

# Bioclimatic analyses for the distributions of *Onthophagus nuchicornis*, *Onthophagus taurus*, and *Digitonthophagus gazella* (Coleoptera: Scarabaeidae) in North America

K.D. Floate,<sup>1</sup> D.W. Watson, R.M. Weiss, O. Olfert

**Abstract**—*Onthophagus nuchicornis* (Linnaeus), *Onthophagus taurus* (Schreber), and *Digitonthophagus gazella* (Fabricius) (Coleoptera: Scarabaeidae: Scarabaeinae: Onthophagini) are species of dung beetles that have been used in relocation programmes to accelerate the degradation of cattle dung on pastures. Exotic in North America, all three species have expanded their distributions since their introduction onto the continent. Here we report development of CLIMEX<sup>®</sup> bioclimatic models using data collected before 2011 that predict the eventual North American distributions of these species. Data collected after 2010 is used to validate these models. Model outputs identify large regions of the central United States of America suitable for establishment of *O. nuchicornis* and *O. taurus* where these species have not been reported. These results indicate that the latter two species may already be present in these regions and undetected, that they have yet to expand into these regions, and (or) that factors restricting migration or dispersal prevent these species from occupying these areas. Model outputs for *D. gazella* suggest that the species has largely reached its predicted maximum distribution. These models can be used to aid the success of future relocation programmes elsewhere in the world and (or) to predict regions where these species are likely to spread without human intervention.

## Introduction

Cattle dung provides habitat for a diverse community of arthropods that are represented by at least 270 species in Canada (Floate 2011). The tunnelling, reproductive, and feeding behaviours of these species accelerate degradation of the dung, which restores nitrogen to the soil and reduces the suitability of pats as breeding sites for pest flies and parasites that affect cattle. Fragmentation also reduces the pat as a barrier to the growth of new forage from beneath the site of deposition. The economic value of these activities in North America may exceed several hundred million dollars (US\$) per year (Fincher 1981; Anderson *et al.* 1984; Nichols *et al.* 2008), such that changes in the geographic distributions of species that provide these ecological services are of general interest.

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae and Aphodiinae) dominate this coprophilous community in terms of their abundance, biomass, and contribution to bioturbation (Kadiri *et al.* 2014). Different species can be classified by functional group as “dwellers”, “rollers”, or “tunnellers”. Dwellers (mainly Aphodiinae) develop from egg-to-adult within the pat. Fragmentation of the pat occurs over a period of weeks via the feeding activity of the larvae. In contrast, rollers and tunnellers can bury or disperse fresh dung pats in hours or days. Adults arrive at fresh pats and remove portions of dung that they bury at some distance from (rollers) or below (tunnellers) the pat. The buried dung provides food for larvae that hatch from eggs laid in the dung at the time of burial. In addition to more rapidly removing the pat from the soil surface, rollers and tunnellers

Received 3 January 2017. Accepted 24 April 2017. First published online 21 June 2017.

**K.D. Floate,<sup>1</sup>** Lethbridge Research and Development Centre, Agriculture and Agri-Food Canada, Lethbridge, Alberta, T1J 4B1, Canada

**D.W. Watson,** North Carolina State University, Raleigh, North Carolina, 27695-7626, United States of America

**R.M. Weiss, O. Olfert,** Saskatoon Research and Development Centre, Agriculture and Agri-Food Canada, Saskatoon, Saskatchewan, S7N 0X2, Canada

<sup>1</sup>Corresponding author (e-mail: Kevin.Floate@agr.gc.ca).

Subject editor: Andrew Smith

doi:10.4039/tce.2017.20

Can. Entomol. 00: 1–21 (2017)

© 2017 Entomological Society of Canada. Parts of this are a work of Her Majesty the Queen in Right of Canada, as represented by the Minister of Agriculture and Agri-Food Canada

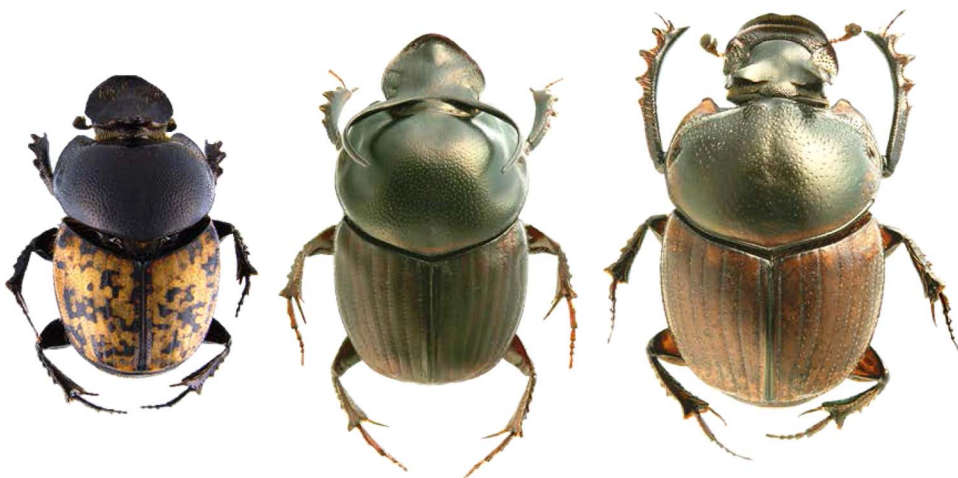
relocate nitrogen (in the form of dung) directly into the root zone of growing plants and, through their tunnelling activities, improve the permeability of the soil to water and air. Because of their greater contributions as ecosystem engineers, studies on dung beetles that are tunnellers or rollers are of particular interest.

*Onthophagus nuchicornis* (Linnaeus), *Onthophagus taurus* (Schreber), and *Digitonthophagus gazella* (Fabricius) are exotic species of tunnellers whose distributions continue to expand in North America (Fig. 1) (Hoebeke and Beucke 1997; MacRae and Penn 2001). *Onthophagus nuchicornis* is a Eurasian species that became established in northeastern North America before the 1840s. First reported in western North America in British Columbia, Canada in 1945, it is now common across southern Canada and adjacent states (Floate and Gill 1998; Tinerella and Fauske 1999; Rounds and Floate 2012; Floate and Kadiri 2013). *Onthophagus taurus* is native to southern Europe, northern Africa, Turkey, and the Middle East. First recovered in North America in 1971 in Florida (Fincher and Woodruff 1975), it has rapidly expanded its distribution northward and recently was recovered near Lake City, Michigan, United States of America (Rounds and Floate 2012). *Digitonthophagus gazella* (formerly *Onthophagus gazella*) is a sub-Saharan species

that was deliberately introduced into the United States of America in the early 1970s (Blume and Aga 1975). It now occurs in the southern states from Florida to Arizona as far north as northwestern Mississippi (Hoebeke and Beucke 1997) and further south into Mexico (Montes de Oca and Halffter 1998). Given their roles in ecosystem function, there is interest in determining the potential future North American distributions of these species.

Species distribution models are commonly used to predict the future establishment of invasive species and are necessarily based on environmental factors; *i.e.*, climate is the dominant factor that governs the distribution and population abundance of most insect species (Andrewartha and Birch 1954). These species distribution models are correlative in that they link climate data for regions where a species currently occurs to climatically similar regions where the species does not yet occur. Correlative species distribution models can be augmented with mechanistic species distribution models to improve the robustness of predictions by incorporating information on the natural history and physiological requirements of the species (Kearney and Porter 2009). CLIMEX<sup>®</sup> (Hearne Scientific Software, South Yarra, Australia) is a software package with aspects of both correlative and mechanistic models. Using a series of annual indices to

**Fig. 1.** Male specimens of (left to right): *Onthophagus nuchicornis* (6.3–8.1 mm in length), *Onthophagus taurus* (6.0–11.5 mm) and *Digitonthophagus gazella* (8.0–13 mm). Photograph credit: H. Goulet (retired, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada).



integrate the weekly responses of a population of a species to climate, CLIMEX<sup>®</sup> models predict not only the likelihood of the establishment of a species, but also how well the species is likely to thrive at a given geographic location (Sutherst *et al.* 2007; Kriticos *et al.* 2015).

Here we present bioclimatic models developed using CLIMEX<sup>®</sup> 3.0 (Sutherst *et al.* 2007) to predict the current and future distributions of *O. nuchicornis*, *O. taurus*, and *D. gazella* in North America. Results for *D. gazella* indicate that this species has largely reached the extent of its potential distribution in North America. Results for *O. nuchicornis* and *O. taurus* identify regions of the continent from which these species have not been reported, but with conditions predicted to be favourable for their establishment. These results indicate that the latter two species may already be present in these regions and undetected, that they have yet to expand into these regions, and (or) that factors restricting migration or dispersal prevent these species from occupying these areas. *Digitonthophagus gazella* and (or) *O. taurus* have been deliberately introduced into Australia (Edwards 2007), New Zealand (Environmental Protection Authority 2011), the United States of America (Lancaster and Hunter 1978; Fincher *et al.* 1983; Markin and Yoshioka 1998), and Brazil (Bianchin *et al.* 1998) in efforts to establish populations to accelerate the degradation of cattle dung. The models developed in the current study for these latter two species should help facilitate redistribution programmes.

## Methods

### Model development

The CLIMEX<sup>®</sup> modelling process has been previously described (Olfert *et al.* 2004, 2012b, 2016b). In brief, CLIMEX<sup>®</sup> derives ecoclimatic indices (EIs) that describe the climatic suitability of specific locations for the reproduction and survival of a given species (Kriticos *et al.* 2015). Our approach combined both correlative and mechanistic supportive data, using the bioclimatic information related to occurrence sites plus seasonal, demographic, and physiological data. The calculation of ecoclimatic indices integrates the weekly responses of a species to climate using a series of annual and weekly indices. An annual

growth index describes the potential for population growth as a function of precipitation, temperature, and photoperiod during the growing season. Up to eight stress indices (cold, wet, hot, dry, cold-wet, cold-dry, hot-wet, hot-dry) are used to simulate population survival during inclement conditions. The weekly growth index is a function of temperature, diapause, and moisture. These indices are comprised of limiting low and high values as well as optimal low and high values. Weekly stress indices include cold stress, heat stress, wet stress, and dry stress. These indices consist of threshold values and stress accumulation values based on linear rates. The growth and stress indices are calculated weekly and then combined into an overall annual index of ecoclimatic suitability (EI), which ranges from EI = 0 for locations at which the species is not able to persist to EI = 100 for locations that are optimal for species survival (Kriticos *et al.* 2015). Five categories of ecoclimatic index values were used in the current paper. These categories, and the corresponding colours used in maps, were as follows: unfavourable (0–2; white); marginal (2–10; green); suitable (10–20; blue); favourable (20–30; yellow), and very favourable (> 30; red).

For model input, climate data were obtained from the CliMond 10 spatial resolution climate data set (Kriticos *et al.* 2012). The CliMond data set was developed for species bioclimatic modelling, including both correlative and process-based mechanistic models. The 10' gridded data set included a hybrid historical data set (based on CRU CL2.0 and WorldClim; centred on 1975). We note that CLIMEX<sup>®</sup> uses air temperatures for input values, whereas our developmental data for *O. nuchicornis*, *O. taurus*, and *D. gazella* is based on soil temperatures (Floate *et al.* 2015). This discrepancy was unavoidable, given that soil temperatures are generally not available for most locations.

For model parameterisation, information was compiled on the natural history and global distribution *O. nuchicornis*, *O. taurus*, and *D. gazella*. Floate *et al.* (2015) examined egg-to-adult development of the three species at constant temperatures of 10–32 °C (in increments of 2 °C). Their results provided values for minimum, optimum, and maximum temperature thresholds for development, degree-day requirements for egg-to-adult development, and diapause requirements.

Locality information was obtained from the published literature, records deposited in the Global Biodiversity Information Facility (2016), the Iberian Scarabaeidae database (Lobo and Martín-Piera 1991; Base de datos sobre Scarabaeidae – [www.biogeografia.org](http://www.biogeografia.org)), records available online for Morocco (Lobo *et al.* 2016), and personal communication with scarab researchers (Supplementary Table S1).

Information obtained for North America by 31 December 2010 was then used to independently refine model parameters in a series of iterative steps to obtain models whose predictions most closely matched North American distributions and reported levels of abundance. For example, models assigned high ecoclimatic index values to regions where the species are known to be abundant.

### Model validation

CLIMEX<sup>®</sup> models were validated with a three-fold approach. First, they were tested for their ability to predict the known global distributions of *O. nuchicornis*, *O. taurus*, and *D. gazella*. Because information on localities from outside of North America was not used in model development, Europe and Australia/New Zealand (varying with species) were used as independent regions for this validation step, serving as an independent occurrence subset. Locality information available for Asia was considered insufficient for this purpose. Second, model outputs that predict patterns of seasonal phenology and the number of generations at different geographic locations were assessed against the published literature. At northern latitudes, surveys from spring (April/May) through autumn (September/October) using dung-baited pitfall traps are best suited for this purpose. At more southern latitudes, year-round operation of dung-baited traps may be most useful. Third, model predictions post-development were assessed against new collection locality information obtained after 31 December 2010. New locality information was obtained from recent publications, additional field surveys, e-mail requests to researchers and curators of insect collections, and from image searches online. Because of their distinctive morphologies, these three species are often photographed and can be reliably identified from other species of scarabs in North America (Fig. 1). The BugGuide website (<http://bugguide.net>) proved to be most useful in this regard.

### Species co-occurrence

The output of CLIMEX<sup>®</sup> models for *O. nuchicornis*, *O. taurus*, and *D. gazella* was combined to compare regions of current and potential future overlap. For each species, grid cells with ecoclimatic index values  $\geq 10$  were plotted on the same map of North America. A belt transect was then drawn through this map, extending from southern Texas (26°N) to northern Canada (60°N), and between 96°W and 98°W. The location of this transect was selected to span the distributions of the three species where they did and did not co-occur in North America north of Mexico. The ecoclimatic index values in this transect were subsequently plotted to spatially assess species overlap.

## Results and discussion

Parameters used in CLIMEX<sup>®</sup> models for *O. nuchicornis*, *O. taurus*, and *D. gazella* are reported in Table 1. Details on model parameterisation and results of validation steps are discussed separately for each species in the following sections.

We note that our interpretation of these models is necessarily affected by several factors. Two of these are sampling effort and access to the data arising from this effort. To illustrate, we note the lack of collection records for *O. nuchicornis* from Nebraska (“suitable” for establishment) and Iowa (“favourable” for establishment) (Fig. 2). The scarab fauna of Nebraska has been extensively surveyed over many years and the results are readily available (Ratcliffe and Paulsen 2008). Hence, it seems likely that the species is indeed absent in the state; at least for now (see next section). In contrast, the dung beetle fauna of Iowa has been much less extensively sampled. The main insect collection of Iowa State University has roughly 100 specimens of *Onthophagus*, none of which are identified to species (G. Courtney, Curator of the Iowa State Insect Collection, personal communication). In a survey limited to two counties in the northeast corner of the state, Worthington and Larsen (2010) recovered 109 scarab beetles (12 species) from dung-baited pitfall traps; none of these were *O. nuchicornis*. However, *O. nuchicornis* does occur in an adjacent county in Wisconsin (Kriska and Young 2002) and also to the south in Missouri (MacRae and Penn 2001). This gives reason to suspect that *O. nuchicornis* is present, but undetected, in Iowa.

**Table 1.** Values for parameter settings for the CLIMEX<sup>®</sup> model projecting *Digitonthophagus gazelle* (*Dg*), *Onthophagus nuchicornis* (*On*), and *Onthophagus taurus* (*Ot*) distribution and abundance in North America.

Index	Parameter	Description	<i>Dg</i>	<i>On</i>	<i>Ot</i>
CLIMEX <sup>®</sup> growth parameters					
Temperature (°C)	DV0	Limiting low temperature	18*	14*	14*
	DV1	Lower optimal temperature	25	18	16
	DV2	Upper optimal temperature	30*	22*	23*
Moisture	DV3	Limiting high temperature	34	32	32
	SM0	Limiting low soil moisture	0.05	0.1	0.1
	SM1	Lower optimal soil moisture	0.35	0.2	0.35
	SM2	Upper optimal soil moisture	1	0.8	0.8
Diapause	SM3	Limiting high soil moisture	2	1.2	1.2
	DPD0	Diapause induction day length		16	
	DPT0	Diapause induction temperature		7	
	DPT1	Diapause termination temperature		6	
	DPD	Diapause development days		180	
	DPSW	Diapause indicator for winter diapause		0	
CLIMEX <sup>®</sup> stress parameters					
Cold stress	TTCS	Cold stress threshold	1	−15	−10
	THCS	Cold stress temperature rate	−0.0008	−0.0007	−0.0009
Heat stress	TTHS	Heat stress temperature threshold	38	32	33
	THHS	Heat stress temperature rate	0.0005	0.4	0.0075
Dry stress	SMDS	Dry stress threshold	0.04	0.075	0.075
	HDS	Dry stress rate	−0.001	−0.005	−0.005
Wet stress	SMWS	Wet stress threshold	3	2	1.35
	HWS	Wet stress rate	0.0004	0.01	0.1
	MTS	Model step time	7	7	7
Degree-days above DVHS	DVCS		32	34	34
	DV4		100	100	100
	MTS		7	7	7
Degree-days per generation	PDD	Minimum degree days above DV0 to complete one generation	209*	230*	210*

\* Based on requirements reported in Floate *et al.* (2015).

A third factor is the accuracy of species determination. In North America, there are no species that might be mistaken for *O. nuchicornis*, *O. taurus*, or *D. gazella*. In Europe, however, *O. taurus* frequently has been mistaken for *Onthophagus illyricus* (Scopoli); *O. nuchicornis* co-occurs and is morphologically similar to *Onthophagus fracticornis* (Preyssler) and *Onthophagus similis* (Scriba). Thus, species misidentifications have the potential to confound model validation (Ljungberg 2002).

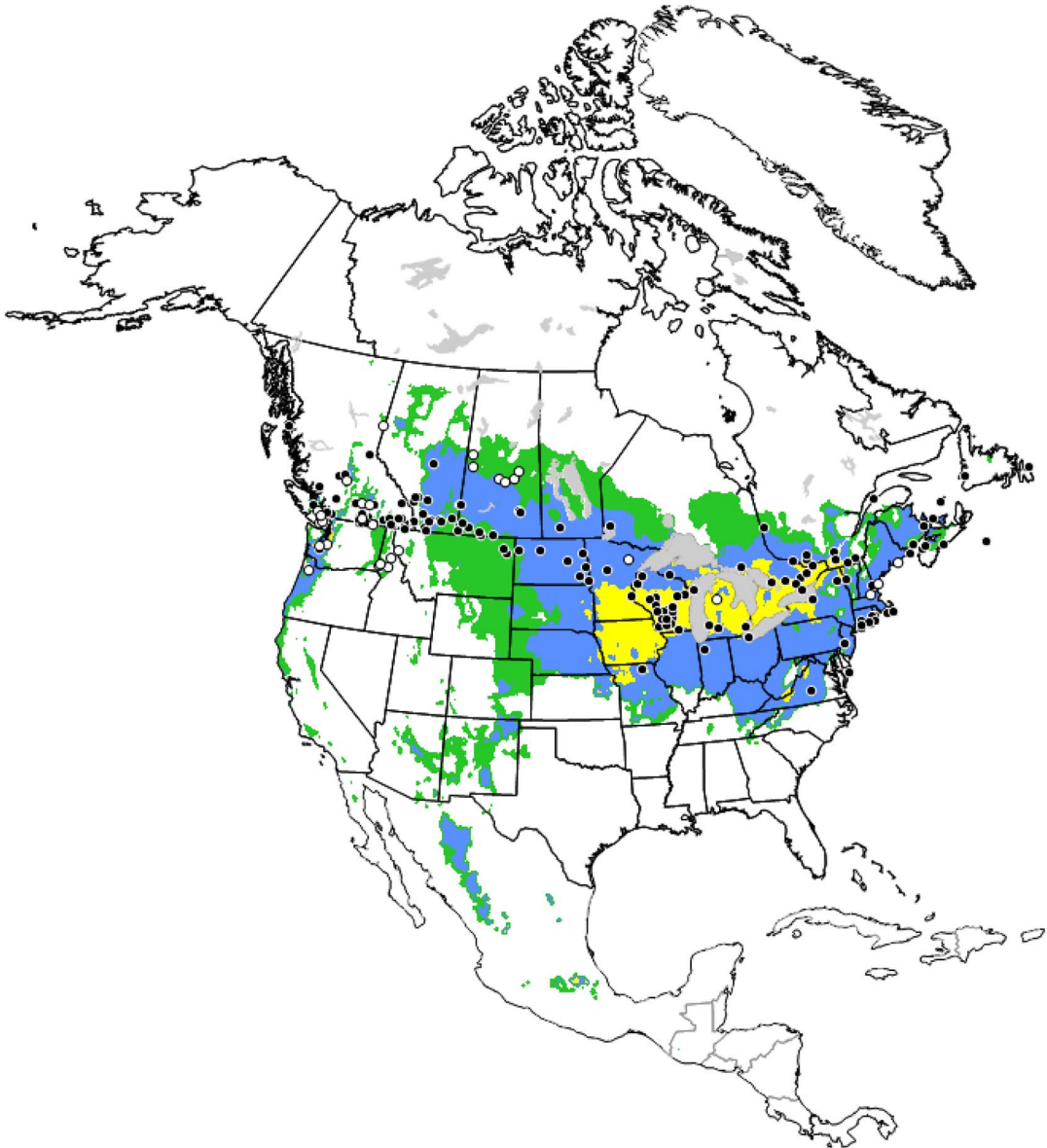
Another factor is our use of air temperatures for model development, rather than soil temperatures (discussed in Floate *et al.* 2015). Immature development and overwintering of the three species typically occurs at soil depths of 10–15 cm or more, varying with soil type and soil moisture (Fincher and Hunter 1989; Tyndale-Biscoe 1990;

Macagno *et al.* 2016). In winter, soil temperatures are warmer than air temperatures, increasingly so with depth and snow cover. Thus, CLIMEX<sup>®</sup> models using air temperatures may underestimate the likelihood of overwintering survival, particularly at the northernmost extent of the distribution of a species. In summer, soil temperatures are cooler than air temperatures. Thus, insects developing underground accumulate fewer degree-days than might be expected based on air temperatures. Hence, use of air temperatures for CLIMEX<sup>®</sup> models may overestimate the predicted number of generations per year (Floate *et al.* 2015).

A further factor is the false assumption that all populations of a given species are physiologically the same. For example, Floate *et al.* (2015) obtained developmental data for *O. taurus* from



**Fig. 2.** Ecoclimatic index values predicting conditions for establishment of *Onthophagus nuchicornis* in North America; white (unfavourable, 0–2); green (marginal, 2–10); blue (suitable, 10–20); yellow (favourable, 20–30). Black circles identify localities of species occurrence used to calculate ecoclimatic index values for North America and elsewhere in the world; white circles are localities identified after model development and assess model rigour.



a single source population. However, results based on other populations might differ. Consider the results reported by Macagno *et al.* (2016) for populations of *O. taurus* from Australia, Italy, and the United States of America. When reared under identical conditions at the same time, each

population displayed significant differences in the soil depth to which they buried brood balls. Similarly, Silva *et al.* (2016) provide evidence that populations of *O. taurus* in eastern North America have expanded into colder and more humid regions beyond what would be expected

based on observations for populations of *O. taurus* in western North America. Hence, for a given species, a biotype may establish in a region predicted to be unsuitable for establishment, based on model parameters obtained for a different biotype.

### ***Onthophagus nuchicornis***

**Model parameterisation.** Model parameters (Table 1) were selected based on developmental requirements and to match reported localities of the species in North America. Temperature parameter DV0 and degree-day requirements per generation (PDD) were set at 14 °C and 230, respectively, based on data in Floate *et al.* (2015). Because their study indicated an upper optimal threshold temperature (DV2) for successful egg-to-adult development of between 22 and 24 °C, the model parameter was set at 22 °C. Because they reported that *O. nuchicornis* was unable to complete development at 32 °C, the limiting high temperature (DV3) was set at 32 °C. Cold stress limited distribution to the north. Floate *et al.* (2015) reported *O. nuchicornis* to have an obligate diapause. Hence, diapause was parameterised to limit southern distributions. Soil moisture parameters were set to permit distribution over a wide range of soil moistures; *e.g.*, the Canadian Maritime and Prairie Provinces, and the Pacific Northwest region of the United States of America.

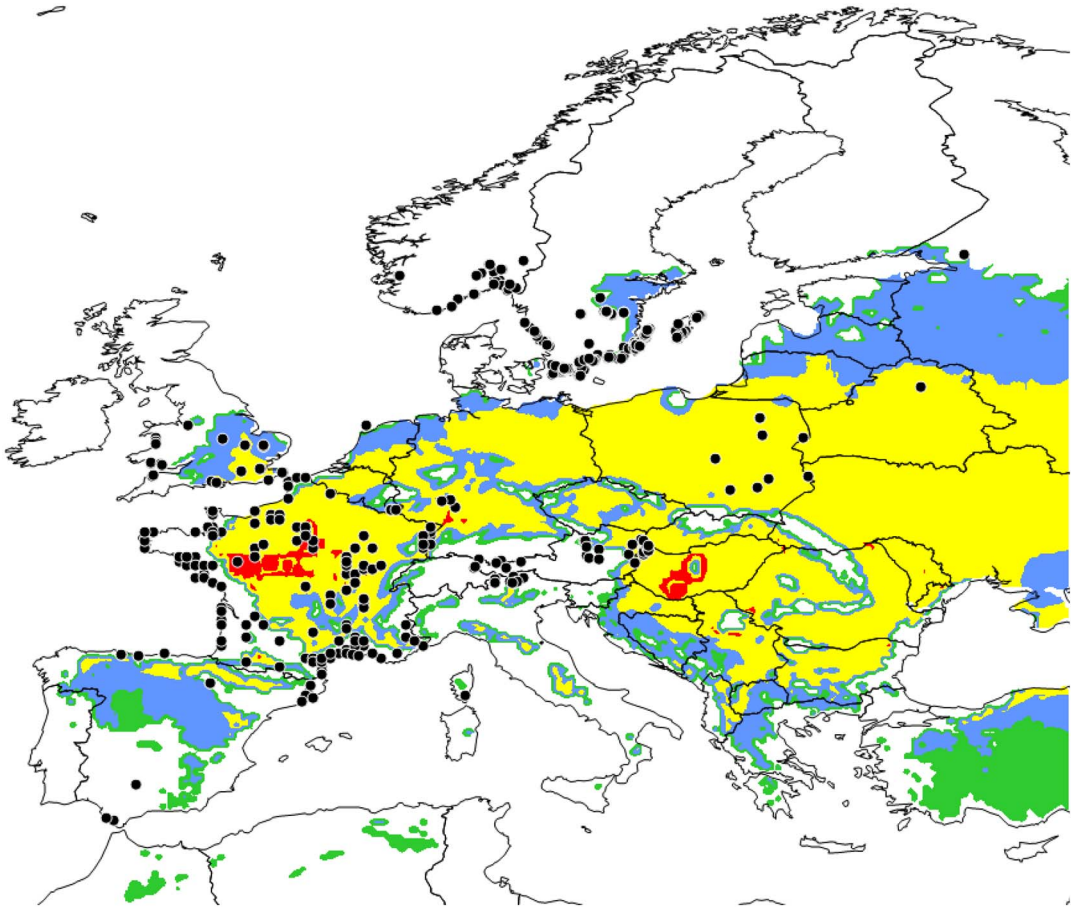
Model output corresponds with the reported transcontinental distribution of *O. nuchicornis* in North America with two apparent discrepancies (Fig. 2). First, the species is common in southern British Columbia where ecoclimatic index values predict conditions to be generally “unfavourable” (EI = 0–2) for establishment. However, these values correspond to high elevation sites in the Rocky Mountains. Collection localities for *O. nuchicornis* correspond to valleys, for which conditions are predicted to be “marginal” (EI = 2–10) or “suitable” (EI = 10–20; *e.g.*, Okanagan Valley). This is not readily apparent from the map. Second, there are essentially no reports of *O. nuchicornis* across broad regions of the central United States of America identified by EI values as “suitable” or “favourable” (EI = 20–30). This discrepancy may indicate that the model over-extrapolates the southernmost extent of the distribution of this species. Potentially, however, it may be that *O. nuchicornis* has yet to establish in these regions. The species has only colonised

the northern Great Plains in the past 60 years and may still be expanding its distribution southward. The earliest reports for the species from Alberta, Saskatchewan, North Dakota, and South Dakota are 1961, 1977, 1981, and the 1990s, respectively (Floate and Gill 1998; Tinerella and Fauske 1999). Thus, the distribution of the species may not have yet reached its maximum southern limits. We also cannot exclude the possibility that *O. nuchicornis* is present in parts of the region, but not yet detected (see previous section). We note that the report for South Dakota (Tinerella and Fauske 1999) is identified as a personal communication with no collection localities provided. For this reason, localities for *O. nuchicornis* in South Dakota are not indicated in Figure 2.

**Model validation.** The model generally is supported with: (i) reported distributions of *O. nuchicornis* outside of North America, (ii) published information on relative abundance and seasonality and number of generations, and (iii) new data obtained since models were completed in December 2010.

(i) *Distributions outside of North America.* The model output agrees with reported distributions of *O. nuchicornis* across continental Europe (Fig. 3), including a recent report of the species from Samsun province on the Black Sea coast in northern Turkey (Sullivan *et al.* 2016). The model predicts the absence of *O. nuchicornis* in Portugal and Morocco, and its limited occurrence in Spain, primarily in the northern parts of the country. These predictions generally fit well with reported localities for this species in the region (see Supplementary material for Dortel *et al.* 2013). The model does not correspond well with distribution records from more northern and western localities (Norway, Sweden; western United Kingdom) or for coastal regions of France and Spain. Variance with reports from Norway and Sweden reflect low temperature index values, which are based on the parameterised value for DVO (14 °C) (Floate *et al.* 2015). The value used for *O. nuchicornis* is higher than that used in previous models for species endemic to northern Europe; *e.g.*, *Peristenus digoneutis* Loan (Hymenoptera: Braconidae) = 13 °C (Olfert *et al.* 2016a); *Contarinia nasturtii* (Kieffer) (Diptera: Cecidomyiidae) = 10 °C (Olfert *et al.* 2006); *Meligethes viridescens* (Fabricius) (Coleoptera: Nitidulidae) = 7 °C (Mason *et al.* 2003); *Sitona lineatus*

**Fig. 3.** Ecoclimatic index values predicting conditions for establishment of *Onthophagus nuchicornis* in Europe; white (unfavourable, 0–2); green (marginal, 2–10); blue (suitable, 10–20); yellow (favourable, 20–30); red (very favourable, > 30). Black circles identify reported localities of occurrence and assess the rigour of ecoclimatic index predictions developed using North American localities.



Linnaeus (Coleoptera: Curculionidae) = 7 °C (Olfert *et al.* 2012a). Variance with predicted distributions in the United Kingdom, France, and Spain reflects a diapause index = 0 for these regions, due to insufficient day lengths or cool temperatures (required to initiate and terminate diapause induction). The discrepancy of the model based on North American distributions, with reported distributions in Europe potentially may reflect differences in conditions for diapause induction and termination between populations on the two continents.

We caution that historical collection localities may not reflect the current distribution of a species. For example, the northern distribution of

*O. nuchicornis* appears to be contracting in Europe. Coope (2000) provides evidence that the species was once common in parts of the British Isles about 120 000 years ago and concludes that the species is now likely extirpated. Records in the Global Biodiversity Information Facility (2016) identify recovery of specimens in southern United Kingdom within the past 10 years, but nothing to indicate that the species is abundant. Skidmore (1991) reports the species to have a “very local” distribution in southern United Kingdom. Information in Bistrom *et al.* (1991), confirmed by T. Roslin (University of Helsinki, Finland, personal communication) indicates that *O. nuchicornis* was once widely scattered in southern regions of

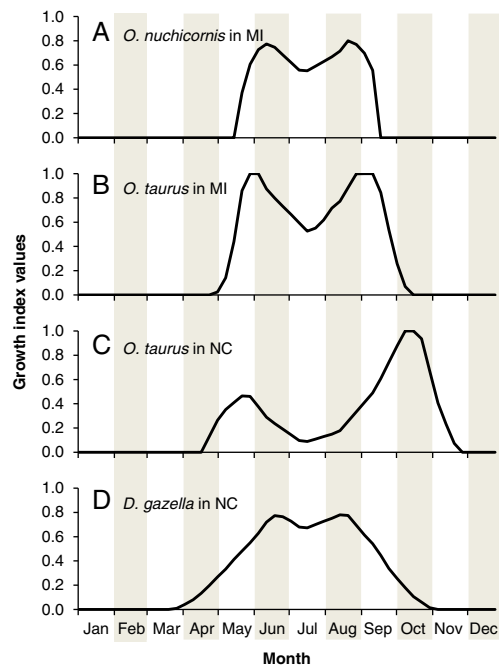


Finland, but has not been collected in the country since the 1950s and is likely extirpated. The two records of *O. nuchicornis* on the southern coast of Spain derive from specimens collected in 1895 (Lobo and Martín-Piera 1991). These distributional changes have been attributed to loss of habitat (Bistrom *et al.* 1991) and climate change. For example, mean July temperatures in southern United Kingdom are estimated to have cooled about 4 °C since the early Eemian interglacial period; ~130 000 to 115 000 years before present (Coope 2000). Predicted changes of dung beetle distributions in western Europe associated with climate change are examined in detail in Dortel *et al.* (2013).

(ii) *Relative abundance, seasonal activity, and number of generations.* The best information on the regional abundance and activity of *O. nuchicornis* in North America derives from surveys in southern Alberta (Floate and Gill 1998; Floate and Kadiri 2013; Kadiri *et al.* 2014) and Michigan (Rounds and Floate 2012). In both regions, *O. nuchicornis* is a dominant member of the local dung beetle community and comprises about 40% of the total trap catch. The former and latter regions are predicted to be “suitable” and “favourable” for establishment, respectively (Fig. 2). The growth index calculated for *O. nuchicornis* in Michigan identifies temperature and moisture conditions favourable for population growth from mid-May until mid-September (Fig. 4A), which corresponds to observed patterns of seasonal activity in both regions. Overwintered adults emerge in May to feed and lay eggs, which develop into adults that emerge in autumn. The autumn peak of adult activity occurs in August in Michigan (Rounds and Floate 2012), and a few weeks later (mid-August through mid-September) in Alberta (Floate and Gill 1998; Floate and Kadiri 2013). The presence of one generation per year is consistent with an obligate diapause requirement for this species.

(iii) *New data.* New data confirms the presence of *O. nuchicornis* in predicted regions of occurrence (Fig. 2) from whence it was not previously reported. The model identifies a region along the coast extending from southern British Columbia to southern Oregon as being “suitable” for establishment. In 2013, we received a specimen collected in late March from Carlton County, Oregon. To our knowledge, this is the first report

**Fig. 4.** Growth index models: **A**, *Onthophagus nuchicornis* (Michigan); **B**, *Onthophagus taurus* (Michigan); **C**, *Onthophagus taurus* (North Carolina); **D**, *Digitonthophagus gazella* (North Carolina). Growth index values range from 0.0 (not suited for population growth) to 1.0 (optimal for population growth). Michigan, MI; North Carolina, NC.



of *O. nuchicornis* in Oregon and extends its reported southern coastal distribution by about 180 km. The model also identifies the aspen parkland region of central Canada as “suitable” or “marginal” for establishment. We tested this prediction by operating dung-baited pitfall traps in the summers of 2012 through 2015. These traps recovered small numbers of *O. nuchicornis* in British Columbia near the community of Tomslake, and in Saskatchewan, near the communities of Duck Lake, Melfort, Nipawin, Peerless, St. Walburg, and Tway (Supplementary Table S1). The collection at Tomslake extends the northernmost reported distribution in North America by about 230 km. We recently became aware of a report of *O. nuchicornis* being released on Hawaii, United States of America where it failed to establish (Anonymous 1910). This finding is consistent with the model’s parameters of this species requiring a cold period for an obligate diapause.

### *Onthophagus taurus*

**Model parameterisation.** Model parameters (Table 1) were selected based on developmental requirements reported in Floate *et al.* (2015) and to match the North American distribution of the species. Temperature parameter DV0 and degree-day requirements per generation (PDD) were set at 14 °C and 210, respectively. Because an upper optimal threshold temperature of about 24 °C was indicated, DV2 was set at 23 °C. Because adult emergence declined at the highest temperature tested (32 °C), DV3 was set at 32 °C. Because this species does not have an obligate diapause, parameters to compute a diapause index were not used.

The model output corresponds with reported localities for *O. taurus* across North America; *i.e.*, states in the eastern and southeastern United States of America, and in California (Hoebeke and Beucke, 1997) (Fig. 5). Because of cold stress, the species is predicted not to establish in most of Canada with the exception of southern Ontario and Québec. These regions are identified as “suitable” (EI = 10–20) or “favourable” (EI = 20–30) for establishment. EI values identify southern Alberta as “marginal” or “suitable”, which reflect results reported in Floate *et al.* (2015). They showed that although *O. taurus* could complete development and overwinter in southern Alberta, high overwintering mortality was expected to prevent population establishment. The model predicts that heat stress is likely to prevent population establishment in parts of Texas. During the growing season, low precipitation (*i.e.*, a low moisture index) is expected to prevent populations from establishing in parts of Texas, New Mexico, Colorado, Wyoming, and Montana.

**Model validation.** The model generally is supported with: (i) reported distributions of *O. taurus* outside of North America, (ii) published information on relative abundance and seasonality and number of generations, and (iii) new data obtained since models were completed in December 2010.

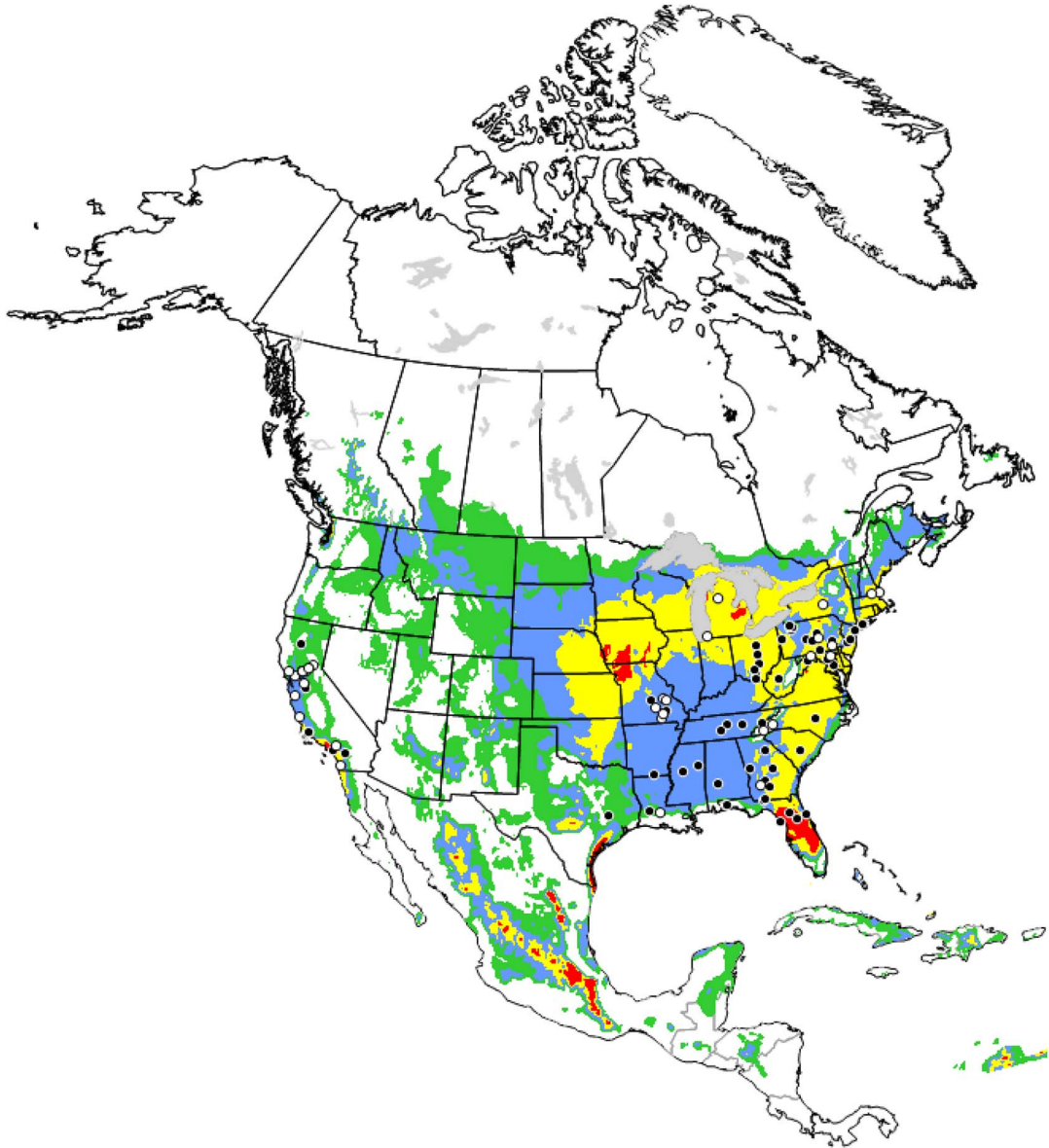
(i) *Distributions outside of North America.* The model output agrees with reported localities for *O. taurus* across western, central, and northern Europe with some exceptions (Fig. 6). One discrepancy is for southern United Kingdom,

where conditions are predicted to be very favourable (EI > 30) for establishment. The species has been reported in the United Kingdom, but not for more than 140 years (Skidmore 1991). It seems unlikely that this distinctive species would go unnoticed for such a long period of time. We speculate that it has been locally extirpated, perhaps as a result of urbanisation and the loss of pastoral habitats. The model does not agree with reports of *O. taurus* from eastern Switzerland and northern Austria, where the species is not expected to establish due to excessive soil moisture (*i.e.*, MI = 0). Conditions on the east coast of Sweden are predicted to be “favourable” for establishment, but the only report of *O. taurus* from that country is from the Island of Gotland (Supplementary Table S1). Cold stress does not limit distribution in Europe.

Releases of *O. taurus* were made in different states of Australia between 1975 and 1984 as part of a national programme to accelerate the degradation of cattle dung. The species is now established in New South Wales, South Australia, Tasmania, Western Australia, and Victoria (Tyndale-Biscoe 1990). The model predicts favourable conditions for establishment in each of these regions (Fig. 7).

(ii) *Relative abundance, seasonal activity, and number of generations.* Surveys that provide insight into the relative abundance and seasonal activity of *O. taurus* in North America have been performed in Florida (Kaufman and Wood 2012) and North Carolina (Bertone *et al.* 2005; Lastro 2006). In north-central Florida, conditions are predicted to be favourable or very favourable for establishment. This prediction accords well with a survey in the region that identified *O. taurus* to be the fifth most common of 39 species recovered (Kaufman and Wood 2012). The model identifies conditions to be favourable for establishment in North Carolina, where *O. taurus* is common and adults are active from March until November; potentially allowing for four to five generations per year (Bertone *et al.* 2005). This observed period of activity corresponds with that predicted using growth index calculations, which show conditions to be favourable for population growth from April through November (Fig. 4C). Using degree-day requirements reported for *O. taurus* (Floate *et al.* 2015), model output predicts three to seven generations per year in North Carolina. However, two to three generations seems

**Fig. 5.** Ecoclimatic index values predicting conditions for establishment of *Onthophagus taurus* in North America; white (unfavourable, 0–2); green (marginal, 2–10); blue (suitable, 10–20); yellow (favourable, 20–30); red (very favourable, > 30). Black circles identify localities of species occurrence used to calculate ecoclimatic index values for North America and elsewhere in the world; white circles are localities identified after model development and assess model rigour.

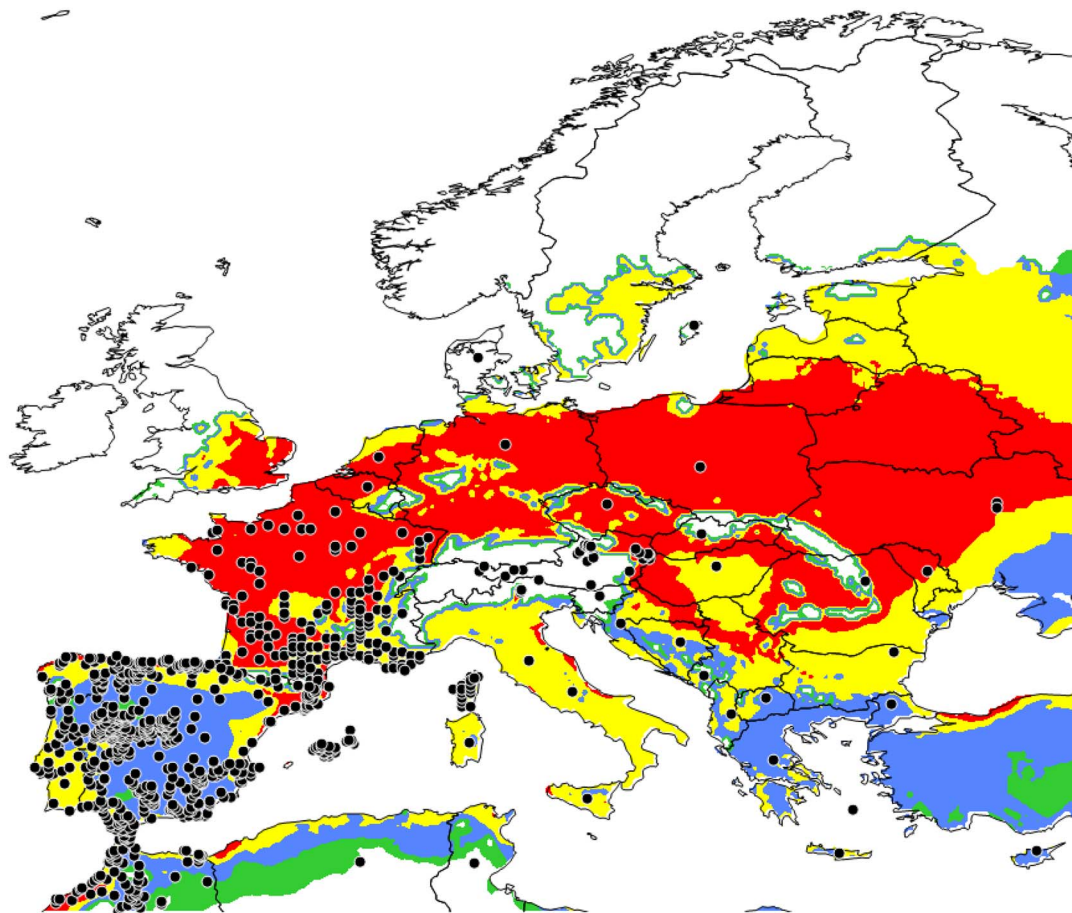


more likely. The model output reflects use of air temperatures rather than soil temperatures, which are cooler during summer months. The model also does not incorporate a period of pre-ovipositional development between generations. In southern Australia, *O. taurus* has a generation time of six to

eight weeks during summer months and overwinters as larvae (Tyndale-Biscoe 1990).

(iii) *New data.* The model predicts conditions to be favourable or very favourable for establishment of *O. taurus* in the United States of America for states bordering the Great Lakes (Fig. 5).

**Fig. 6.** Ecoclimatic index values predicting conditions for establishment of *Onthophagus taurus* in Europe; white (unfavourable, 0–2); green (marginal, 2–10); blue (suitable, 10–20); yellow (favourable, 20–30); red (very favourable, > 30). Black circles identify reported localities of occurrence and assess the rigour of ecoclimatic index predictions developed using North American localities.

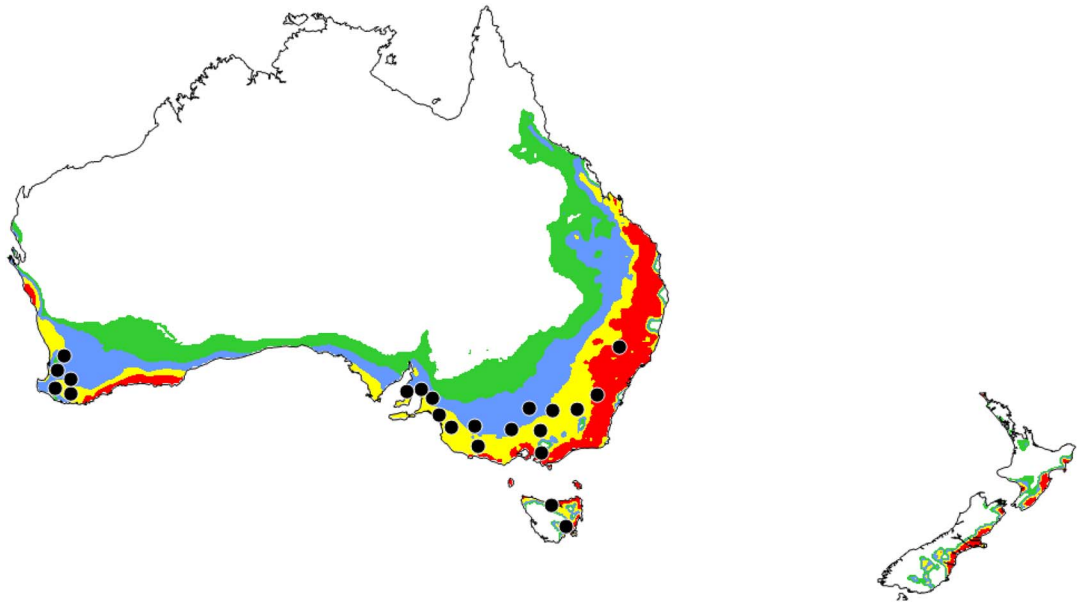


Before 2011, the species was not known to the authors to occur in Michigan. A survey in 2011 detected a resident population of *O. taurus* in the northern lower peninsula of Michigan (Rounds and Floate 2012). This represents the furthest northwestern occurrence of the species in North America to date. Subsequent examination of photographs on bugguide.net identifies additional localities for *O. taurus* in the Great Lakes region (Supplementary Table S1). The model predicts favourable conditions for establishment in southern Ontario. We are unaware of any Canadian records for this species, but expect reports for southern Ontario to be forthcoming.

The growth index calculated for *O. taurus* in Michigan identifies conditions favourable for population growth from May through September (Fig. 4B). This prediction corresponds to the observed pattern of seasonal activity reported for the state by Rounds and Floate (2012). Based on degree-day requirements for *O. taurus* (Floate *et al.* 2015), model output predicts two to three generations. As mentioned previously, model output is based on air temperature and does not incorporate a period for pre-ovipositional development. Hence, one generation per year seems more likely. The peak recovery of adults in August reported by Rounds and Floate (2012) is



**Fig. 7.** Ecoclimatic index values predicting conditions for establishment of *Onthophagus taurus* in Australia and New Zealand; white (unfavourable, 0–2); green (marginal, 2–10); blue (suitable, 10–20); yellow (favourable, 20–30); red (very favourable, > 30). Black circles identify reported localities of occurrence and assess the rigour of ecoclimatic index predictions developed using North American localities.



therefore attributed to the emergence of the  $F_1$  generation developing from eggs laid in spring.

As part of a national programme, releases of *O. taurus* began in 2013 at selected sites on the North Island of New Zealand. Small numbers have since been recovered at these sites (S. Forgie, Dung Beetle Innovations, Auckland, New Zealand, personal communication), coinciding with predictions for model establishment (Fig. 7).

### ***Digitonthophagus gazella***

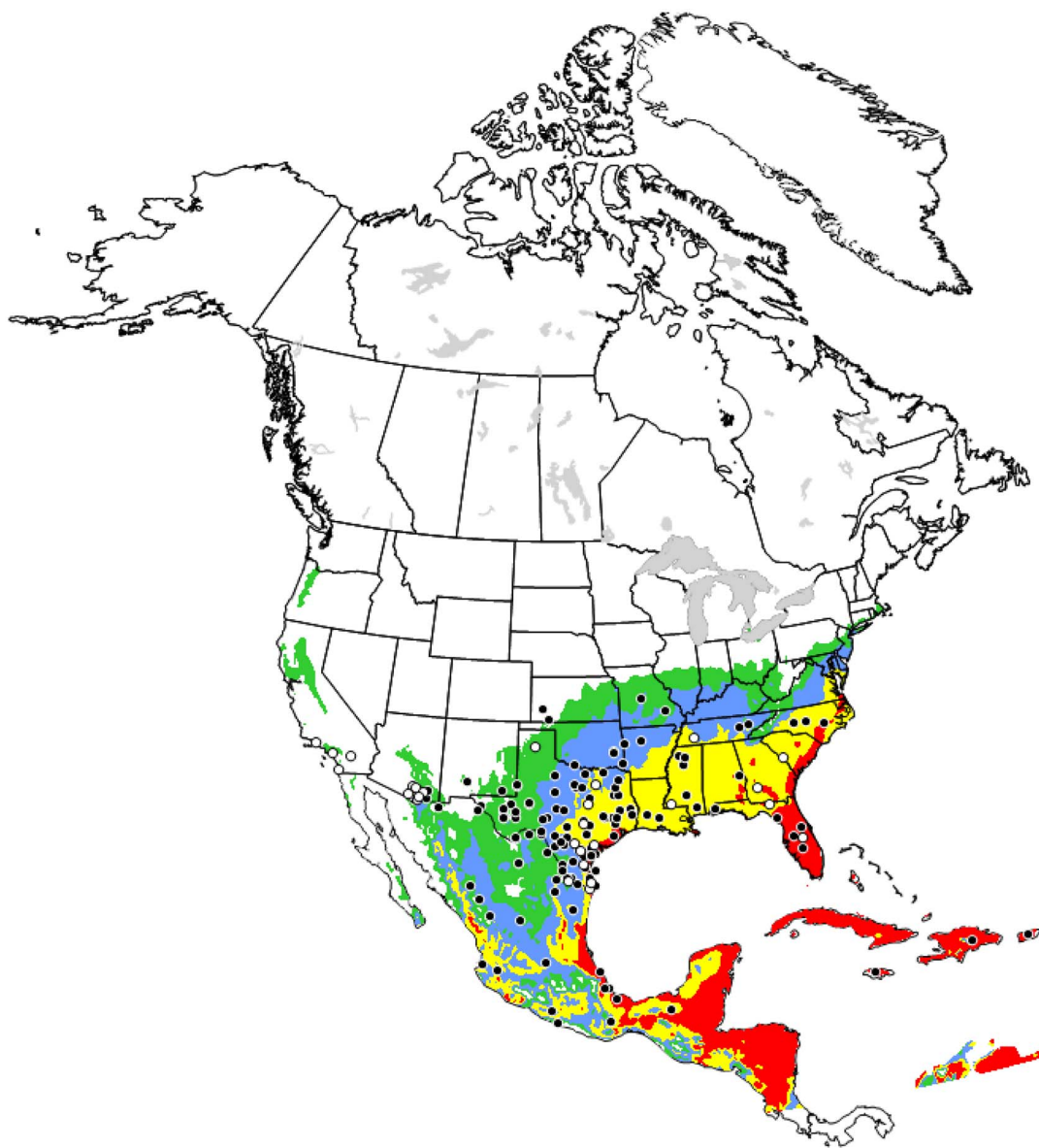
**Model parameterisation.** Model parameters (Table 1) were selected based on developmental requirements reported in Floate *et al.* (2015) and to match reported localities of the species in North America. Temperature parameter DV0 and degree-day requirements per generation (PDD) were set at 18 °C and 209, respectively. Results in Floate *et al.* (2015) indicated a lower optimal temperature (DV1) of between 24 °C and 26 °C; hence, DV1 was set at 25 °C. Also based on results in Floate *et al.* (2015), the upper optimal threshold temperature (DV2) was set at 30 °C. The limiting high temperature (DV3) was set at 34 °C, given that adult emergence

appeared to decline between 30 °C and 32 °C, and no data were available for 34 °C (Floate *et al.* 2015). The lower soil moisture threshold (SM0) was set very low in order to permit the species to occur in central Australia. Cold stress was used to limit distribution of the species across the northern United States of America.

Model predictions match the reported localities for *D. gazella* across North America, which are mainly in southeastern North America, including the Gulf Coast and Mexico (Hoebke and Beucke 1997) (Fig. 8). There are fewer reports for southern regions of California, Arizona, and New Mexico. In parts of Texas, heat stress is predicted to limit species distribution. During the growing season, low precipitation (low MI) is predicted to limit potential growth in Texas, New Mexico, Colorado, Wyoming, and Montana.

**Model validation.** (i) *Distributions outside of North America.* Génier and Moretto (2017) recently identified *D. gazella* as one of 16 species that form a species complex. They reported that the distribution of *D. gazella* in Africa extends from South Africa northward to Uganda, and

**Fig. 8.** Ecoclimatic index values predicting conditions for establishment of *Digitonthophagus gazella* in North America; white (unfavourable, 0–2); green (marginal, 2–10); blue (suitable, 10–20); yellow (favourable, 20–30); red (very favourable, > 30). Black circles identify localities of species occurrence used to calculate ecoclimatic index values for North America and elsewhere in the world; white circles are localities identified after model development and assess model rigour.

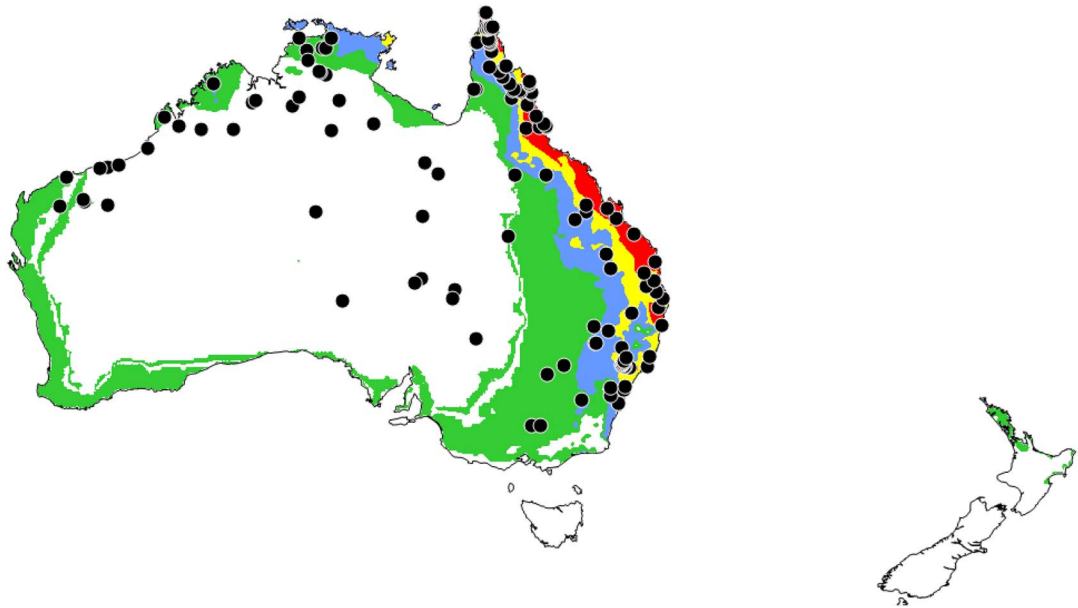


includes Madagascar. Model predictions are consistent with this finding. *Digitonthophagus gazella* also has been reported from Saudi Arabia, Oman, Ethiopia, and Nigeria (Supplementary Table S1), and from localities in Asia Minor, India, and Sri Lanka (Balthasar 1963 – cited in Hoebeke and

Beucke 1997). Results of Génier and Moretto (2017), however, indicate that these latter reports are likely not for *D. gazella*, but for other members of this species complex.

Model predictions generally coincide with reported localities for *D. gazella* in Australia and

**Fig. 9.** Ecoclimatic index values predicting conditions for establishment of *Digitonthophagus gazella* in Australia and New Zealand; white (unfavourable, 0–2); green (marginal, 2–10); blue (suitable, 10–20); yellow (favourable, 20–30); red (very favourable, > 30). Black circles identify reported localities of occurrence and assess the rigour of ecoclimatic index predictions developed using North American localities.



Hawaii. In Australia, *D. gazella* is well documented from coastal regions, particularly along the east coast where conditions are predicted to range from marginal to very favourable for establishment (Fig. 9). However, there are collection localities further inland in regions where *D. gazella* is predicted not to establish. This anomaly merits further investigation. These populations may be genetically distinct from populations elsewhere, or local conditions may permit their persistence in regions otherwise identified as unfavourable. The model also predicts conditions for establishment of *D. gazella* on the Hawaiian Islands as being generally favourable or very favourable (data not shown). Releases of the species were made in Hawaii in 1957 and again in 1973 (Markin and Yoshioka 1998). It is now among the most common dung beetles species on Oahu (Harris *et al.* 1982) and also on Maui (K.D.F., personal observation).

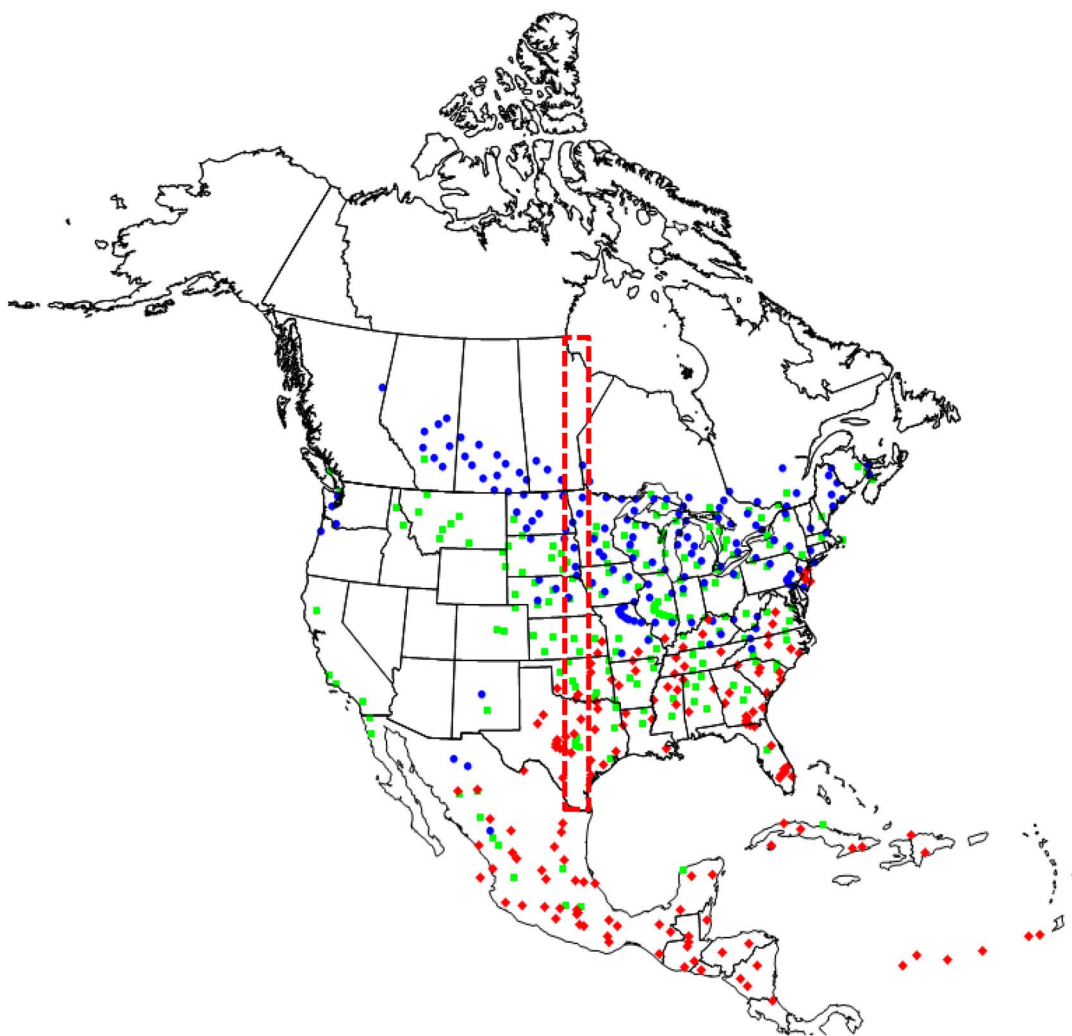
Model predictions also reflect the establishment of *D. gazella* in Mexico (Rivera-Cervantes and Garcia-Real 1991; Montes de Oca and Halffter 1998), the West Indies (Ivie and Philips 2008) (Fig. 8), and in numerous localities in Central and

South America (Fig. 8, see summary in (Noriega *et al.* 2010).

(ii) *Relative abundance, seasonal activity, and number of generations.* Model predictions generally coincide with the abundance of this species where such data are available (Fig. 8). *Digitonthophagus gazella* is a common member of the dung beetle community in the West Indies (Ivie and Philips 2008), southern Texas (Howden and Scholtz 1986), north-central Florida (Kaufman and Wood 2012), and parts of North Carolina (Bertone *et al.* 2005). In each of these regions, the model predicts conditions for establishment to be favourable or very favourable. Based on its short period of seasonal activity in North Carolina, Bertone *et al.* (2005) concluded that establishment of *D. gazella* in more northerly regions along the Atlantic coast was unlikely. The model is in accordance with this expectation (Fig. 8).

An apparent exception emphasises the reliance of the model on climatic parameters that may not reflect local conditions altered by human activity. Conditions in the largely rainfall-free Coachella Valley of southeastern California region are predicted to be marginal for establishment of

**Fig. 10.** Ecoclimatic index values predicting conditions for establishment for *Digitonthophagus gazella* (red), *Onthophagus nuchicornis* (blue), and *Onthophagus taurus* (green) ( $EI > 9.9$ ). The rectangle (red dashed line) delineates the area that was used for Fig. 11.



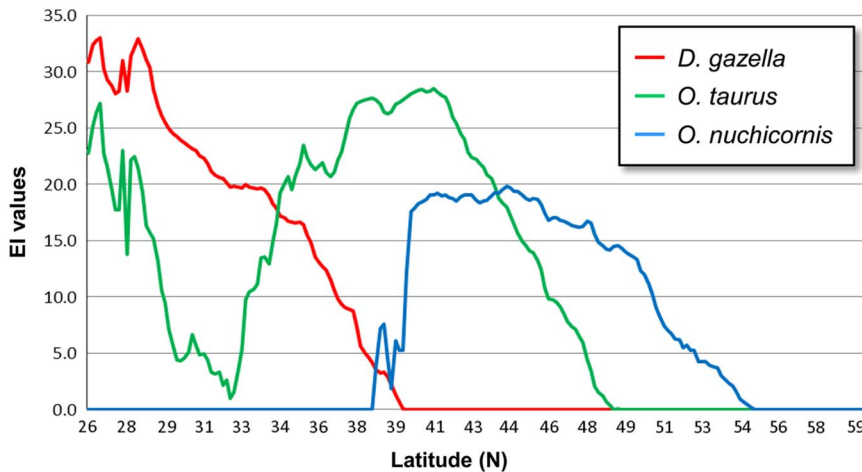
*D. gazella* (Fig. 8), but high populations have established from releases made in 1975 (Legner 1986; Legner and Warkentin 1991). This discrepancy is explained by the reliance of the region on irrigation to maintain cattle pastures. During regular 21-day cycles of irrigation, adults usually colonise dung pats within an hour of deposition. During periods outside of this irrigation regime, adults may remain dormant in the soil for up to six months until the irrigation schedule begins anew (Legner and Warkentin 1991). *Digitonthophagus gazella* also has been reported to colonise dog faeces in urban areas (Cave 2005). Thus, cattle

need not be present for *D. gazella* to establish in localised pockets where irrigation in urban or agricultural settings provides sufficient soil moisture. Irrigation also may explain the aforementioned occurrence of *D. gazella* at sites in the interior of Australia, where conditions are predicted to be unfavourable for establishment (Fig. 9).

Model output corresponds with periods of seasonal activity reported in field surveys. Adults are active in North Carolina from early June through late October, which potentially allows time for three to four generations per year (Bertone *et al.* 2005). Growth index calculations



**Fig. 11.** Average ecoclimatic index (EI) values for *Digitonthophagus gazella*, *Onthophagus nuchicornis*, and *Onthophagus taurus* between 26°N and 60°N (averaged between 96°W and 98°W; see Fig. 10). Ecoclimatic index values of 10–20, 20–30, and > 30, respectively, are considered to be suitable, favourable, and very favourable for establishment.



predict conditions to be favourable for population growth from April to early November (Fig. 4D). Based on degree-day requirements for *D. gazella* (Floate *et al.* 2015), model output predicts two to three generations per year.

(iii) *New data.* Information for North America obtained since model development reflects previous reports of *D. gazella* from southern regions of California, Arizona, and Texas (Fig. 8). A report from northern Texas is consistent with previous recoveries of the species from southern Kansas on the boundary of a region predicted to be marginal for species establishment. In the absence of further information, *D. gazella* appears to have largely reached the extent of its potential distribution in North America.

As part of a national programme, releases of *D. gazella* began in 2013 at selected sites in New Zealand. Small numbers have since been recovered at these sites (S. Forgie, Dung Beetle Innovations, Auckland, New Zealand, personal communication), coinciding with predictions for model establishment (Fig. 9).

In their recent paper, Génier and Davis (2017) questioned the taxonomy of *D. gazella* (and see Génier and Moretto 2017). They conclude that the correct name of the species that has been widely distributed should be *D. dorcas* (Olivier). However, to conserve the name in prevailing

usage, they have asked the International Commission on Zoological Nomenclature for a ruling on the name *D. gazella* (Fabricius). When a case is submitted to the International Commission on Zoological Nomenclature, the name in prevailing usage is protected until a final decision is reached. Hence, we continue to refer to the species as *D. gazella*.

Excluding *D. gazella*, other members of its species complex are reported to be restricted to the Afrotropical region, the Arabian Peninsula, the eastern portion of the Saharo-Arabian region, and the continental Indomalayan region (Génier and Moretto 2017). However, if other species of this complex do occur beyond these limits, it may help explain discrepancies between observed distributions and our CLIMEX<sup>®</sup> model predictions. For example, the populations in the interior of Australia (Fig. 9), predicted to be unfavourable for establishment of *D. gazella*, may be of a different member of this complex. We note that Duncan *et al.* (2009) used localities reported for *D. gazella* in South Africa to model predicted distributions in Australia. If the South African localities represent a mixture of cryptic species, their findings may need to be reassessed. Studies on the morphology and molecular profiles of *D. gazella* in different regions will help reconcile these matters.

## Species co-occurrence

Predicted regions of species co-occurrence in North America are shown in Figure 10. Results indicate that 19.1% of the continent north of Mexico has a climate rated as “suitable” or better for *D. gazella*. This compares with 21.3 and 27.9% for *O. nuchicornis* and *O. taurus*, respectively.

Comparisons of ecoclimatic index values for the three species within the “belt” transect are shown in Figure 11. Southern Texas is identified as the most favourable region for *D. gazella*, with a steady decline in ecoclimatic index values until reaching 0 at 39.9°N. Thus, the northernmost limit for *D. gazella* is predicted to be the Kansas/Nebraska border. Within this same transect, ecoclimatic index values identify the predicted distribution for *O. nuchicornis* to extend from central Kansas (38.5°N) to central Manitoba (55°N). The region of peak suitability (ecoclimatic index values of 15–20) is predicted to extend from the Kansas/Nebraska border northward to the North Dakota/Manitoba border. Ecoclimatic index values for *O. taurus* exhibit a bimodal peak. The first peak identifies ecoclimatic index values that exceed 25 in southern Texas (26°N) and declining close to 0 in central Texas near Dallas. The decline in ecoclimatic index values reflects a combination of suboptimal moisture and temperature values during July and August. The second peak (ecoclimatic index values >20) corresponds to the region extending from central Oklahoma northward to northern Nebraska; *i.e.*, between 37°N and 42°N. The northernmost occurrence of *O. taurus* is predicted to be the southernmost extent of Manitoba; *i.e.*, 49.1°N. These predicted regions of co-occurrence do not reflect the distribution of these species in western North America where, for example, no overlap is predicted between *O. nuchicornis* and *D. gazella*.

## Conclusions

The CLIMEX<sup>®</sup> models presented here are consistent with the best available information for the distributions of *O. nuchicornis*, *O. taurus*, and *D. gazella* in North America. Results for the first two species indicate that they are likely to establish, or already have established, in regions where they are not yet reported. For *O. nuchicornis*, this includes the central plains of the United States of America south from North Dakota to Nebraska, and east from Nebraska to the Atlantic Coast (Fig. 2).

For *O. taurus*, this includes the region north from Oklahoma into South Dakota, and west from Missouri into Colorado (Fig. 5). If not already present in these regions, results of the CLIMEX<sup>®</sup> models can be used to optimise the success of redistribution programmes for these species to accelerate dung degradation. Any such programmes, however, will need to assess the risk to native species of dung beetles before initiation. *Digitonthophagus gazella* appears to have largely reached its predicted North American distribution.

## Acknowledgements

For information on collection localities in Oregon, California, and Iowa, the authors thank Anton Clifford (Bailey Nurseries, Carleton, Oregon), Larry Bezark, and Gregory Courtney. For information on collection localities outside of North America, the authors thank Giuseppe Carpaneto, Shaun Forgie, Andrey Frolov, Dennis Keith, Jason Mate, Hong Thai Pham, Thomas Roslin, and Stefano Ziani for their personal communications. Debbie Nordstrom provided assistance with generation of CLIMEX<sup>®</sup> models. The authors particularly thank Arlen Benn, Shelby Dufton, Nancy Melnychuk, and Jennifer Otani for operating dung-baited pitfall traps in British Columbia, Alberta, and Saskatchewan. They also thank the many individuals who indirectly provided collection localities either by posting photographs online (*e.g.*, BugGuide) or by entering this information into freely accessible online databases (*e.g.*, Global Biodiversity Information Facility, Jorge Lobo – [www.biogeografia.org/biogeografia/index.php/dung-beetles](http://www.biogeografia.org/biogeografia/index.php/dung-beetles)). The authors thank two anonymous reviewers for their insightful comments on an earlier draft of this manuscript. This is Lethbridge Research and Development Centre publication number 38717002.

## Supplementary material

To view supplementary material for this article, please visit <http://dx.doi.org/10.4039/tce.2017.20>

## References

- Anderson, J.R., Merritt, R.W., and Loomis, E.C. 1984. The insect-free cattle dropping and its relationship to increased dung fouling of rangeland pastures. *Journal of Economic Entomology*, **77**: 133–141.

- Andrewartha, H.G. and Birch, L.C. 1954. The distribution and abundance of animals. The University of Chicago Press, Chicago, Illinois, United States of America.
- Anonymous. 1910. Report of the Entomologist. Hawaii Board of Commissioners of Agriculture and Forestry, Division of Forestry, Hawaiian Gazette Company, Honolulu, Hawaii, United States of America.
- Bertone, M., Green, J., Washburn, S., Poore, M., Sorenson, C., and Watson, D.W. 2005. Seasonal activity and species composition of dung beetles (Coleoptera: Scarabaeidae and Geotrupidae) inhabiting cattle pastures in North Carolina. *Annals of the Entomological Society of America*, **98**: 309–321.
- Bianchin, I., Alves, R.G.O., and Koller, W.W. 1998. Efeito de carrapaticidas/inseticidas “pour-on” sobre adultos do besouro coprófago africano *Onthophagus gazella* Fabr. (Coleoptera: Scarabaeidae). *Anais da Sociedade Entomológica do Brasil*, **27**: 275–279.
- Bistrom, O., Silfverberg, H., and Rutanen, I. 1991. Abundance and distribution of coprophilous Histerini (Histeridae) and *Onthophagus* and *Aphodius* (Scarabaeidae) in Finland (Coleoptera). *Entomologica Fennica*, **2**: 53–66.
- Blume, R.R. and Aga, A. 1975. *Onthophagus gazella*: mass rearing and laboratory biology. *Environmental Entomology*, **4**: 735–736.
- Cave, R.D. 2005. Observations of urban dung beetles utilizing dog feces (Coleoptera: Scarabaeidae). *The Coleopterists Bulletin*, **59**: 400–401.
- Coope, G.R. 2000. The climatic significance of coleopteran assemblages from the Eemian deposits in southern England. *Netherlands Journal of Geosciences*, **79**: 257–267.
- Dortel, E., Thuiller, W., Lobo, J.M., Bohbot, H., Lumaret, J.P., and Jay-Robert, P. 2013. Potential effects of climate change on the distribution of Scarabaeidae dung beetles in western Europe. *Journal of Insect Conservation*, **17**: 1059–1070.
- Duncan, R.P., Cassey, P., and Blackburn, T.M. 2009. Do climate envelope models transfer? A manipulative test using dung beetle introductions. *Proceedings of the Royal Society B: Biological Sciences*, **276**: 1449–1457.
- Edwards, P. 2007. Introduced dung beetles in Australia 1967–2007: current status and future directions. Dung Beetles for Landcare Farming Committee, Sinnamon Park, Australia.
- Environmental Protection Authority. 2011. Environmental risk management authority decision: application ERMA200599. Environmental Protection Authority, Wellington, New Zealand.
- Fincher, G.T. 1981. The potential value of dung beetles in pasture ecosystems. *Journal of the Georgia Entomological Society*, **16**: 316–333.
- Fincher, G.T. and Hunter, J.S. 1989. Overwintering studies on *Onthophagus gazella* (F.) and *Onthophagus bonasus* (F.) in two different textural classes of soil in east-central Texas, United States of America. *Southwestern Entomologist*, **14**: 133–138.
- Fincher, G.T., Stewart, T.B., and Hunter, J.S.I. 1983. The 1981 distribution of *Onthophagus gazella* Fabricius from releases in Texas and *Onthophagus taurus* Schreber from an unknown release in Florida (Coleoptera: Scarabaeidae). *The Coleopterists Bulletin*, **37**: 159–163.
- Fincher, G.T. and Woodruff, R.E. 1975. A European dung beetle, *Onthophagus taurus* Schreber, new to the U.S. (Coleoptera: Scarabaeidae). *The Coleopterists Bulletin*, **29**: 349–350.
- Floate, K.D. 2011. Arthropods in cattle dung on Canada's grasslands. In *Arthropods of Canadian grasslands. Volume 2. Inhabitants of a changing landscape*. Edited by K. D. Floate. Biological Survey of Canada, Ottawa, Ontario, Canada. Pp. 71–88.
- Floate, K.D. and Gill, B.D. 1998. Seasonal activity of dung beetles (Coleoptera: Scarabaeidae) associated with cattle dung in southern Alberta and their geographic distribution in Canada. *The Canadian Entomologist*, **130**: 131–151.
- Floate, K.D. and Kadiri, N. 2013. Dung beetles (Coleoptera: Scarabaeidae) associated with cattle dung on native grasslands of southern Alberta, Canada. *The Canadian Entomologist*, **145**: 647–654.
- Floate, K.D., Watson, D.W., Coghlin, P., and Olfert, O. 2015. Degree-day models for development of the dung beetles *Onthophagus nuchicornis*, *O. taurus*, and *Digitonthophagus gazella* (Coleoptera: Scarabaeidae), and the likelihood of *O. taurus* establishment in southern Alberta, Canada. *The Canadian Entomologist*, **147**: 617–627.
- Génier, F. and Davis, A.L.V. 2017. *Digitonthophagus gazella auctorum*: an unfortunate case of mistaken identity for a widely introduced species (Coleoptera: Scarabaeidae: Scarabaeinae: Onthophagini). *Zootaxa*, **4221**: 497–500.
- Génier, F. and Moretto, P. 2017. *Digitonthophagus Balthasar, 1959*: taxonomy, systematics, and morphological phylogeny of the genus revealing an African species complex (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa*, **4248**: 1–110.
- Global Biodiversity Information Facility. 2016. Global Biodiversity Information Facility [online] Available from [www.gbif.org](http://www.gbif.org) [accessed 31 January 2015].
- Harris, R.L., Onaga, K., Blume, R.R., Roth, J.P., and Summerlin, J.W. 1982. Survey of beneficial insects in undisturbed cattle droppings on Oahu, Hawaii. *Proceedings of the Hawaiian Entomological Society*, **24**: 91–95.
- Hoebcke, E.R. and Beucke, K. 1997. Adventive *Onthophagus* (Coleoptera: Scarabaeidae) in North America: geographic ranges, diagnoses, and new distributional records. *Entomological News*, **108**: 345–362.
- Howden, H.F. and Scholtz, C.H. 1986. Changes in a Texas dung beetle community between 1975 and 1985 (Coleoptera: Scarabaeidae, Scarabaeinae). *The Coleopterists Bulletin*, **40**: 313–316.
- Ivie, M.A. and Philips, T.K. 2008. Three new species of *Canthonella* Chapin from Hispaniola, with new records and nomenclatural changes for West Indian dung beetles. *Zootaxa*, **1704**: 1–14.

- Kadiri, N., Lumaret, J.-P., and Floate, K.D. 2014. Functional diversity and seasonal activity of dung beetles (Coleoptera: Scarabaeoidea) on native grasslands in southern Alberta, Canada. *The Canadian Entomologist*, **146**: 291–305.
- Kaufman, P.E. and Wood, L.A. 2012. Indigenous and exotic dung beetles (Coleoptera: Scarabaeidae and Geotrupidae) collected in Florida cattle pastures. *Annals of the Entomological Society of America*, **105**: 225–231.
- Kearney, M. and Porter, W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**: 334–350.
- Kriska, N.A. and Young, D.K. 2002. An annotated checklist of Wisconsin Scarabaeoidea (Coleoptera). *Insecta Mundi*, **16**: 31–48.
- Kriticos, D.J., Maywald, G.F., Yonow, T., Zurcher, E.J., Herrmann, N.I., and Sutherst, R.W. 2015. Exploring the effects of climate on plants, animals and diseases. CLIMEX version 4 – user guide, Commonwealth Scientific and Industrial Research Organisation, Canberra, Australia.
- Kriticos, D.J., Webber, B.L., Leriche, A., Ota, N., Macadam, I., Bathols, J., and Scott, J.K. 2012. CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods in Ecology and Evolution*, **3**: 53–64.
- Lancaster, J.L. and Hunter, J.S. 1978. Introducing dung beetles as an aid in manure disposal and fly control. *Arkansas Farm Research*, **27**: 4.
- Lastro, E. 2006. Dung beetles (Coleoptera: Scarabaeidae and Geotrupidae) in North Carolina pasture ecosystem. MSc thesis. North Carolina State University, Raleigh, North Carolina, United States of America.
- Legner, E.F. 1986. The requirement for reassessment of interactions among dung beetles, symbovine flies, and natural enemies. *Entomological Society of America*, **61**: 120–131.
- Legner, E.F. and Warkentin, R. 1991. Influence of *Onthophagus gazella* on hornfly, *Haematobia irritans* density in irrigated pastures. *Entomophaga*, **36**: 547–553.
- Ljungberg, H. 2002. Notes on North European *Onthophagus* Latr. (Coleoptera: Scarabaeidae). *Entomologisk Tidskrift*, **123**: 35–49.
- Lobo, J.M., Cabrero-Sañudo, F., Samper, J.R., Ruiz, J.L., Muñoz, J.H., Dellacasa, M., and Dellacasa, G. 2016. Información taxonómica y biogeográfica sobre los Scarabaeoidea coprófagos de Marruecos. [online] Available from [www.biogeografia.org/biogeografia/index.php/proyecto-instituto-de-estudios-ceuties](http://www.biogeografia.org/biogeografia/index.php/proyecto-instituto-de-estudios-ceuties) [accessed 31 January 2015].
- Lobo, J.M. and Martín-Piera, F. 1991. La creación de un banco de datos zoológico sobre los Scarabaeidae (Coleoptera: Scarabaeoidea) Ibero-Baleares: una experiencia piloto. *Elytron*, **5**: 31–37.
- Macagno, A.L.M., Moczek, A.P., and Pizzo, A. 2016. Rapid divergence of nesting depth and digging appendages among tunneling dung beetle populations and species. *The American Naturalist*, **187**: E143–E151.
- MacRae, T.C. and Penn, S.R. 2001. Additional records of adventive *Onthophagus* Latreille (Coleoptera: Scarabaeidae) in North America. *The Coleopterists Bulletin*, **55**: 49–50.
- Markin, G. and Yoshioka, E.R. 1998. Biological control of the horn fly, *Haematobia irritans* L., in Hawaii (Diptera: Muscidae). *Proceedings of the Hawaiian Entomological Society*, **33**: 43–50.
- Mason, P.G., Olfert, O., Sluchinski, L., Weiss, R.M., Boudreault, C., Grossrieder, M., and Kuhlmann, U. 2003. Actual and potential distribution of an invasive canola pest, *Meligethes viridescens* (Coleoptera: Nitidulidae), in Canada. *The Canadian Entomologist*, **135**: 405–413.
- Montes de Oca, E. and Halfpiter, G. 1998. Invasion of Mexico by two dung beetles previously introduced into the United States. *Studies on Neotropical Fauna and Environment*, **33**: 37–45.
- Nichols, E., Spector, S., Louzada, J., Larsen, T., Amequita, S., and Favila, M.E. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation*, **141**: 1461–1474.
- Noriega, J.A., Horgan, F.G., Larsen, T.H., and Valencia, G. 2010. Records of an invasive dung beetle species, *Digitonthophagus gazella* (Fabricius, 1787) (Coleoptera: Scarabaeidae), in Peru. *Acta Zoológica Mexicana*, **26**: 451–456.
- Olfert, O., Hallett, R., Weiss, R.M., Soroka, J., and Goodfellow, S. 2006. Potential distribution and relative abundance of swede midge, *Contarinia nasturtii*, an invasive pest in Canada. *Entomologia Experimentalis et Applicata*, **120**: 221–228.
- Olfert, O., Haye, T., Weiss, R., Kriticos, D., and Kuhlmann, U. 2016a. Modelling the potential impact of climate change on future spatial and temporal patterns of biological control agents: *Peristenus digoneutis* (Hymenoptera: Braconidae) as a case study. *The Canadian Entomologist*, **158**: 579–594.
- Olfert, O., Weiss, R.M., Cárcamo, H.A., and Meers, S. 2012a. The influence of abiotic factors on an invasive pest of pulse crops, *Sitona lineatus* (L.) (Coleoptera: Curculionidae), in North America. *Psyche*, Article 746342. <https://doi.org/10.1155/2012/746342>.
- Olfert, O., Weiss, R.M., and Elliott, R.H. 2016b. Bioclimatic approach to assessing the potential impact of climate change on wheat midge (Diptera: Cecidomyiidae) in North America. *The Canadian Entomologist*, **148**: 52–67.
- Olfert, O., Weiss, R.M., Turkington, K., Beckie, H., and Kriticos, D. 2012b. Bioclimatic approach to assessing the potential impact of climate change on representative crop pests in North America. In *Climate change and the Canadian agricultural environment*. Edited by A.J.A. Ivany and R.E. Blackshaw. Canadian Weed Science Society, Pinawa, Manitoba, Canada. Pp. 47–69.
- Olfert, O., Weiss, R.M., Woods, S., Philip, H., and Dosdall, L. 2004. Potential distribution and relative abundance of an invasive cereal crop pest, *Oulema melanopus* (Coleoptera: Chrysomelidae), in Canada. *The Canadian Entomologist*, **136**: 277–287.



- Ratcliffe, B. and Paulsen, M.J. 2008. The scarabaeoid beetles of Nebraska (Coleoptera: Scarabaeoidea). Bulletin of the University of Nebraska State Museum, **22**: 1–568.
- Rivera-Cervantes, L.E. and Garcia-Real, E. 1991. New locality records for *Onthophagus gazella* Fabricius (Coleoptera: Scarabaeidae) in Jalisco, Mexico. The Coleopterists Bulletin, **45**: 370.
- Rounds, R.J. and Floate, K.D. 2012. Diversity and seasonal phenology of coprophagous beetles at Lake City, Michigan, United States of America, with a new state record for *Onthophagus taurus* (Schreber) (Coleoptera: Scarabaeidae). The Coleopterists Bulletin, **66**: 169–172.
- Silva, D.P., Vilela, B., Buzatto, B.A., Moczek, A.P., and Hortal, J. 2016. Contextualized niche shifts upon independent invasions by the dung beetle *Onthophagus taurus*. Biological Invasions, **18**: 3137–3148.
- Skidmore, P. 1991. Insects of the British cow-dung community. Richmond Publishing, Slough, United Kingdom.
- Sullivan, G.T., Ozman-Sullivan, S.K., Lumaret, J.-P., Baxter, G., Zalucki, M.P., and Zeybekoğlu, Ü. 2016. Dung beetles (Coleoptera: Scarabaeidae) utilizing water buffalo dung on the Black Sea coast of Turkey. Turkish Journal of Zoology, **40**: 80–86.
- Sutherst, R.W., Maywald, G.F., and Kriticos, D.J. 2007. CLIMEX version 3: user's guide. Hearne Scientific Software, South Yarra, Australia.
- Tinerella, P.P. and Fauske, G.M. 1999. Occurrence of *Onthophagus nuchicornis* (Coleoptera: Scarabaeidae) in North Dakota. Entomological News, **110**: 22–26.
- Tyndale-Biscoe, M. 1990. Common dung beetles in pastures of south-eastern Australia. Division of Entomology, Commonwealth Scientific and Industrial Research Organisation, Canberra, Australia.
- Worthington, R.J. and Larsen, K.J. 2010. An annotated checklist of scarab beetles (Coleoptera: Scarabaeidae) from northeastern Iowa. The Great Lakes Entomologist, **43**: 77–90.