition window. However, due to the disconnected nature of their rocky shore habitat, individuals may not be able to disperse to currently uninhabited sites within that extended range. Additionally, although locations may be thermally suitable for incubation, predation by introduced mammals, competition and habitat modification may prevent successful establishment of populations.

**Main conclusions:** Our models contribute to understanding fundamental physiological constraints on an important life history stage that will inform conservation management actions, including potential future translocations.

## KEYWORDS

climate change, degree-days, embryonic development, mechanistic microclimate model, *Oligosoma suteri*, temperature-dependent

## 1 | INTRODUCTION

A species' geographical boundaries are determined by both the physical environment (e.g. microclimate and physical barriers to dispersal)

and biological interactions (e.g. predation and competition). However, fundamental constraints on species' distributions are delineated largely by physiological limitations (Kearney & Porter, 2009). While a single biotic or abiotic variable is unlikely to capture all factors that



set distributional limits (Gaston, 2009), temperature remains a key climatic variable in determining the distribution of species (Gaston, 2003, 2009; Jeffree & Jeffree, 1994). Climate change is driving shifts in species distributions (e.g. Böhm et al., 2016; Thomas et al., 2004), as organisms track optimal habitats or adapt to changing conditions in situ by modifying their behaviour and physiology (e.g. Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Thomas et al., 2004). Climate change is likely to surpass habitat loss as the main driver of biodiversity change during the 21st century (Leadley et al., 2010), emphasizing the need to identify factors that constrain geographical boundaries and to predict the magnitude and direction of potential shifts (Araújo, Thuiller, & Pearson, 2006). These predictions are of particular importance for rare and endangered species and species with restricted distributions and/or limited dispersal ability (e.g. Mitchell, Rodriguez, Kuchling, Arnall, & Kearney, 2016).

Extreme temperatures, those that exceed thermal tolerance limits, are generally associated with higher latitudes and can have significant, negative fitness consequences for terrestrial ectotherms, such as reptiles (Kingsolver, Diamond, & Buckley, 2013; Sinervo et al., 2010). Extreme or sustained low temperatures have the greatest impact on the embryonic stage of oviparous species, as eggs cannot relocate themselves into more favourable microsites. Cold temperatures can prevent oviparous reptiles from inhabiting higher latitudes and elevations, because the incubation period required to complete development in ovo is longer than the period of time during which nutrients (i.e. yolk reserves) remain available (e.g. Parker & Andrews, 2007). Even in locations where hatching may occur, if embryonic temperatures are suboptimal, hatchling phenotypes may be negatively impacted (e.g. deformed limbs), reducing recruitment and, ultimately, population persistence (see Deeming, 2004 for a review).

Many reptiles also exhibit temperature-dependent sex determination. If climatic temperatures shift so that only one sex is produced, a population may ultimately become extinct (e.g. Grayson et al., 2014). Thus, in oviparous reptiles, the embryonic stage is a major consideration for defining boundaries of geographical distributions via incubation temperature (Deeming, 2004), even allowing for adults to change microhabitats or alter nesting behaviour (e.g. Doody et al., 2006). For terrestrial ectotherms, species-specific upper critical temperatures typically fail to predict their biogeography (Sunday, Bates, & Dulvy, 2012). However, when cool incubation temperatures prevent oviparous species from inhabiting colder regions, embryonic thermal tolerances and developmental rates are key components of distributional limits (Parker & Andrews, 2007).

Degree-day models are a useful tool for predicting distributions of species and timing of events based on temperature-dependent developmental processes (e.g. Hartley & Lester, 2003; Parker & Andrews, 2007; Schultze, Sabbatini, & Luo, 2016). Degree-day models establish a baseline temperature and the number of “thermal units” above that threshold required for an organism to develop from one point in its lifecycle to another (Baskerville & Emin, 1969; Birchard, 2004; Wilson & Barnett, 1983). They are typically parameterized from developmental times measured under controlled constant temperature conditions. For example, three days spent at a

constant two degrees above the threshold accumulates six ( $3 \times 2$ ) degree-days. Once parameterized, however, degree-day models can predict developmental times under the fluctuating temperature regimes characteristic of field conditions. Here, we parameterize a degree-day model to explore the current and future distribution of New Zealand's only endemic, oviparous lizard (Whitaker, 1968).

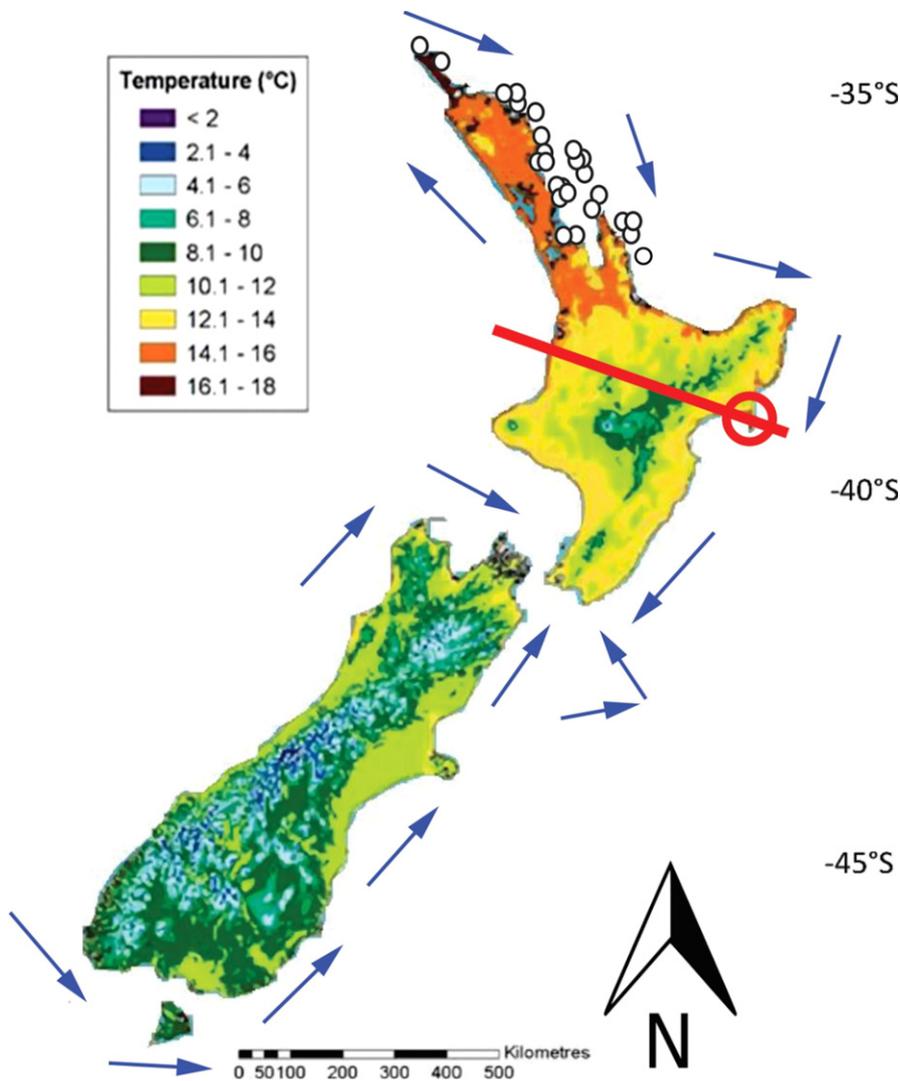
Reptiles in New Zealand underwent significant range contractions following human colonization, due to habitat loss and predation by introduced mammals (Nelson, Hitchmough, & Monks, 2014; Towns & Daugherty, 1994; Towns, Hitchmough, & Perrott, 2016). Thus, the present distribution of *O. suteri* (Figure 1;  $-36^\circ$  S to  $-35^\circ$  S) is considered relictual, with populations once more widespread around the North Island coastline (Towns, Neilson, & Whitaker, 2002), possibly as far south as the biogeographical limit created by the “Taupo Line” (Chapple & Hitchmough, 2016; Figure 1). Additionally, the lack of phylogenetic structure in *O. suteri*, coupled with its restricted distribution and strong relationship between frequency of occurrence and latitude (i.e. southern limit corresponds with a  $10^\circ$ C mean winter [July] isotherm at sea level; Towns, 1975b; Towns, Parrish, & Westbrooke, 2003), has led to predictions that the southern limit results from ecophysiological constraints (Hare, Longson, Pledger, & Daugherty, 2004; Hare, Pledger, & Daugherty, 2008; Towns, 1975b). In particular, the low levels of genetic divergence may be a result of range contractions to warmer northern refugia during glacial maxima, followed by rapid range expansions during interglacials (Hare, Pledger, et al., 2008), via swimming, and rafting in a southward direction along the East Auckland Current (Heath, 1985; Hare, Pledger, et al., 2008; Figure 1). Thus, climate warming could benefit this species, potentially enabling expansion of its current range to cooler, more southern locations (Hare, Pledger, et al., 2008).

We used data on timing of oviposition and incubation duration to: (a) parameterize a degree-day model for embryonic development of *O. suteri* from controlled incubation regimes; (b) investigate the current thermally mediated distributional limits of *O. suteri* along New Zealand's entire coastline; and (c) evaluate the sensitivity of *O. suteri* to increasing temperatures. We expected that the current distribution of *O. suteri* would not match its potential thermal distributional limits. We also expected that, with warming, the potential range could extend further south, possibly as far as Te Waipounamu/South Island.

## 2 | MATERIALS AND METHODS

### 2.1 | Study species

The egg-laying skink, *O. suteri*, is an oviparous, littoral and nocturnal skink that inhabits boulder and stone beaches or rocky platforms (Whitaker, 1968), from the high tide line to the vegetation edge (Towns, 1975b). Current-day populations are mainly restricted to offshore islands that are free from introduced mammalian predators (Towns et al., 2003). Egg-laying skinks are semiaquatic and have physiological adaptations to deal with a semimarine lifestyle (Janssen, Towns, Duxbury, & Heitkonig, 2015) suggesting they may easily disperse across water (Hare, Pledger, et al., 2008). In the wild, nesting



**FIGURE 1** The current distribution of *Oligosoma suteri* (white circles; data from the Department of Conservation's Atlas of the Amphibians and Reptiles of New Zealand) superimposed on a map of mean annual air temperatures for New Zealand from 1971–2000 (NIWA Cliflo: <https://cliflo.niwa.co.nz/>). The extant distribution of *O. suteri* is in areas ranging from mean annual air temperatures of 12.1–18°C, with the southernmost population on the Alderman Islands (36°58' S 176°05' E). The mean air temperature (MAT) in several locations outside the current distribution reaches temperatures similar to “northern” New Zealand (e.g. Gisborne [−39°49' S 176°91' E]; red circle, MAT >14°C). The red line indicates the Taupo Line (McCann, 1955, 1956). Blue arrows in the ocean indicate the prevailing ocean currents (modified from Heath, 1985), and likely routes for dispersal of *O. suteri*

occurs from late December to mid February (Towns, 1975a); the earliest observed oviposition date, 21 December, was recorded in the laboratory (Hare, Daugherty, & Cree, 2002). Oviposition may be earlier in warmer locations (i.e. lower latitudes), since embryonic development depends on temperature, and eggs undergo some development (up to stage 32, according to the staging series for *Lacerta* [*Zootoca*] *vivipara* developed by Dufaure & Hubert, 1961 and reproduced in Porter, 1972) prior to oviposition (Hare et al., 2002). Females dig nests in sand, beneath boulders and rocks of 100–300 mm in diameter (Whitaker, 1968; Vaughn Stenhouse unpublished data). In laboratory settings, females favour warm nest sites over cool (Chapple, Keall, Daugherty, & Hare, 2017). The duration of incubation decreases with increasing temperature in the laboratory (Hare et al., 2002). The longest known incubation period that resulted in successful hatching is 149 days (~5 months, at constant 18°C), and the shortest recorded is 48 days (~2 months, at constant 26°C; Hare, 2001). However, hatching success and embryo and hatchling survival rates are low for eggs held at constant temperatures of 18°C (Hare et al., 2002, 2004). In the wild, hatching occurs between March and April (Towns, 1975a; Whitaker, 1968). The current distributional range of *O. suteri* falls entirely within the climatic region of “Northern New Zealand” the only

region where mean annual air temperatures are above 12.5°C (Leathwick, Wilson, & Stephens, 2002).

## 2.2 | Degree-day model

To build the degree-day model (Petitt, Allen, & Barfield, 1991), we used data on incubation period for *O. suteri* eggs held under three constant laboratory regimes (detailed in Hare et al., 2002). Briefly, since the range of temperatures experienced in natural nests was unknown, incubation temperatures were selected over a range of temperatures that eggs were thought to experience in the wild (Hare et al., 2002). Eggs were randomly distributed among three incubation regimes: 18, 22 and 26°C. When the incubation period for 18°C eggs exceeded the hypothesized maximum development period (using temperature coefficient  $Q_{10} = 105$  days), and embryos were beginning to fail (i.e. beads of water built up on the outside of eggs, indicating water loss from eggs, or embryos stopped moving) half of the 18°C eggs were transferred to 22°C to induce hatching (Hare et al., 2002). Average incubation period increased from 51.5 days at 26°C, to 73.8 days at 22°C and to 137.9 days at 18°C (Hare et al., 2002). Incubation at 18°C (compared to 22 and 26°C) resulted in

reduced hatching rates and high levels of hatching abnormalities, which reduced locomotor fitness and survival (Hare, Daugherty, & Chapple, 2008; Hare et al., 2002, 2004).

Using data on incubation duration vs. temperature, we calculated the number of degree-days and associated temperature threshold required for complete embryonic development of *O. suteri*, using the linearized Law of Total Effective Temperature (Equation 1):

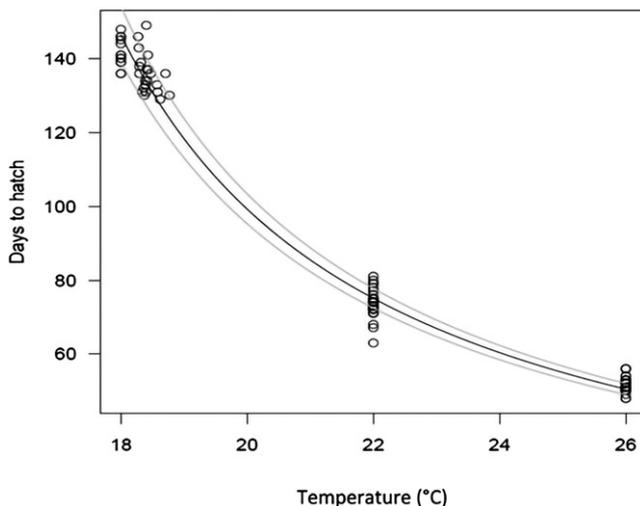
$$DT = k + t_0D \quad (1)$$

where  $D$  is incubation duration,  $T$  is temperature,  $k$  is a thermal constant measured in units of degree-days and  $t_0$  is a baseline temperature of theoretical zero development (Ikemoto & Takai, 2000). The values for  $t_0$  and  $k$  were estimated from the slope and intercept, respectively, of a reduced major axis regression of  $DT \sim D$  (Figure 2). We accounted for the shift of 22 eggs from 18 to 22°C by calculating a constant temperature equivalent ( $T_{\text{equiv}}$ ) for these eggs, based on the amount of time spent incubating at the two temperatures (Equation 2):

$$T_{\text{equiv}} = [(days\ at\ 18^\circ C \times 18) + (days\ at\ 22^\circ C \times 22)]/D \quad (2)$$

### 2.3 | Soil temperature model

To model soil (i.e. incubation) temperatures likely to be experienced in the field, we used the NicheMapR microclimate model, which computes vertical profiles of hourly substrate temperatures at 10, user-defined depths, based on a one-dimensional, partial differential equation using above and below-ground boundary conditions (Kearney & Porter, 2016). The inputs include: environmental parameters



**FIGURE 2** Relationship between incubation temperature ( $T$ ) and developmental time ( $D$ ) for eggs of *Oligosoma suteri* incubated at three constant incubation temperatures (data from: Hare et al., 2002). Fitted lines are the mean (black line)  $\pm$  95% confidence intervals (grey lines) of a degree-day model derived from major axis regression of  $DT$  versus  $D$ , back-transformed on to axes of  $D$ – $T$ . For model-fitting, temperature is assumed to be a constant, thus for 22 eggs switched between 18 and 22°C late in their incubation period, a constant temperature equivalent was used, based on a weighted average of the two periods (Equation 2)

(maximum and minimum daily values of air temperature, wind speed, relative humidity, cloud cover and shading and soil properties) as well as location and terrain (latitude, longitude, elevation, slope, aspect and hillshade). Latitudes and longitudes were extracted at a 15 km horizontal resolution from the “microclim” dataset (Kearney, Isaac, & Porter, 2014). The spatial extent of the model was restricted to a single pixel-width around the New Zealand coastline (i.e., within 15 km of the shoreline), generating 346 unique sites. For simulations, we modelled all terrain with a slope of 0, due to the relatively coarse spatial resolution (15 km) of location data, and because *O. suteri* inhabits flat areas (Whitaker, 1968). To simulate the current climate, we used the NicheMapR default “global\_climate” dataset (Kearney & Porter, 2016), which provides 1961–1990 “climate normals” for each location (New, Lister, Hulme, & Makin, 2002). To simulate different substrates, we ran separate models using “sand” and “rock” soil parameters (Kearney et al., 2014). The microclimate model has a previously reported accuracy of 2–3°C RMSE from observed temperatures at a given depth (Kearney et al., 2014).

### 2.4 | Predictions of accumulated degree-days

To evaluate accumulated degree-days at any given site (for a given depth and given substrate), hourly soil temperatures output from the microclimate model were entered into the degree-day model for *O. suteri* embryos:

$$dd = \sum (M_{st} - t_0) \times 0.042 \quad (3)$$

where  $dd$  is degree-days,  $M_{st}$  is the modelled soil temperature,  $t_0$  is the minimum development threshold temperature from equation 1 and 0.042 is the hourly fraction of 1 day. If  $M_{st} < t_0$ , then  $M_{st} - t_0$  for that hour was assigned a value of zero, reflecting that those temperature conditions would not contribute to development.

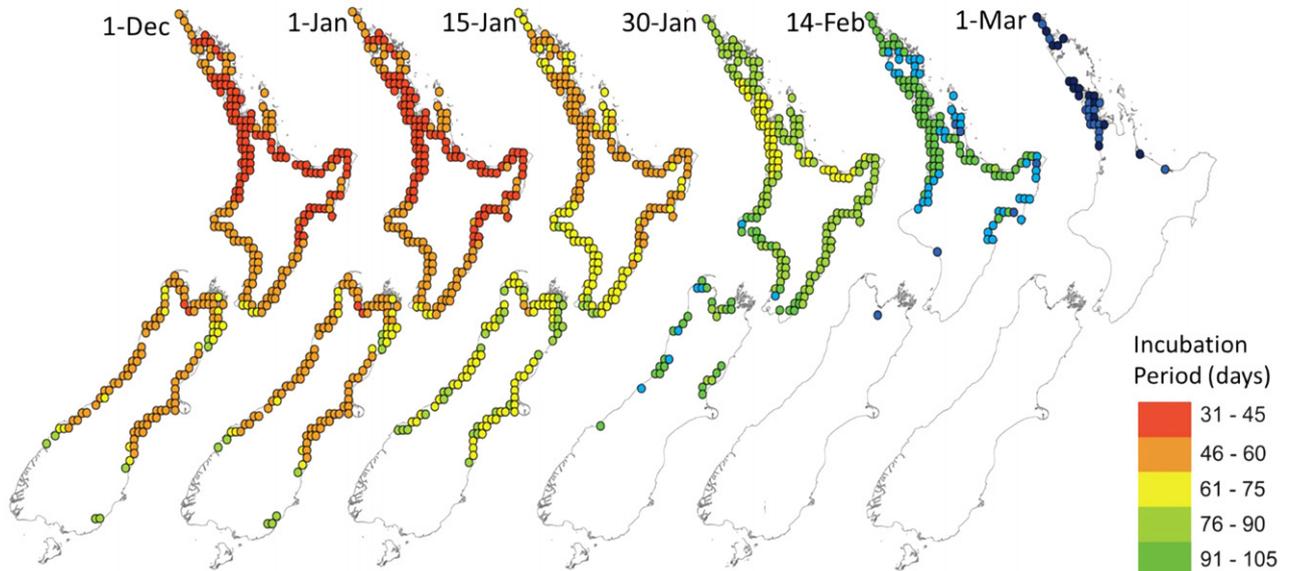
Accumulated degree-days were calculated for each site based on eight possible start dates, selected liberally to encompass known oviposition and hatching dates (1 December, 16 December, 1 January, 15 January, 30 January, 14 February, 1 March, 15 March), three possible depths (25 mm, 100 mm and 300 mm) and two possible substrate types (sand and rock). We liberally estimated 6 months for the maximum possible incubation period, as no data exist on in ovo nutrient availability (i.e. how long yolk can last, relative to how long incubation takes). Sites that did not reach the required number of degree-days within 6 months were considered “unsuitable.”

We also identified a subset of more conservative predictions, those based on: (a) nest depths spanning those recorded in the wild (100 and 300 mm; Whitaker, 1968; Vaughn Stenhouse unpublished data); (b) the four oviposition dates spanning the range documented in the wild (1, 15 and 30 January and 14 February); and (c) a reduced maximum incubation duration of four months, reflecting conditions known to facilitate successful development (Towns, 1975a; Whitaker, 1968).

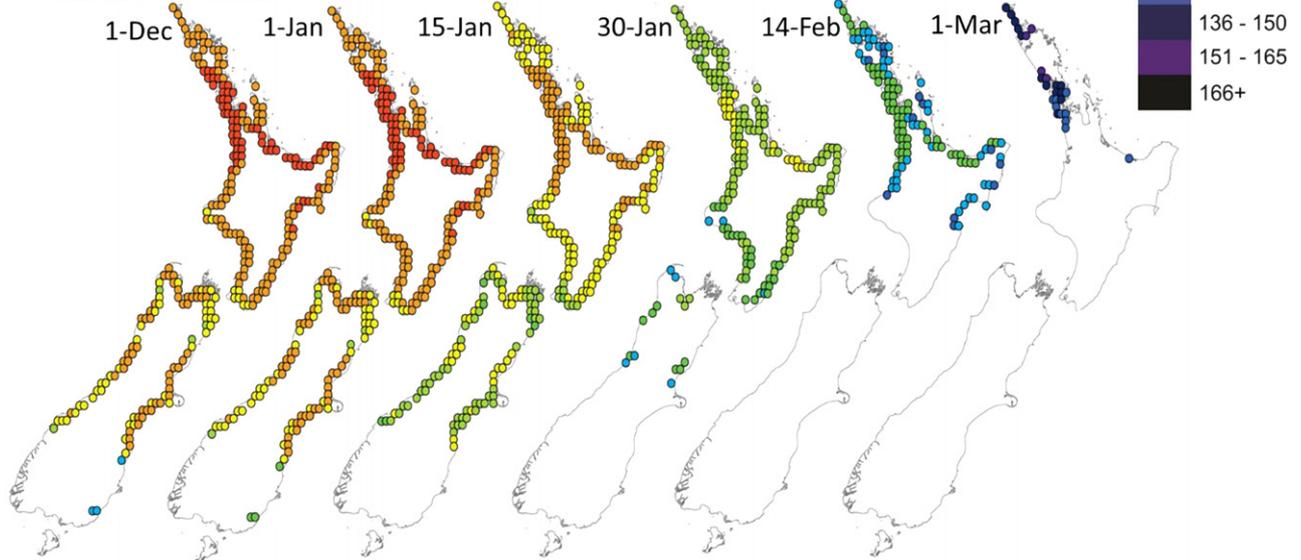
We compared predicted distribution of sites thermally suitable for embryonic development to current distribution records for *O. suteri* from the New Zealand Department of Conservation’s Atlas of the



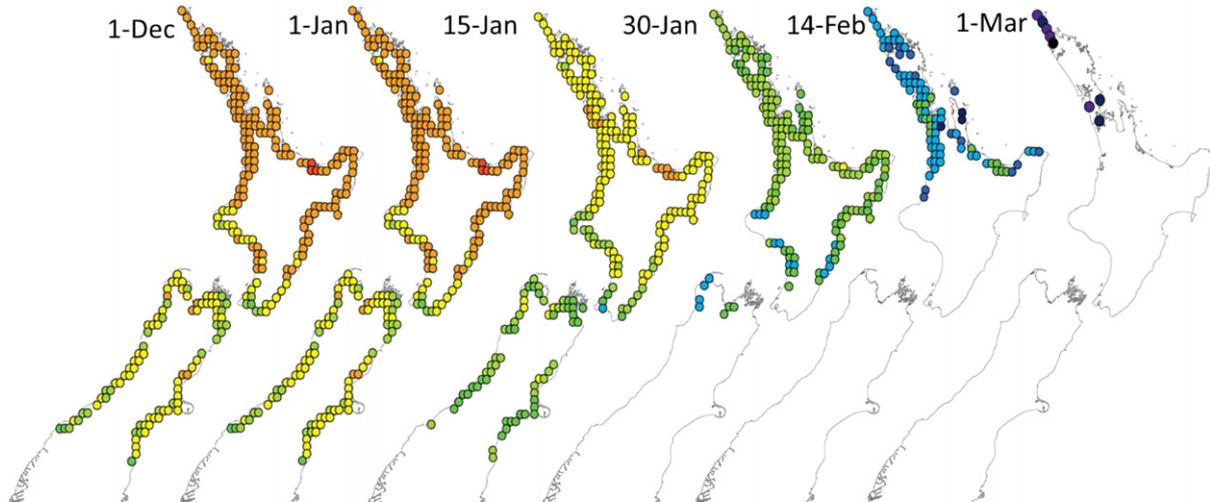
## (a) Rock 25 mm



## (b) Rock 100 mm



## (c) Rock 300 mm





**FIGURE 3** The predicted number of days to hatch for *Oligosoma suteri* eggs laid within rocky substrates, calculated at a 15 km resolution around the New Zealand coastline. Six modelled oviposition dates are shown for nests at three depths: (a) nest of 25 mm depth. (b) Nests of 100 mm depth. (c) Nests of 300 mm depth. Model outputs for oviposition dates of 16th December (identical to 1st December model) and 15th March (no data/blank map) are omitted to reduce clutter. The scale bars represent the duration of incubation (days) predicted from the modelled soil temperatures. Only sites that reached a minimum of 616 degree-days within 6 months are shown. Figures of nests within sand substrate at the same depths are available in Supplementary Materials S1. Please note, if a maximum incubation period of 4 months is assumed, then the set of potentially viable sites is those where predicted incubation period is <120 days

Amphibians and Reptiles of New Zealand (BHW, 2017). Where data points were located at a trigonometry station (i.e. an ordnance survey point) on an island or headland, they were manually moved to the nearest rocky beach. Aerial imagery (sourced from the LINZ Data Service: <https://data.linz.govt.nz/>) was used to guide the final placements.

## 2.5 | Sensitivity to increasing temperatures

To determine how climate warming may affect duration of incubation and timing of oviposition, we used the current climate and two higher temperatures, representative of average predicted increases in temperature for New Zealand over the next century (MfE 2008). Six oviposition dates (1 January, 15 January, 30 January, 14 February, 1 March, 15 March) were used in place of eight to reduce computational requirements. Climate warming is predicted to impact New Zealand fairly uniformly (i.e. with relatively little variation in temperature increase by region). Thus, we tested sensitivity of *O. suteri* development to increasing temperatures in a spatially uniform manner. In addition, the upper thermal tolerance of developing *O. suteri* embryos is unknown, which meant that we could not identify a spatially explicit (i.e. northern) lethality limit for incubation temperatures under extreme warming conditions. We used temperature increases of 0.9 and 2.1°C, which are the “best estimate” predictions for, respectively, 2040 and 2090, based on the A1B emissions scenario (MfE, 2008). The average temperature increases were then incorporated into the degree-day model (equation 4):

$$dd = \sum [(M_{st} + T) - t_0] \times 0.042 \quad (4)$$

where  $T$  was the increase in temperature of 0.9 or 2.1°C. Increases in mean air temperature were used as a proxy for increases in soil temperature.

Analyses were conducted in R (R-Development-Core-Team, 2015) using the packages “smatr” (Warton, Duursma, Falster, & Taskinen, 2015) and “NicheMapR” (Kearney & Porter, 2016), and graphs were created using package “ggplot2” (Wickham & Chang, 2014). Maps were created using ArcMap™ 10.1 (Environmental Systems Research Institute [Esri] ArcGIS: Redlands, CA, USA, 2012).

## 3 | RESULTS

### 3.1 | Degree-day model

Regression analyses of incubation periods observed under laboratory conditions estimated that  $616 \pm 45.3$  degree-days above a

developmental threshold temperature of  $13.8 \pm 0.53^\circ\text{C}$  are required for complete development of *O. suteri* embryos (i.e. from time of egg laying to time of hatching [estimate  $\pm$  95% CI; Figure 2]).

### 3.2 | Thermal distributional limits of *O. suteri*

Under current climatic conditions, the most important variable affecting whether or not the 616 degree-day incubation threshold was reached was date of oviposition and latitude. For oviposition between 1 December and 15 January, thermally suitable nest environments were predicted to be present more than 1,000 km further south than the southernmost record for *O. suteri* and about 800 km further south than the Taupo Line (Figure 3; Appendix S1 in Supporting Information). The number of suitable sites decreased for oviposition dates after 30 January, with no sites reaching the number of degree-days required within the 6-month timeframe for oviposition dates on 15 March (Figure 3; Appendix S1 in Supporting Information). Substrate (rock vs. sand) and nest depth made little difference, except for oviposition dates 30 January and 1 March, where sand substrate contained more suitable sites at both the 100 and 300 mm depths, compared with the rock substrate (Figure 3; Appendix S1 in Supporting Information).

When more conservative models were used (oviposition dates from 1 January, with maximum duration of incubation of 4 months at 100 and 300 mm depths), the number of suitable sites was reduced by 9.4% (100 mm) and 21.95% (300 mm) for 14 February oviposition dates for both substrates (Figure 3; Appendix S1 in Supporting Information; sites with incubation >120 days). The duration of incubation was longer for rock than sand substrate, ranging from 2 days longer at 25 mm nest depths to 11 days longer at 300 mm nest depths.

### 3.3 | Effects of temperature increases on incubation duration

On average, increasing temperature reduced duration of incubation by ~10 days compared to the current climate. With temperature increases of 0.9 and 2.1°C, duration of incubation in sand substrates was, on average, 13–16 days shorter than in rocky substrates (all depths combined), and duration of incubation ranged from 59 to 77 days between 25 and 300 mm depths (both substrates combined) (Figure 4a–f). Simulating a rock substrate (Figure 4a–c) increased the range of successful oviposition dates until 15 March, compared to sand substrate, which was similar to the current climate, extending to only 1 March (Figure 4d–f).

## 4 | DISCUSSION

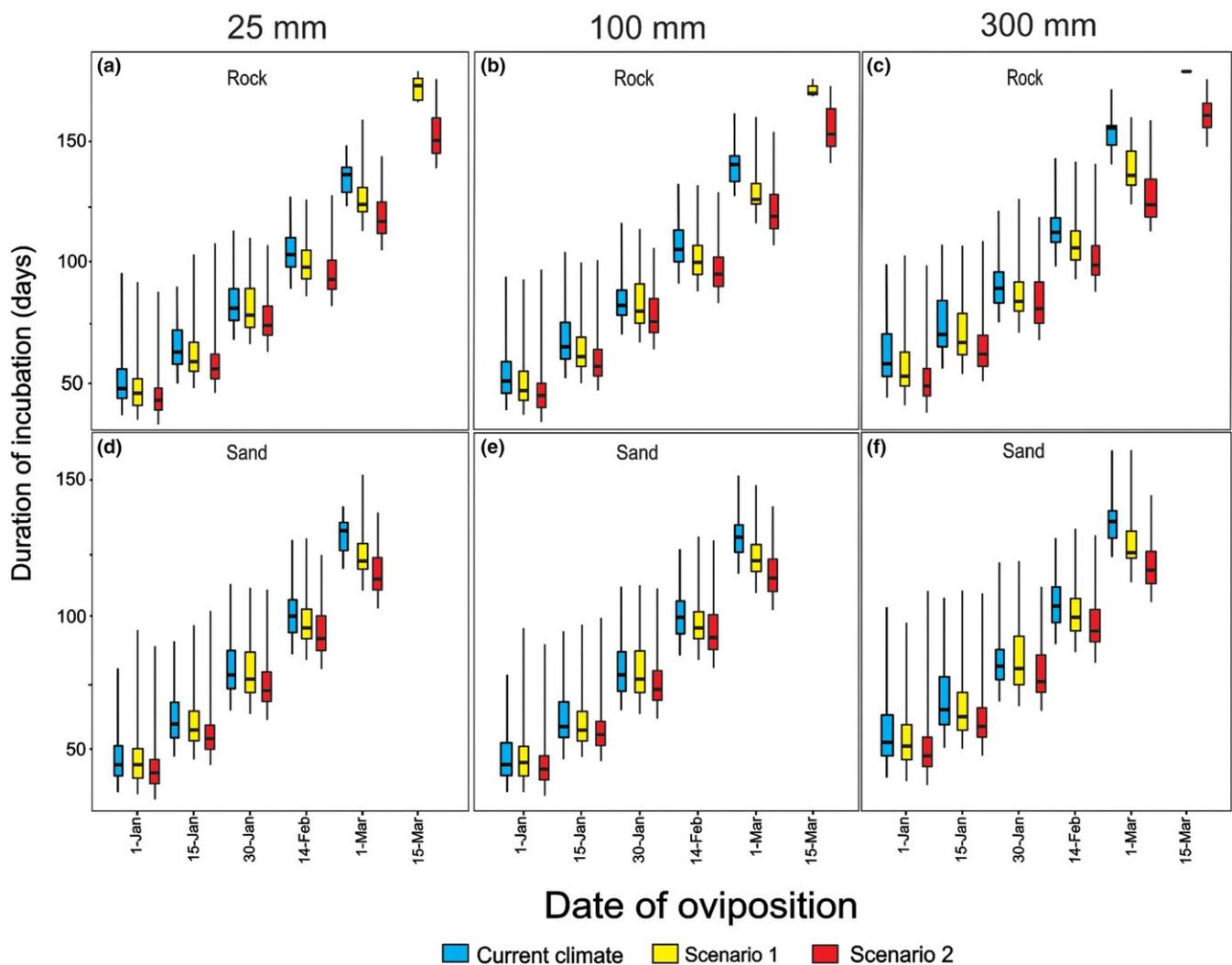
We found that climatically viable nesting sites for *O. suteri* may currently exist south of the Taupo Line, where the species is not currently known to occur. Climate change could increase the potential geographical range yet further southwards, as well as increasing the breadth of dates available for oviposition in northern sites and reducing average incubation length by ~10 days.

### 4.1 | Current distribution of *O. suteri*: models and hypotheses

Our models of the current distribution of *O. suteri* predict that successful embryonic development of eggs could extend up to 200 km further south to the Taupo Line. However, the negative effects of cool-constant temperatures observed in eggs and hatchlings of *O.*

*suteri* (Hare et al., 2002; Hare et al., 2004; Hare, Daugherty et al., 2008) suggest population establishment might not occur in all locations. The longest known incubation time for successful hatching of an egg of *O. suteri* is 149 days at constant 18°C (Hare, 2001). Wild-laid nests experiencing such low average temperatures would not hatch until austral autumn/early winter. For example, hatchlings from eggs laid at higher latitudes and later in the season (e.g. 1 March), would hatch in mid-August (austral winter), when resources and foraging opportunities may be reduced, and predation may be greater due to slower locomotion of hatchlings with lower body temperatures (Hare, Daugherty et al., 2008).

At lower extremes of a temperature range, assumptions of the relationship of linearity between temperature and development rate break down (Georges, Beggs, Young, & Doody, 2005). We used regression analyses to calculate an assumed minimum development threshold of 13.8°C for *O. suteri*, above which embryonic



**FIGURE 4** Modelled dates of oviposition and predicted duration of incubation (days) of *Oligosoma suteri* using the conservative dataset (see text for explanation). Data are presented for each nest depth (25, 100 and 300 mm) for nests in rock substrate (a–c) and sand substrate (d–f). Models were created under the current climate (blue), and climate warming: yellow +0.9°C and red +2.1°C. Boxes indicate median with first and third quartiles, and whiskers are maximum and minimum values across the 15 km pixels representing the New Zealand coastline. Under climate change, mean days to hatch for both substrate types decrease with advancing oviposition date. See text for more details about climate change simulations



development may begin. The estimated minimum development temperature is slightly higher than that predicted for tuatara (11.1°C; Cree, 2014), but little is known for other New Zealand lizards. Therefore, the lower development threshold of 13.8°C for *O. suteri* is a conservative estimate.

The mismatch between the relictual and predicted potential distribution within Te Ika a Māui/North Island is probably a result of the detrimental effects of habitat modification and introduced mammalian predators. Subfossil remains for many of New Zealand's herpetofauna have been found throughout New Zealand in locations where no surviving populations exist (Towns & Daugherty, 1994; Worthy, 2016), indicating previously wider distributions. Although no subfossils are known for *O. suteri* (Worthy, 2016), it is possible they were once more widespread. Although *O. suteri* are probably capable of overwater dispersal over large distances (Hare, Pledger, et al., 2008), populations are often isolated by extensive areas of unoccupied coastline, even on a relatively large island (e.g. Newman & Towns, 1985). Neither can we rule out the possibility that the current southern limit of *O. suteri* distribution is a result of slow, southward dispersal since the Last Glacial Maximum (Hare, Pledger, et al., 2008), when temperatures were between 3 and 6°C lower than present (Elliot, Neall, & Wallace, 2005).

Evaluation of sites predicted as "suitable" by our models will need to consider additional biotic processes and constraints in addition to development-based predictions in order to confidently define accurate range limits, for example, vegetation dynamics, interspecific interactions, dispersal and disturbance (Kearney et al., 2010). Such models will more closely reflect environmental limitations, environmental tolerances and other biotic factors that may limit species distributions at one or both ends of a latitudinal and/or temperature gradient.

#### 4.2 | Temperature increases and incubation success of *O. suteri*

We confirmed our prediction that, under increasing temperatures, the thermally dependent development niche of *O. suteri* can be met further south, including in Te Waipounamu/South Island. However, our model could be strengthened by inclusion of an upper thermal threshold for embryonic development, which is not known from empirical data. This information would indicate which sites (probably northernmost sites, if any) could exceed an upper critical threshold for embryonic development under warmer climates. Parental effects (e.g. oviposition-site choice) may be important in mediating the effects of incubation environment (Deeming, 2004), as nest site selection by females has a significant impact on offspring phenotype (Schwanz, 2016). Maternal nest site choice could compensate, at least partially, for increased temperatures, such as those predicted by climate change (Doody et al., 2006; Telemeco, Elphick, & Shine, 2009). However, adult *O. suteri* females tend to favour warmer nesting locations (Chapple et al., 2017). Thus, behavioural adaptations, such as maternal nest site choice, may not respond fast enough to keep pace with climate change, thereby affecting embryo mortality

and population viability via increased sublethal effects (e.g. reduced growth rate of juveniles).

Hatching earlier in the season could increase both foraging time and potential growth of hatchlings before the onset of winter. However, mismatch between hatching phenology and food availability and/or predator prevalence is possible. In addition, increasing environmental temperatures will impact all life-stages, not just embryos, and may have negative consequences for adults. For example, common lizards (*Lacerta (Zootoca) vivipara*) reproduce earlier in the season and have faster growth and lower adult survival under warmer, compared with cooler, conditions (Bestion, Teyssier, Richard, Clobert, & Cote, 2015). The maximum recorded body temperature of *O. suteri* is 25°C in a captive adult (Towns, 1975b). As a group, endemic lizards of New Zealand have not been reported to voluntarily exceed a body temperature of 34°C (Hare & Cree, 2016). Potentially, under warmer conditions, *O. suteri* may halt foraging and basking by day, and become more strictly nocturnal. Warmer climates also increase reproductive costs to adults (Shine, 2005) by lengthening the time spent in retreats, while avoiding upper critical temperatures, thereby reducing foraging time and causing energetic shortfalls (Kearney, Shine, & Porter, 2009). Thus, climate change may have a positive effect on *O. suteri*, in terms of decreasing incubation duration, but could impact other aspects of life history in unforeseen ways and/or via other facets of climate change.

#### 4.3 | Model application and limitations

Understanding of the causes of species' geographical range limits remains incomplete, both because empirical studies have lagged behind developments in theory (Gaston, 2009) and because plastic responses to climate warming have occurred (Franks, Weber, & Aitken, 2014). For example, some insect species appear to be able to keep pace with current warming (Donnelly et al., 2012), as they generally have shorter life cycles. However, without long-term datasets, difficulties can arise when attempting to detect long-term responses to gradual warming in species with long generation times (Donnelly et al., 2012). Although simpler models are more likely to be generalizable to new situations (Elith, Kearney, & Phillips, 2010), models that explicitly incorporate multiple aspects of an organism's fundamental niche and/or behaviour can improve our ability to differentiate between suitable and unsuitable sites, especially for populations living in marginal habitats at the boundaries of the species' range (Kearney, Porter, Williams, Ritchie, & Hoffmann, 2009).

For this study, we modelled temperature-limited distributions at a relatively coarse spatial resolution (15 × 15 km pixels). Quantifying the variables that underlie a species' fundamental niche, such as below-ground thermal conditions, is generally improved with high spatial resolution microclimate layers (Carter et al., 2015). Using higher resolution layers increases computation time for process-explicit models (i.e. those that describe aspects of the fundamental niche), making them currently impractical for large geographical extents, even for the entire coastline of New Zealand (Kearney & Porter, 2009). However, our lower resolution "first pass" model can

be used to define areas where a higher resolution surface should be generated to confirm model predictions and help inform management decisions (Carter et al., 2015). Given the limited data available for *O. suteri* (i.e. incubation duration, oviposition dates from the field), a more conservative approach was warranted. Future work would benefit from improved data on the functional relationship between embryonic development and temperature, including (a) the impact of fluctuating incubation conditions, which are more indicative of those encountered in real nests, on development rates and (b) the upper thermal tolerances of developing embryos. However, even based on this conservative approach, the potential distribution for this species is still predicted to extend much further south than the current distribution.

#### 4.4 | Assisted colonization

Predictive distribution models are becoming increasingly important to address issues not only in ecology and biogeography but also in conservation biology (Guisan & Thuiller, 2005) for assessment of conservation management issues, such as reserve selection and planning (Araújo, Cabeza, Thuiller, Hannah, & Williams, 2004; Ferrier, Watson, Pearce, & Drielsma, 2002), or for mapping suitable sites for assisted colonizations (Mitchell et al., 2016; Pearce & Lindenmayer, 1998). Our modelling approach could be applied to other species of conservation concern that are range limited by temperature (e.g. plants, invertebrates and reptiles). Conversely, this approach may enable potential invasion hotspots to be predicted, as has been done for exotic reptiles in the pet trade (Kikillus, 2010). Species distribution models, both correlative and process based, can be used to classify sites for reintroductions by identifying suitable habitat and predict changes in habitat suitability under current and future climates (Mitchell et al., 2016; Thomas, 2011).

With climate change, new areas may become available for species that are currently thermally limited, such as temperate species (Cree, 1994). New Zealand has over 100 endemic species of reptiles (Hitchmough et al., 2016). Many are found on offshore, predator-free islands, in mainland sanctuaries or in population distributions significantly smaller than their previous distributions (Nelson et al., 2016; Towns & Daugherty, 1994). Their capacity for dispersal may be limited due to large tracts of unsuitable habitat, even for those species capable of across-water dispersal. Our models provide a useful tool for evaluating potential sites for translocation to aid their spread to areas in which they could, or would, normally reside.

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#### ORCID

Anna L. Carter  <http://orcid.org/0000-0003-4392-277X>

David G. Chapple  <http://orcid.org/0000-0002-7720-6280>

Kelly M. Hare  <http://orcid.org/0000-0002-9473-5256>

Stephen Hartley  <http://orcid.org/0000-0002-9049-5072>

Nicola J. Nelson  <http://orcid.org/0000-0002-1641-6030>

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## DATA ACCESSIBILITY

The climate data used in this study are available from the NIWA (National Institute of Water and Atmospheric Research, Ltd (New Zealand)) Cliflo database (<https://cliflo.niwa.co.nz/>). The distribution records of the study species are available from the New Zealand Department of Conservation's Atlas of the Amphibians and Reptiles



of New Zealand (<http://www.doc.govt.nz/our-work/reptiles-and-frogs-distribution/atlas/>). The incubation data are available from the Victoria University of Wellington Library Archive for theses and dissertations (KMH (2001) MSc thesis; <http://libguides.victoria.ac.nz/theses-and-dissertations>).

#### BIOSKETCH

The authors are a team of international collaborators bringing together their expertise to investigate environmental constraints on fauna in the Pacific. They are listed alphabetically after V.S. V.S. is an MSc student who developed the ideas, performed the analyses and wrote the draft manuscript. A.L.C. provided technical knowledge with microclimate models. D.G.C. and K.M.H. conceived the initial ideas on which this study was based, and provided the species data used in the models. S.H. developed the degree-day model and co-supervised V.S. N.J.N. was the primary supervisor of V.S. All authors were involved in writing and editing sections of the manuscript prior to submission.

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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