*Environmental Entomology*, 53(6), 2024, 1147–1156
https://doi.org/10.1093/ee/nvae100
Advance Access Publication Date: 20 October 2024
Research

ENTOMOLOGICAL SOCIETY OF AMERICA
SHARING INSECT SCIENCE GLOBALLY

OXFORD

Pollinator Ecology and Management

# The establishment and potential spread of *Osmia cornuta* (Hymenoptera: Megachilidae) in North America

**Michael P. Getz, Lincoln R. Best[1], Andony P. Melathopoulos, Timothy L. Warren[*]**

Department of Horticulture, Oregon State University, Corvallis, OR, USA *Corresponding author, email: tim.warren@oregonstate.edu

Subject Editor: Sandy DeBano

Received on 12 June 2024; revised on 18 September 2024; accepted on 25 September 2024

Mason bees, subgenus *Osmia* Panzer (Hymenoptera: Megachilidae), are economically and ecologically significant pollinators. In eastern North America, the rapid spread of 2 non-native species from Asia, *Osmia cornifrons* Radoszkowski and *Osmia taurus* Smith, has coincided with declines in native *Osmia* populations, raising concern about the effects of further exotic arrivals. Here we investigate the recent establishment in British Columbia, Canada of the European orchard bee, *Osmia cornuta* Latreille, previously thought to be limited to Europe and its periphery. We document *O. cornuta* records ranging more than 170 km, including sightings of live adults and the discovery of a multigenerational nest with hundreds of cocoons. We tested whether these cocoons could be discriminated from other *Osmia* species by training a machine learning classifier on features extracted from images. The best performing model could not reliably discriminate cocoons by species, raising the possibility *O. cornuta* could be inadvertently intermingled in future commercial shipments. Recent occurrence records of *O. cornifrons* and *O. taurus* were spatially isolated, suggesting ongoing anthropogenic dispersal of these species. We predicted the suitability of North American habitats for *O. cornuta* by estimating its native climate niche. This analysis indicated broad regions of the Pacific Northwest and eastern North America contain potentially suitable habitat. Our findings document the establishment of *O. cornuta* in North America and the potential for its expansion. Our study demonstrates the utility of accessible biodiversity data archives and public observation programs in tracking non-native species spread and highlights the need for future monitoring of exotic *Osmia*.

*Key words:* species introduction, niche modeling, community science, mason bee, computer vision

## Introduction

The mason bees, subgenus *Osmia* (*Osmia*) Panzer (Hymenoptera: Megachilidae), hereafter *Osmia* s.s., are economically and ecologically significant pollinators that are widely distributed throughout the Holarctic region. Of the 29 bees in subgenus *Osmia*, several are managed agricultural pollinators in their native ranges, including *Osmia lignaria* Say in North America, *Osmia cornifrons* Radoszkowski in northern Asia, and *Osmia cornuta* Latreille in Europe (Branstetter et al. 2021). Mason bees are ideal for husbandry and agricultural use, as they can be more effective pollinators of rosaceous trees than *Apis mellifera* L. and *Bombus terrestris* L. (Bosch and Blas 1994, Vicens and Bosch 2000, Jaumejoan et al. 2023), they readily build nests in provided artificial cavities, and are easily transported in their cocoon stage (Torchio et al. 1987, Sedivy and Dorn 2014).

Two non-native *Osmia* s.s., *O. cornifrons* and *Osmia taurus* Smith, have recently spread widely in eastern North America. *O. cornifrons* first established in Maryland as a result of a prolonged, intentional introduction effort involving multiple shipments of thousands of bees from Japan as early as 1965, with evidence of establishment in 1977 (Rust 1974, Batra 1998). In contrast, the closely related *O. taurus*, also native to Japan, was introduced unintentionally to the eastern United States; its first documented records in North America were in Maryland and West Virginia in 2002 (Droege and Maffei 2023). Both species have broadly increased their range in the last 20 years. Their shared range now extends from the Carolinas to southern Ontario and Quebec, and west into several midwestern states (Normandin et al. 2017, MacIvor et al. 2022, Gutierrez et al. 2023). *Osmia taurus* was recorded as far south as Georgia and Florida, and *O. cornifrons* records extend west to Colorado, Utah, and Oregon (Gutierrez et al. 2023).

There is growing concern about the extent to which exotic *Osmia* species could threaten native ecosystems. In a multidecade monitoring study in the mid-Atlantic United States, the annual

© The Author(s) 2024. Published by Oxford University Press on behalf of Entomological Society of America.
This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs licence (https://creativecommons.org/licenses/by-nc-nd/4.0/), which permits non-commercial reproduction and distribution of the work, in any medium, provided the original work is not altered or transformed in any way, and that the work is properly cited. For commercial re-use, please contact reprints@oup.com for reprints and translation rights for reprints. All other permissions can be obtained through our RightsLink service via the Permissions link on the article page on our site—for further information please contact journals.permissions@oup.com.



Downloaded from academic.oup.com/ee/article/53/6/1147/7828291 by guest on 14 November 2026

abundance of *O. taurus* increased and *O. cornifrons* remained stable, while all 6 native *Osmia* species populations, including *O. lignaria*, declined significantly (LeCroy et al. 2020). One possible cause for these apparent population declines is transmission of fungal pathogens from non-native to native species (Prenter et al. 2004, Crowl et al. 2008). Consistent with this view, native North American mason bees *O. lignaria* and *Osmia georgica* had higher levels of chalkbrood-causing fungi (*Ascosphaera naganensis* and *Ascosphaera fusiformis*, first described in Japan), in areas where *O. cornifrons* and *O. taurus* were present (Hedtke et al. 2015, LeCroy et al. 2023). In addition to transmitting disease, exotic bees can compete with native species for food and nesting resources and alter plant communities through selective pollination (Goulson 2003, Thomson 2004, Stout and Morales 2009, Russo et al. 2021).

*Osmia* s.s. have several attributes that contribute to their wide distributions. As cavity nesters, they can disperse globally by building nests in materials used for international shipping (Goulson 2003). *Osmia* s.s. are generally polylectic, which supports flexible adaptation to new environments, although some species have known floral preferences such as *Osmia ribifloris* for *Arctostaphylos* (Haider et al. 2014). Exotic *Osmia* can benefit from commercial beekeeping operations, which provide housing, food, and further opportunity for anthropogenic dispersal. Furthermore, the shipment of cocoons—either by large commercial operators or by small-scale hobbyists—may accelerate the inadvertent dispersal of *Osmia* s.s. (MacIvor et al. 2022). Although some states regulate the import of non-native insects, there are currently no federal limits on domestic shipments of *Osmia* s.s within the continental United States or Canada (USDA 2018).

Many intentional introductions of *Osmia* s.s. have failed, suggesting that habitat suitability plays a critical role in determining successful establishment. For instance, prior to the successful introduction of *O. cornifrons* to Maryland in 1977, there was a failed attempt in Utah in 1965. Similarly, when researchers released thousands of European orchard bees (*O. cornuta*) in Logan, Utah in 1978, they assumed the species would establish permanently (Torchio and Asensio 1985). Several *O. cornuta* nests were found the following year, but there were no records thereafter (Torchio and Asensio 1985). The same group then attempted to introduce *O. cornuta* to 4 almond orchards in Dixon, California in 1985; again, there was no lasting establishment (Torchio and Asensio 1985, Torchio et al. 1987). These failed introductions may have resulted from inhospitable climate conditions. As univoltine bees, *Osmia* s.s. are highly sensitive to the quantity and timing of rainfall, which affects spring emergence and foraging success, and to seasonal temperature variation, which influences developmental rate and the viability of overwintering (Kemp and Bosch 2005, White et al. 2009, Radmacher and Strohm 2011, Pitts-Singer et al. 2014, Westreich et al. 2023). Consistent with this environmental sensitivity, *O. lignaria* survived at a higher rate when introduced to locations with climates that closely matched their original range (Kemp and Bosch 2005). To model the climatic niche of insects and other animals, many studies have used the abundant presence records of the Global Biodiversity Information Facility (GBIF) database (Silva et al. 2014, Curtis and Bradley 2016, De Marco and Nóbrega 2018, Polidori and Sánchez-Fernández 2020, Encarnação et al. 2021, Di Febbraro et al. 2023).

The successful spread of *O. cornifrons* and *O. taurus* raises the possibility that other exotic *Osmia* could similarly establish in North America with potential negative consequences for native bees. This study investigates the recent establishment of *O. cornuta*—thought to be limited to Europe and its periphery—in southern British Columbia, Canada. We document numerous sightings of *O. cornuta* adults as well as a multigenerational nest with hundreds of cocoons. We evaluate the visual features of these cocoons to assess whether *O. cornuta* could go undetected in shipments of other *Osmia* s.s. cocoons. To examine potential range expansion dynamics of *O. cornuta*, we map where similar exotic mason bees, *O. taurus* and *O. cornifrons,* have been observed following their introductions to North America. We then predict the suitability of North American habitats for *O. cornuta* by estimating its native European climate niche.

## Materials and Methods

### *Osmia cornuta* Sample Collection and Occurrence Records

In April 2023, Gordon Cyr, the owner and operator of a mason bee farm in Black Creek, Vancouver Island, harvested a cache of cocoons from a prefabricated mason bee house after observing distinctly red adult mason bees nearby. Suspecting they were *O. cornuta*, Cyr contacted the Native Bee Society of British Columbia (NBSBC), which arranged for the transport of 30 cocoons to Oregon State University (OSU)—suspended in ethyl alcohol—for identification and dissection. In January 2024, Cyr harvested 80 cocoons from the same nesting site, which he again sent to OSU. We separately obtained *O. lignaria* and *O. cornifrons* cocoons from Willamette Valley beekeepers as part of an Oregon mason bee health project. Cocoons from all sources were coarsely cleaned of nesting materials, with occasional frass and mud cap fragments remaining; all 3 species use mud as a nesting material.

We accessed 4 iNaturalist records of adult *O. cornuta* from British Columbia, Canada: a 29 March 2023 record from North Vancouver, BC (153554196) contributed by Jasna Guy, a Master Melittologist volunteer for the NBSBC; 2 concurrent observations (204882854, 204883055) of a male and a female *O. cornuta* on 30 March 2024 contributed by Jeremy Gatten, Wildlife Biologist, LGL Limited; and a 15 April 2024 record of a female *O. cornuta* (207021500) contributed by Bonnie Zand, a director and taxonomist for the NBSBC. We visually verified the identifications made for all photos.

### Cocoon and Specimen Analysis

We imaged a batch of 390 *Osmia* cocoons using a Raspberry Pi 4 with a Pi Cam HQ 12MP module, 6 mm lens (Adafruit) at a constant height (20 mm), and a ring LED surrounding the lens that provided consistent lighting for all samples. After imaging, we dissected the cocoons, removed any samples containing underdeveloped or parasitized bees, and identified the adult specimens to species and sex (Amiet et al. 2004). Of the resulting 317 samples, 130 were *O. lignaria*, 81 were *O. cornifrons*, and 106 were *O. cornuta*. For all adult specimens, we measured intertegular distances using digital calipers to 0.01 mm accuracy under a dissecting scope (Leica).

We implemented the analysis of cocoon images in Python 3.11.5. We corrected for lens distortion using the OpenCV Camera Calibration procedure (Bradski 2000). We segmented cocoons in images by first training a YOLO object detection model (yolov8s) and used the resulting bounding boxes as inputs for Segment-Anything (Meta; Jocher et al. 2023, Kirillov et al. 2023). Segmentation creates an image mask of the cocoon, thereby removing the background. We calculated cocoon length and width with OpenCV by fitting a rectangle to the resulting cocoon mask. Area ($cm^2$) and average color values on a scale of 0-255 were extracted from the cocoon mask. To estimate discriminability among cocoons from visual characteristics,

Downloaded from academic.oup.com/ee/article/53/6/1147/7828291 by guest on 14 November 2026

we used the scikit-learn package to train a support vector machine (SVM) model on the extracted features (length, width, area, and red, green, and blue color values; Pedregosa et al. 2011). We used a 10-fold cross-validated grid search to tune SVM parameters: gamma (influence range for each training example), *C* (complexity of decision boundary), and kernel type (linear, radial basis function, or polynomial). Using the best parameters from the grid search (*C* = 100, gamma = 0.1, kernel = radial basis function), we performed 1,000 iterations of 10-fold cross-validation. Using a one-vs-rest format, we tested whether *O. cornuta* and *O. lignaria* could be reliably classified. We evaluated the performance of the SVM by averaging precision and recall across all iterations. For a particular class (e.g., *O. lignaria* or *O. cornuta*), precision is the ratio of true positives to total positive determinations. Recall is the proportion of actual positives correctly classified (i.e., true positives divided by true positives and false negatives).

### Mapping Distributions of GBIF Occurrence Records

We generated North American species observation maps for *O. cornifrons* and *O. taurus* using the Global Biodiversity Information Facility (GBIF) database, a repository for expert-identified specimen records and community science observations. Expert-identified physical specimens accounted for 72.7% of *O. cornifrons* records and 92.0% of *O. taurus* records; the remaining records are 'Research Grade' iNaturalist observations. The 'Research Grade' designation requires a date, georeferenced coordinates, an associated photo or sound, at least 2 confirmatory identifications to species level or lower, and at least two-thirds of identifications must agree. GBIF is an aggregate dataset without standardized sampling protocols, which can be difficult to interpret due to uneven sampling efforts throughout time and space. For this reason, we focused our analysis on the spatial extent where each species was observed, rather than the density of sampling in particular regions. Using Python 3.11.5, we mapped the locations of all North American GBIF records for both species (between 23° to 60° latitude and -126° to -64° longitude) from 1977 to 2006 and from 2007 to 2023. We chose the first period to include the 1977 introduction of *O. cornifrons* to the Northeast United States and 5 years following the first North American record of *O. taurus* in 2002 (Batra 1998, Droege and Maffei 2023). The second period captures the expansion dynamics of each species following introduction and includes the 2008 release of iNaturalist. We projected a grid of equally sized bins (22,500 km$^2$) over this area, with the projection centered at -95° longitude. Distinguishing *O. cornifrons* from *O. taurus* in photographs poses challenges, as the determination can depend on microscopic features. Therefore, we separately identified bins with only iNaturalist records and bins with at least one expert-identified physical specimen.

### Comparing the European *O. cornuta* Climate Niche to North America

We predicted the suitability of North American habitats for *O. cornuta* using R, by estimating the climate niche of *O. cornuta* in its native range. At each of the 32,413 *O. cornuta* occurrence locations (1960-2023; excluding recent North American observations), we extracted values for the 19 bioclimatic variables and elevation from the WorldClim database (Supplementary Table S1; Fick and Hijmans 2017). These 19 WorldClim variables, derived from temperature or precipitation measures, capture general conditions as well as seasonal trends (Kriticos et al. 2012, Fick and Hijmans 2017). To reduce the effects of uneven sampling density, we filtered the full set of occurrence data to include at most 1 record per pixel at the resolution of the WorldClim dataset (30 arc seconds, ~1 km$^2$), resulting in 6,494 points. All data were *z*-score normalized, so that each feature distribution had mean of 0 and standard deviation of 1. We then applied principal components analysis (PCA) to the native-range data to transform the 20 environmental variables, which are highly collinear, to 4 orthogonal components used for subsequent analysis (De Marco and Nóbrega 2018). These first 4 components, chosen on the basis of scree plot inspection, accounted for 85.2% of variance (Jolliffe 2002). The most positive loadings of the first principal component included maximum temperature of the warmest month and mean temperature of the warmest quarter, whereas the most negative loadings included annual precipitation and precipitation of the driest month. Variables with the most positive loadings on the second axis included temperature seasonality and annual range, whereas minimum temperature of the coldest month and mean temperature of the coldest quarter had the most negative loadings. We estimated *O. cornuta*'s environmental niche by calculating the Mahalanobis distance ($D^2$) in this 4-dimensional PCA space from each of the 6,494 locations to the centroid of these points. We used Mahalanobis distance for niche modeling as it calculates distance to the mean of a multivariate distribution, considering all data and reducing the impact of outliers (Farber and Kadmon 2003).

We then extracted the same 20 environmental variables across North America at the full resolution of the WorldClim dataset (~1 km$^2$; from -130° to -63° longitude and 25° and 54° latitude). We mapped these data (normalized using the European means and standard deviations) to the native-range PCA feature space. Then, for each point in North America, we calculated $D^2$ to the European centroid. Smaller $D^2$ values implied higher similarity to the native climate niche (Etherington et al. 2009).

## Results

Prior to 2023, the range of the European orchard bee (*O. cornuta*) was limited to continental Europe and its immediate periphery, including the Mediterranean islands, North Africa, and far western Asia. From 1960 to 2023, 32,416 *O. cornuta* records were logged to the GBIF database (Fig. 1A). The highest density of observations was in central Europe (e.g., Belgium, Holland, and Germany); the spatial range of GBIF records extended from Lagoudera, Cyprus to Oslo, Norway (from south to north), and from the Caspian coast in Iran to Serra da Estrela Nature Park, Portugal (from east to west).

In 2023 and 2024, there were multiple observations of *O. cornuta* in British Columbia, the westernmost province of Canada. In March 2023, a volunteer from the NBSBC encountered an isolated male *O. cornuta* at a residential park in North Vancouver, BC. The image record, uploaded to iNaturalist, was the first valid GBIF entry of *O. cornuta* in North America. In April 2023, in Black Creek, Vancouver Island (Fig. 1B; 160 km from North Vancouver), a beekeeper harvested a set of cocoons from a nest where he had observed putative *O. cornuta* adults. We dissected 30 cocoons from this nest to determine species and sex; all were *O. cornuta* (11 male, 19 female). Sex was determined by the 13 antennal segments and 7 exposed tergites of males, and 12 antennal segments and 6 exposed tergites of females. Males were identified to species by their tergite 7 with wide, rounded lateral lobes, tergite 6 lacking posterolateral teeth or angles, black pubescence of mesepisternum, and rufescent dorsum of the metasoma (Fig. 2A-C). Females were identified to species by their red metasomal scopa, concave clypeus with laterally protruding horns, black vestiture of head and thorax, and red metasomal tergites (Fig. 2D-F). Intertegular distances of adults (male, mean 3.3 ± 0.42 mm;

Downloaded from academic.oup.com/ee/article/53/6/1147/7828291 by guest on 14 November 2026

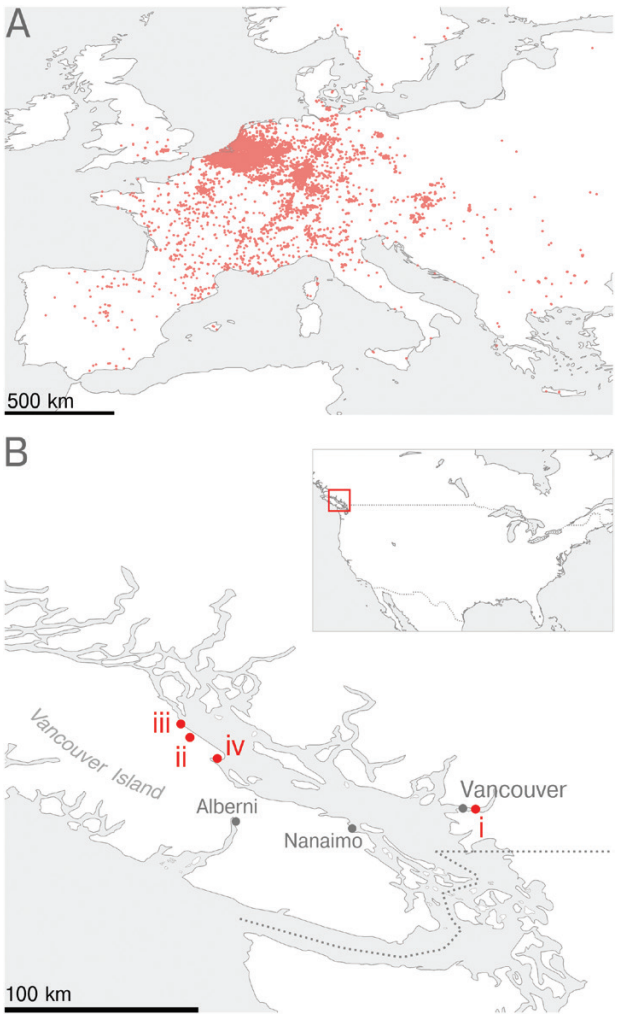



**Fig. 1.** Occurrence records of the European orchard bee, *O. cornuta*, in Europe and North America. A) Locations of 32,295 GBIF occurrence records for *O. cornuta* from 1960 to 2023. Not shown are 118 records to the east between 28.0 and 51.1°C longitude. B) Four distinct records of *O. cornuta* in British Columbia, Canada in 2023 and 2024: (i) an adult male observed in spring 2023 in North Vancouver, BC, (ii) a nest with cocoons found in 2023 and 2024 in Black Creek, Vancouver Island, (iii) a male and female *O. cornuta* sharing a nest with *O. lignaria*, (iv) an adult female *O. cornuta*.

female, mean 3.8 ± 0.22 mm) matched prior European estimates and were higher than the respective sexes of *O. lignaria* and *O. cornifrons* samples (Fig. 2G; Bosch and Vicens 2002). We further examined a second batch of 80 cocoons from the same location in 2024. Of these, 77 were *O. cornuta* (57 male, 20 female). One cocoon was *O. lignaria* and 2 contained underdeveloped larvae. In spring 2024, there were additional, independent observations of adult *O. cornuta* on Vancouver Island. In March 2024, a taxonomist from the NBSBC observed a female and male *O. cornuta* about 15 km northwest of Black Creek on an artificial mason bee house alongside *O. lignaria* (Fig. 1B). In April 2024, a female *O. cornuta* was spotted in a mason bee nesting block in Comox, ~25 km from Black Creek. Together, these observations indicate multigenerational establishment of *O. cornuta* in British Columbia over a range of at least 170 km.

We tested whether visual features of cocoons, such as size and color, permitted the discrimination of *O. cornuta* from *O. lignaria* and *O. cornifrons*. *Osmia* cocoons have a broadly similar appearance, though there was apparent variability in size and color both within and across species (Fig. 3A). We used a standardized imaging pipeline to extract area, length, width, and average red, green, and blue color value for each cocoon (Fig. 3B). Cocoon areas overlapped across the 3 species (Fig. 3C), with ranges of 0.25-0.76 $cm^2$ for *O. cornifrons* ($n = 81$), 0.30-0.92 $cm^2$ for *O. lignaria* ($n = 130$), and 0.39-1.17 $cm^2$ for *O. cornuta* ($n = 106$). *O. cornuta* female cocoons (mean: 0.89 ± 0.15 $cm^2$) were distinctly larger than all other groups, whereas the size of *O. cornuta* male cocoons (mean: 0.64 ± 0.16 $cm^2$) overlapped with *O. lignaria* females (mean: 0.70 ± 0.13 $cm^2$) (Fig. 3C). Cocoon aspect ratios (length/width) also overlapped across species (ranges: *O. cornuta:* 1.52-2.00, *O. lignaria*: 1.55-2.54, and *O. cornifrons*: 1.45-2.63). The ranges of red, blue, and green values for average cocoon color similarly overlapped (Fig. 3D). To test whether species could be classified by combining information across the data dimensions, we trained a SVM on the extracted visual features. We evaluated the model using precision-recall curves to determine whether the native *O. lignaria* could be separated from the non-natives, and whether *O. cornuta* could be reliably detected (Fig. 3E). An ideal classifier would achieve perfect (1.0) recall for *O. cornuta*, so that no instances of the species are missed. The highest precision of our best SVM model at 1.0 recall was 0.79. At 0.9 recall, *O. cornuta* precision was 0.87. The model performed more poorly for *O. lignaria*, which has features intermediate to *O. cornifrons* and *O. cornuta* (Fig. 3C and D). The highest precision for *O. lignaria* at a recall above 0.5 was 0.92 (at recall = 0.54), while at 0.9 recall, precision was 0.82. The sawtooth shape of the *O. lignaria* precision-recall curve (Fig. 3E) indicates sensitivity to changes in dataset splits (Davis and Goadrich 2006). The SVM marginally outperformed human sorters, as 79% of *O. lignaria* and *O. cornifrons* cocoons submitted by Oregon beekeepers were labeled accurately.

To characterize the spread of non-native *Osmia* previously introduced to North America, we mapped historical records of *O. taurus* and *O. cornifrons*. For both species, we binned GBIF point records over 2 time periods (1977-2006 and 2007-2023) into 918 equal-area regions (Fig. 4; 22,500 $km^2$; 23-60°C latitude), to generalize the spatial range of occurrences. From 1977 to 2006, *O. cornifrons* records were concentrated around the US Mid-Atlantic (Fig. 4A). From 2007 to 2023, there were iNaturalist observations and physical records of *O. cornifrons* throughout the eastern United States; discontinuous records are found across the Great Plains, in Rocky Mountain states, and in the Pacific Coast states (Fig. 4B). *Osmia taurus* records were similarly initially concentrated in the Mid-Atlantic following its discovery in Maryland and West Virginia in 2002 (Fig. 4C; Droege and Maffei 2023). From 2007 to 2023, there was a vouchered specimen of *O. taurus* as far south as Jupiter Island, FL; iNaturalist observations extend throughout the central United States, southern Ontario, and as far west as Boise, ID (Fig. 4D). These data suggest that the observed range of *O. cornifrons* and *O. taurus* increased rapidly, and in a spatially discontinuous fashion, following their respective introductions.

The rapid spread of *O. cornifrons* and *O. taurus* from the Mid-Atlantic raises the question of whether *O. cornuta* might similarly expand its range from the Pacific Northwest. To determine regions with suitable habitat for *O. cornuta* range expansion, we estimated the bee's climate niche using occurrence data from its native range. We reduced 20 environmental variables (the 19 WorldClim bioclimatic variables and elevation) to 4 orthogonal principal components, which explained 85.2% of all native-range variance (Fig. 5A and B). In the native range, the distribution of Mahalanobis distances ($D^2$) to the centroid was heavily right-skewed, ranging from 0.015 to 106.62 (unitless) with a mean of 4.0 (Fig. 5C, top axis). Based on this distribution, we set a suitability threshold at 61.65, which

Downloaded from academic.oup.com/ee/article/53/6/1147/7828291 by guest on 14 November 2026

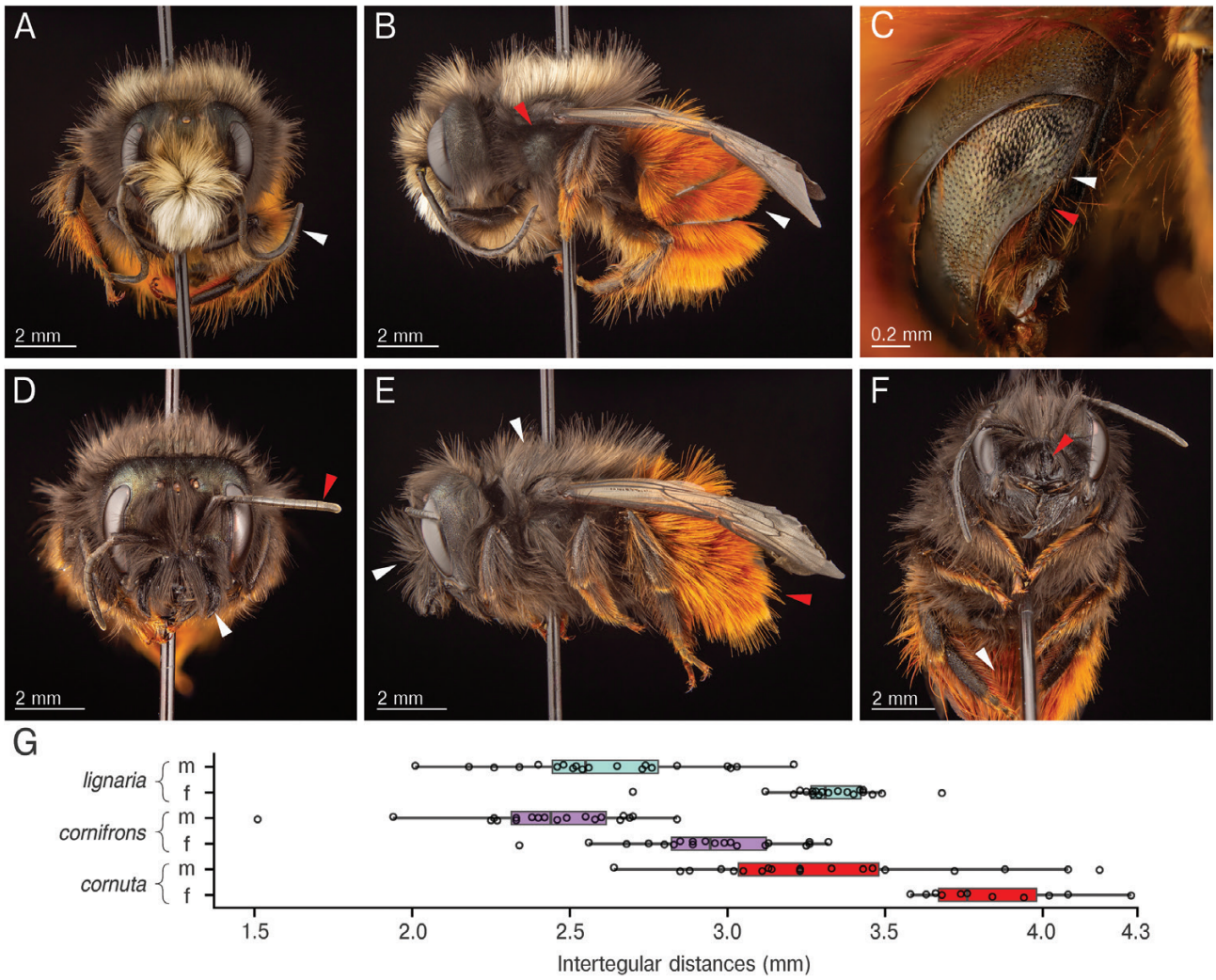



**Fig. 2.** Physical characteristics of Black Creek *O. cornuta* specimens. A) Male face with 11 flagellar segments (arrow). B) Male lateral habitus with black mesepisternum (red arrow) and rufescent metasoma (white arrow). C) Male tergite 6 & tergite 7 detail (hairs shaved for clarity). Tergite 7 is wide and rounded laterally and lacks teeth (red arrow), whereas tergite 6 lacks angles and teeth (white arrow). D) Female face with 10 flagellar segments (red arrow) and lateral horns (white arrow). E) Female lateral habitus with rufescent metasoma (red arrow) and black head and mesosoma (white arrows). F) Female ventral habitus with concave clypeus (red arrow) and red scopal hairs (white arrow). G) Box and whisker plot for the intertegular distances of *O. cornuta*, *O. lignaria*, and *O. cornifrons*. Boxes mark the interquartile range (IQR) from Q1 to Q3 and median. The whiskers mark the minimum and maximum values within 1.5 times the IQR. Open circles are measured values; circles outside the whiskers are considered outliers. Image credit: Mark Gorman

includes >99.9% of all values and removed 3 outliers. We calculated $D^2$ to the native-range centroid across North America (24-55°C latitude; ~1 km$^2$ resolution), to determine regions of potential suitability. North American $D^2$ values ranged from 2.7 to 741.0 with a mean of 83.4 ± 46.9 (Fig. 5C, bottom axis), and 35.8% of locations had $D^2$ values below the 61.65 suitability cutoff. Two prominent regions in North America have $D^2$ values below the native-range threshold, indicating climate similarity (Fig. 5D). One region extends from Vancouver and Vancouver Island—the locations of *O. cornuta* detection—south to the Olympic Peninsula in Washington and the Willamette Valley in Oregon, inland through eastern Washington and northern Idaho through the Columbia River Valley, and through the major river valleys of southern British Columbia. A second, much larger region of high similarity in the central and eastern United States ranges from the Ozarks in northwest Arkansas, through the Mid-Atlantic and north to Michigan, southern Ontario, New England, and Nova Scotia. The Mid-Atlantic, where *O. taurus* and *O. cornifrons* first established, exhibits some of the lowest $D^2$ values in the range. The climate similarity map shows patchy, discontinuous regions of suitability throughout the American West, including the California Bay Area and in Utah near the Great Salt Lake. The site of a prior failed *O. cornuta* introduction in Logan, Utah is outside the range of estimated suitability, whereas another site, Dixon, California, is on the edge of estimated suitability. This model suggests that the Vancouver area was well suited to permit *O. cornuta* establishment, and that *O. cornuta* could be supported by habitats throughout the Pacific Northwest and eastern North America.

## Discussion

In this study, we documented multiple recent records in British Columbia, Canada of the European orchard bee, *Osmia cornuta*, a species previously thought to be limited to Europe and its periphery. These records, ranging over 2 years and 170 km, included a multigenerational nest containing hundreds of cocoons (Fig. 1). The

Downloaded from academic.oup.com/ee/article/53/6/1147/7828291 by guest on 14 November 2026

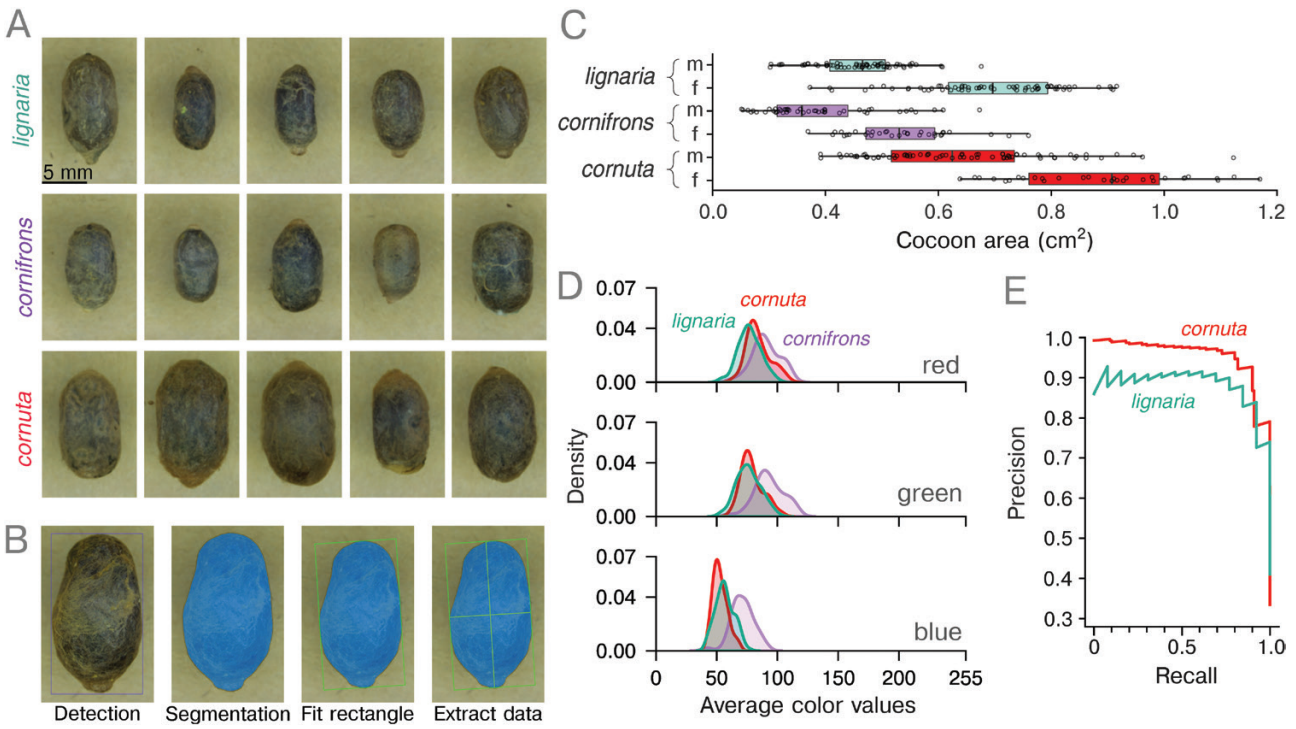



**Fig. 3.** Visual features of *Osmia* cocoons provide a limited basis for interspecies discrimination. A) Randomly selected cocoon images for native *O. lignaria* (top row), *O. cornifrons* (middle row) and *O. cornuta* (bottom row). B) Pipeline for visual feature extraction involving automated detection, segmentation, and then fitting to extract length, width, area, and average color values. C) Measured cocoon areas for all 3 species, separated by sex. Box and whisker plot follows as in Fig. 2G. D) Smoothed histogram (via kernel density estimation) shows the distribution of average color values for each species measured on red, green, and blue channels. E) Averaged precision-recall curves for *O. lignaria* and *O. cornuta* obtained by training a SVM model on the cocoon feature data over 1,000 cross-validated iterations. Precision is the ratio of true positives to total positive determinations. Recall is the proportion of actual positives correctly classified.

physical features of these cocoons overlapped with those of other *Osmia* species (Figs 2 and 3), providing limited basis for classification (Fig. 3). This raises the possibility that *O. cornuta* will be inadvertently mixed into cocoon shipments of other mason bees. The rapid, discontinuous, and continent-wide expansion of *O. cornifrons* and *O. taurus* further suggests the potential for anthropogenic dispersal of *O. cornuta* (Fig. 4). We estimated the climatic niche of *O. cornuta* using occurrence data in its native range and found that broad regions of the Pacific Northwest, southeastern Canada, and the central and eastern United States provide suitable habitat (Fig. 5). Given access to artificial dispersal vectors and favorable habitat, *O. cornuta* could spread quickly in North America.

The proximity of recent records to international ports suggests *O. cornuta* arrived in western Canada on commercial container ships. Across a wide variety of taxa, the introduction and invasion of foreign organisms has become more frequent with globalized trade (Perrings et al. 2005, Bertelsmeier 2021, Fenn-Moltu et al. 2023). This is especially the case with insects, which are small, mobile, and can stay dormant during development (Bertelsmeier 2021, Fenn-Moltu et al. 2023). Cavity-nesting *Osmia* s.s. are particularly prone to long-distance dispersal through shipping materials, where they can remain undetected as cocoons during transit (Russo 2016). The initial 2023 sighting of *O. cornuta* was only about 7 km from the Port of Vancouver, the fourth largest in North America. Subsequent Vancouver Island sightings were within 50-80 km of several international ports (e.g., Nanaimo, Alberni; Fig. 1B). Similarly, *O. taurus* was first detected in North America <30 km from the Port of Baltimore, and a lone adult was found in 2013 <10 km away from the Port of Montreal (Normandin et al. 2017, Droege and Maffei 2023; Fig. 3B). The emergence of *O. cornuta* on Vancouver Island parallels the recent, well-publicized invasion by the northern giant hornet (*Vespa mandarinia*), which was first encountered <5 km from the Port of Nanaimo (Zhu et al. 2020). This pattern of exotic insect detection near ports highlights the role of international commercial exchange points in species introduction.

Our findings suggest that inadvertent shipments of cocoons could contribute to the future spread of *O. cornuta* in North America. The initial records of *O. cornuta* on Vancouver Island—in which adults and cocoons were observed alongside native *O. lignaria*—indicate the species are likely to intermingle in shared nesting blocks. Once mixed, *Osmia* s.s. cocoons will be difficult to distinguish reliably on the basis of individual visual features such as size and color (Fig. 3). A SVM, which combines information across multiple features, performed better for *O. cornuta* than *O. lignaria*. To select for only *O. lignaria*, high precision is required to prevent inadvertent inclusion of non-native cocoons. The best performance the SVM obtained for *O. lignaria* was 0.91 precision at 0.54 recall (i.e., 1 in 10 identifications were wrong, and nearly half of the true positives went undetected). This exceeds the performance of volunteer beekeepers in Oregon; of 211 cocoons we received with *O. lignaria* or *O. cornifrons* labels, 79% were correctly identified. However, given that commercial *Osmia* rearing operations produce millions of cocoons a year, this performance would result in a significant number of errors and wasted cocoons, making it infeasible to control inadvertent dispersal of non-native species. Identifying and removing the exotic *O. cornuta* from mixed groups of cocoons would require perfect recall for the species. For *O. cornuta*, the SVM achieved 1.0 recall but only at a precision of 0.79. With this performance, 1 in 5 *O. lignaria* or *O. cornifrons* cocoons would be misclassified as *O. cornuta*, potentially removing native pollinators

Downloaded from academic.oup.com/ee/article/53/6/1147/7828291 by guest on 14 November 2026

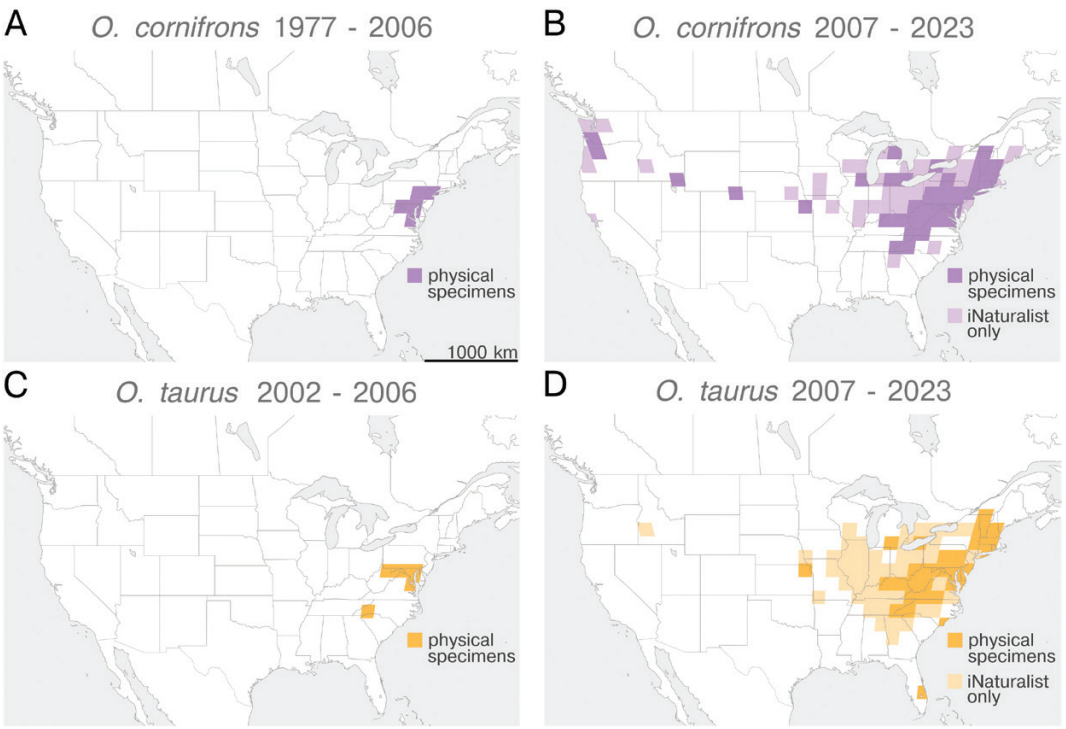



**Fig. 4.** GBIF occurrence records suggest broad, discontinuous spread of *O. cornifrons* and *O. taurus* in North America. A) Locations with GBIF occurrence records of *O. cornifrons* from 1977, the first year it was recorded as established in the United States (Batra 1998), through 2006. Data are binned into equal-area regions (22,500 km$^2$). B) Binned *O. cornifrons* records from 2007 to 2023, including physical specimens identified by experts and photo records from iNaturalist, which was released in 2008. Darker colors denote bins that contain at least one physical specimen, and lighter colors denote bins where only iNaturalist observations were recorded. C) Locations of bins with *O. taurus* records from 2002 to 2006. The first record of *O. taurus* in North America was in Baltimore, MD, 2002 (Droege and Maffei 2023). D) Binned *O. taurus* occurrence records between 2007 and 2023, including physical specimens and iNaturalist observations.

from the population. Alternative classification approaches (e.g., deep learning) could potentially exhibit improved performance, though a much larger and more representative dataset will be necessary to account for geographic variation in species size and color.

The observed range of non-natives *O. taurus* and *O. cornifrons* in North America has rapidly expanded in the past 20 years, with a notable increase relative to a recent study (Gutierrez et al. 2023). Their rapid yet discontinuous range expansion further suggests that *O. cornuta* could spread widely throughout the United States and Canada via anthropogenic dispersal. These isolated records may have resulted from long-distance shipments of purchased cocoons. While the records on their own do not imply successful long-term establishment, these isolated locations may serve as case studies to investigate the conditions for successful *Osmia* introductions. Furthermore, the broad spatial distribution of *O. taurus* and *O. cornifrons* raises the possibility of increasing ecological pressure on native *Osmia*, e.g., through transmission of chalkbrood-causing fungi or competition for floral and nesting resources (LeCroy et al. 2020, 2023).

Our climate niche model indicates broad regions of the Pacific Northwest and eastern North America have environmental conditions similar to *O. cornuta*'s native range. This similarity-based approach to identifying suitable habitat is not exhaustive; *O. cornuta* could succeed in climate conditions distinct from its native range or quickly adapt to new habitats. The analysis, however, highlights the most probable regions for *O. cornuta* spread, and provides a potential explanation for the failure of prior introductions in North America. The Logan, UT introduction site is outside the area of predicted suitable habitat, whereas the Dixon, CA location is just on the edge, indicating marginal suitability. The regions of predicted *O. cornuta* habitat suitability overlap conspicuously with occurrence record maps of *O. taurus* and *O. cornifrons* (compare Fig. 4B and D with Fig. 5). This similarity suggests *O. cornuta* could exhibit similar rapid expansion dynamics to its non-native congeners if introduced to central or eastern North America (e.g., through the mason bee cocoon trade).

*Osmia cornuta* could negatively affect native North American bees through pathogen transmission and direct competition for resources. *Osmia cornuta* is known to host *Chaetodactylus osmiae* mites that infest mason bee nest cells, *Monodontomerus obscurus* wasps that parasitize cocoons, and chalkbrood fungi (Krunic et al. 2005). *O. cornuta* are pollen generalists, with preferences for rosaceous trees and shrubs, as well as *Salix*, *Quercus*, and *Acer* (Kratschmer et al. 2020)—groups also favored by *O. lignaria* (Rust 1990, Kraemer and Favi 2005, Kraemer et al. 2014, Pinilla-Gallego and Isaacs 2018). When co-released in orchards, the bee species exhibited identical pollen preferences (Torchio and Asensio 1985). The similarities between *O. lignaria* and *O. cornuta* in size (Fig. 2B), biological requirements (Torchio and Asensio 1985, Bosch and Kemp 2003, 2004), and diet suggest they could compete for nesting and floral resources where their ranges overlap. It will be important for future studies to determine *O. cornuta*'s pathogenic and parasitic associates in North America, and to study its interactions with native insects and plants.

Our study highlights the utility of community science monitoring, both for detecting biological invasions and predicting exotic species' spread. Notably, most North American *O. cornuta* records were contributed by affiliates of the NBSBC, and the *O. cornuta* cocoon collection was reported to the same organization. In many cases,

Downloaded from academic.oup.com/ee/article/53/6/1147/7828291 by guest on 14 November 2026

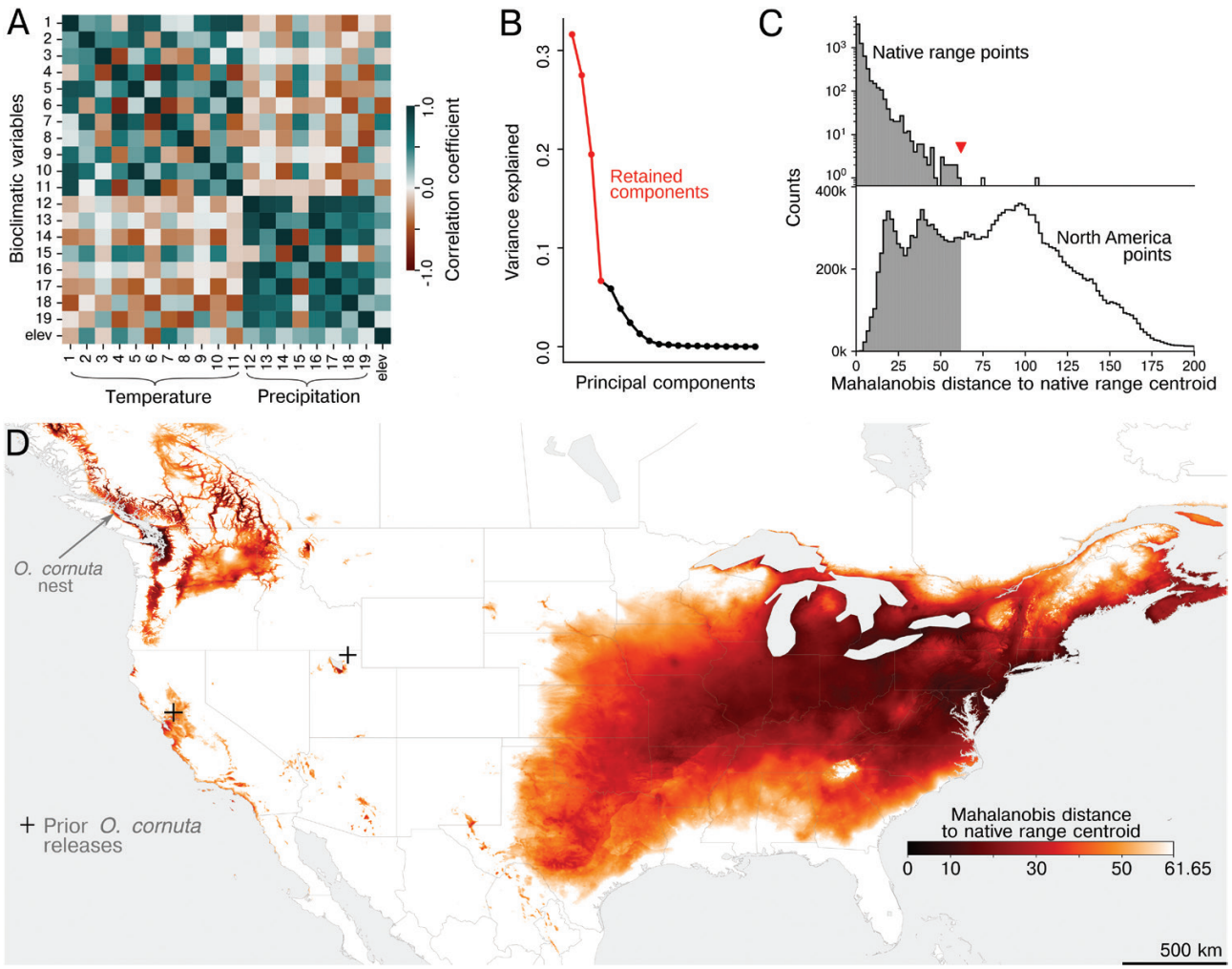



**Fig. 5.** Large regions of North America have habitat similar to the native range of *O. cornuta*. A) Covariance matrix of data extracted at native-range locations for the 19 WorldClim bioclimatic variables and elevation. B) Scree plot indicating variance explained by the 20 principal components calculated from the native-range climate data. The first 4 components (highlighted) were used for subsequent analyses. C) Histograms of Mahalanobis distance ($D^2$) distributions for the native range (top axis) and North American points (bottom axis). For both distributions, $D^2$ was calculated to the native-range centroid. The vertical axis for native-range data is log-scaled to visualize the right tail of the distribution. The arrowhead at $D^2 = 61.65$ denotes a habitat suitability threshold that encompasses > 99.9% of native-range points and excludes 3 outliers. D) Mahalanobis distance suitability model for *O. cornuta* in North America based on the WorldClim bioclimatic variables and elevation. Darker colors, with $D^2$ closer to zero, indicate locations more similar to the native range. The Utah location where *O. cornuta* was previously released but did not establish is outside the range of predicted similarity. The British Columbia records of *O. cornuta* are in regions of high climate similarity.

community naturalist programs (e.g., Bee Atlases, Native Bee/Plant Societies, Natural Heritage Programs) have been shown to improve the quality of public records by increasing awareness of target species and sharing expertise through identification workshops, surveying events, or by moderating non-expert accessions (Pocock et al. 2015, Kosmala et al. 2016, Anderson et al. 2020). Community reporting will be a critical resource for tracking the spread of *O. cornuta* adults, which are easily identifiable by their bright red coloring and detectable by hobbyists with backyard mason bee houses. However, there are known limitations to grassroots reporting, such as spatial bias around human population centers (Amano and Sutherland 2013, Bowler et al. 2022) and potential taxonomic errors (Pereira et al. 2024). To estimate population size, assess range accurately, or create historical distribution benchmarks, targeted studies with standardized monitoring are essential.

Our work indicates that *O. cornuta* is likely to spread following introduction. There is a need for researchers to determine the impact of this species on native *Osmia*, as well as to understand its potential benefits such as increased pollination services to agriculture. Such research would help resolve whether policymakers should dedicate resources to preventing the spread of this species. The commercial *Osmia* cocoon trade demands particular attention—both as a potential vector for unintended long-distance dispersal and as an opportunity for conducting large-scale monitoring. The future development of an automated cocoon sorting method could enable producers to cull non-native *Osmia* from retail shipments; analogously, camera-based monitoring of adult bees around nesting blocks could inform beekeepers when exotic species are present (Wittmann et al. 2024). The early detection of *O. cornuta* in Canada provides an opportunity to respond while the bee's range remains manageably small.

## Acknowledgments

We thank Seth Arendell for imaging, dissecting, and identifying the cocoons, Julia Jones, Lauren Ponisio, and Posy Busby for feedback on a draft version of this paper, and Weng-Keen Wong for discussions regarding analytical methods.

Downloaded from academic.oup.com/ee/article/53/6/1147/7828291 by guest on 14 November 2026

## Author contributions

Michael Getz (Conceptualization [equal], Data curation [lead], Formal analysis [lead], Investigation [lead], Methodology [lead], Project administration [supporting], Software [lead], Validation [lead], Visualization [lead], Writing—original draft [equal], Writing—review & editing [equal]), Lincoln Best (Conceptualization [equal], Data curation [supporting], Formal analysis [supporting], Investigation [supporting], Methodology [supporting], Project administration [supporting], Resources [supporting], Supervision [supporting], Writing—review & editing [supporting]), Andony Melathopoulos (Conceptualization [supporting], Funding acquisition [supporting], Investigation [supporting], Methodology [supporting], Project administration [supporting], Supervision [supporting], Writing—review & editing [supporting]), and Timothy Warren (Conceptualization [equal], Data curation [supporting], Formal analysis [supporting], Funding acquisition [lead], Investigation [equal], Methodology [equal], Project administration [lead], Software [supporting], Supervision [lead], Validation [supporting], Visualization [supporting], Writing—original draft [equal], Writing—review & editing [equal])

## Supplementary data

Supplementary data are available at *Environmental Entomology* online.

## Funding

This project was funded by the Oregon State University College of Agricultural Sciences Strategic Advantage Award.

## Data Availability

Data are available upon request to the corresponding author.

## References

Amano T, Sutherland WJ. 2013. Four barriers to the global understanding of biodiversity conservation: wealth, language, geographical location and security. Proc. Biol. Sci. 280(1756):20122649. https://doi.org/10.1098/rspb.2012.2649

Amiet F, Herrmann M, Müller A, et al. 2004. Apidae 4: *Anthidium, Chelostoma, Coelioxys, Dioxys, Heriades, Lithurgus, Megachile, Osmia, Stelis*. Fauna Helv. 9(4):273.

Anderson RP, Araújo MB, Guisan A, et al. 2020. Optimizing biodiversity informatics to improve information flow, data quality, and utility for science and society. Front. Biogeogr. 12(3):1–14. https://doi.org/10.21425/F5FBG47839

Batra S. 1998. Hornfaced bees for apple pollination. Am. Bee J. 138(5):361–365.

Bertelsmeier C. 2021. Globalization and the anthropogenic spread of invasive social insects. Curr. Opin. Insect Sci. 46:16–23. https://doi.org/10.1016/j.cois.2021.01.006

Bosch J, Blas M. 1994. Foraging behaviour and pollinating efficiency of *Osmia cornuta* and *Apis mellifera* on almond (Hymenoptera, Megachilidae and Apidae). Appl. Entomol. Zool. 29(1):1–9. https://doi.org/10.1303/aez.29.1

Bosch J, Kemp WP. 2003. Effect of wintering duration and temperature on survival and emergence time in males of the orchard pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). Environ. Entomol. 32(4):711–716. https://doi.org/10.1603/0046-225x-32.4.711

Bosch J, Kemp WP. 2004. Effect of pre-wintering and wintering temperature regimes on weight loss, survival, and emergence time in the mason bee *Osmia cornuta* (Hymenoptera: Megachilidae). Apidologie 35(5):469–479. https://doi.org/10.1051/apido:2004035

Bosch J, Vicens N. 2002. Body size as an estimator of production costs in a solitary bee. Ecol. Entomol. 27(2):129–137. https://doi.org/10.1046/j.1365-2311.2002.00406.x

Bowler DE, Callaghan CT, Bhandari N, et al. 2022. Temporal trends in the spatial bias of species occurrence records. Ecography 2022(8):e06219. https://doi.org/10.1111/ecog.06219

Bradski G. 2000. The OpenCV Library. Dr. Dobb's J Softw Tools.

Branstetter MG, Müller A, Griswold TL, et al. 2021. Ultraconserved element phylogenomics and biogeography of the agriculturally important mason bee subgenus *Osmia* (*Osmia*). Syst. Entomol. 46(2):453–472. https://doi.org/10.1111/syen.12470

Crowl TA, Crist TO, Parmenter RR, et al. 2008. The spread of invasive species and infectious disease as drivers of ecosystem change. Front. Ecol. Environ. 6(5):238–246. https://doi.org/10.1890/070151

Curtis CA, Bradley BA. 2016. Plant distribution data show broader climatic limits than expert-based climatic tolerance estimates. Naya DE, editor. PLoS One 11(11):e0166407. https://doi.org/10.1371/journal.pone.0166407

Davis J, Goadrich M. 2006. The relationship between Precision-Recall and ROC curves. In: Proceedings of the 23rd International Conference on Machine learning - ICML'06. Pittsburgh, Pennsylvania: ACM Press; p. 233–240. https://doi.org/10.1145/1143844.1143874

De Marco P, Nóbrega CC. 2018. Evaluating collinearity effects on species distribution models: an approach based on virtual species simulation. Bosso L, editor. PLoS One 13(9):e0202403. https://doi.org/10.1371/journal.pone.0202403

Di Febbraro M, Bosso L, Fasola M, et al. 2023. Different facets of the same niche: Integrating citizen science and scientific survey data to predict biological invasion risk under multiple global change drivers. Global Change Biol. 29(19):5509–5523. https://doi.org/10.1111/gcb.16901

Droege S, Maffei C. 2023. Insect species occurrence data from multiple projects worldwide with focus on bees and wasps in North America. Kearneysville, WV, USA: United States Geological Survey. https://doi.org/10.15468/6AUTVB

Encarnação J, Teodósio MA, Morais P. 2021. Citizen science and biological invasions: a review. Front. Environ. Sci. 8:602980. https://doi.org/10.3389/fenvs.2020.602980

Etherington TR, Ward AI, Smith GC, et al. 2009. Using the Mahalanobis distance statistic with unplanned presence-only survey data for biogeographical models of species distribution and abundance: a case study of badger setts. J. Biogeogr. 36(5):845–853. https://doi.org/10.1111/j.1365-2699.2008.02041.x

Farber O, Kadmon R. 2003. Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance. Ecol. Model. 160(1-2):115–130. https://doi.org/10.1016/s0304-3800(02)00327-7

Fenn-Moltu G, Ollier S, Caton B, et al. 2023. Alien insect dispersal mediated by the global movement of commodities. Ecol. Appl. 33(1):e2721. https://doi.org/10.1002/eap.2721

Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37(12):4302–4315. https://doi.org/10.1002/joc.5086

Goulson D. 2003. Effects of introduced bees on native ecosystems. Annu. Rev. Ecol. Evol. Syst. 34(1):1–26. https://doi.org/10.1146/annurev.ecolsys.34.011802.132355

Gutierrez GM, LeCroy KA, Roulston TH, et al. 2023. *Osmia taurus* (Hymenoptera: Megachilidae): a non-native bee species with invasiveness potential in North America. Lupi D, editor. Environ. Entomol. 52(2):149–156. https://doi.org/10.1093/ee/nvad005

Haider M, Dorn S, Sedivy C, et al. 2014. Phylogeny and floral hosts of a predominantly pollen generalist group of mason bees (Megachilidae: Osmiini): phylogeny and floral hosts of *Osmia*. Biol. J. Linn. Soc. Lond. 111(1):78–91. https://doi.org/10.1111/bij.12186

Hedtke SM, Blitzer EJ, Montgomery GA, et al. 2015. Introduction of non-native pollinators can lead to trans-continental movement of bee-associated fungi. Nascimento FS, editor. PLoS One 10(6):e0130560. https://doi.org/10.1371/journal.pone.0130560

Downloaded from academic.oup.com/ee/article/53/6/1147/7828291 by guest on 14 November 2026

Jaumejoan X, Arnan X, Hagenbucher S, et al. 2023. Different effects of local and landscape context on pollen foraging decisions by two managed orchard pollinators, *Osmia cornuta* and *Bombus terrestris*. Agric. Ecosyst. Environ. 353:108528. https://doi.org/10.1016/j.agee.2023.108528

Jocher G, Chaurasia A, Qiu J. 2023. Ultralytics YOLOv8. https://github.com/ultralytics/ultralytics [accessed 1 July 2023].

Jolliffe IT. 2002. Principal component analysis. 2nd ed. New York: Springer (Springer series in statistics).

Kemp WP, Bosch J. 2005. Effect of temperature on *Osmia lignaria* (Hymenoptera: Megachilidae) Prepupa–adult development, survival, and emergence. J. Econ. Entomol. 98(6):1917–1923. https://doi.org/10.1603/0022-0493-98.6.1917

Kirillov A, Mintun E, Ravi N, et al. 2023. Segment Anything. https://github.com/facebookresearch/segment-anything [accessed 1 July 2023].

Kosmala M, Wiggins A, Swanson A, et al. 2016. Assessing data quality in citizen science. Front. Ecol. Environ. 14(10):551–560. https://doi.org/10.1002/fee.1436

Kraemer ME, Favi FD. 2005. Flower phenology and pollen choice of *Osmia lignaria* (Hymenoptera: Megachilidae) in Central Virginia. Environ. Entomol. 34(6):1593–1605. https://doi.org/10.1603/0046-225x-34.6.1593

Kraemer ME, Favi FD, Niedziela CE. 2014. Nesting and pollen preference of *Osmia lignaria lignaria* (Hymenoptera: Megachilidae) in Virginia and North Carolina orchards. Environ. Entomol. 43(4):932–941. https://doi.org/10.1603/EN13219

Kratschmer S, Petrović B, Curto M, et al. 2020. Pollen availability for the Horned mason bee (*Osmia cornuta*) in regions of different land use and landscape structures. Ecol. Entomol. 45(3):525–537. https://doi.org/10.1111/een.12823

Kriticos DJ, Webber BL, Leriche A, et al. 2012. CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. Methods Ecol. Evol. 3(1):53–64. https://doi.org/10.1111/j.2041-210x.2011.00134.x

Krunic M, Stanisavljević L, Pinzauti M. 2005. The accompanying fauna of *Osmia cornuta* and *Osmia rufa* and effective measures of protection. Bull. Insectol. 58(2):141–152.

LeCroy KA, Savoy-Burke G, Carr DE, et al. 2020. Decline of six native mason bee species following the arrival of an exotic congener. Sci. Rep. 10(1):18745. https://doi.org/10.1038/s41598-020-75566-9

LeCroy KA, Krichilsky E, Grab HL, et al. 2023. Spillover of chalkbrood fungi to native solitary bee species from non-native congeners. J. Appl. Ecol. 60(6):1067–1076. https://doi.org/10.1111/1365-2664.14399

MacIvor JS, de Keyzer CW, Marshall MS, et al. 2022. Establishment of the non-native horned-face bee *Osmia cornifrons* and the taurus mason bee *Osmia taurus* (Hymenoptera: Megachilidae) in Canada. PeerJ 10:e14216. https://doi.org/10.7717/peerj.14216

Normandin E, Vereecken NJ, Buddle CM, et al. 2017. Taxonomic and functional trait diversity of wild bees in different urban settings. PeerJ 5:e3051. https://doi.org/10.7717/peerj.3051

Pedregosa F, Varoquaux G, Gramfort A, et al. 2011. Scikit-learn: machine learning in Python. J. Mach. Learn. Res. 12:2825–2830.

Pereira FW, Zamoner M, Gonçalves RB. 2024. The potential of iNaturalist for bee conservation research—A study case in a southern Brazilian metropolis. Insect Conserv. Diver. 17(2):386–395. https://doi.org/10.1111/icad.12711

Perrings C, Dehnen-Schmutz K, Touza J, et al. 2005. How to manage biological invasions under globalization. Trends Ecol. Evol. 20(5):212–215. https://doi.org/10.1016/j.tree.2005.02.011

Pinilla-Gallego MS, Isaacs R. 2018 Jul 31. Pollen Use by *Osmia lignaria* (Hymenoptera: Megachilidae) in Highbush Blueberry Fields. Ann. Entomol. Soc. Am 111(6):335–340. https://doi.org/10.1093/aesa/say028

Pitts-Singer TL, Cane JH, Trostle G. 2014. Progeny of *Osmia lignaria* from distinct regions differ in developmental phenology and survival under a common thermal regime. J. Insect Physiol. 67:9–19. https://doi.org/10.1016/j.jinsphys.2014.05.018

Pocock MJ, Roy HE, Preston CD, et al. 2015. The Biological Records Centre: a pioneer of citizen science. Biol. J. Linn. Soc. 115(3):475–493.

Polidori C, Sánchez-Fernández D. 2020. Environmental niche and global potential distribution of the giant resin bee Megachile sculpturalis, a rapidly spreading invasive pollinator. Global Ecol. Conserv. 24:e01365. https://doi.org/10.1016/j.gecco.2020.e01365

Prenter J, MacNeil C, Dick JTA, et al. 2004. Roles of parasites in animal invasions. Trends Ecol. Evol. 19(7):385–390. https://doi.org/10.1016/j.tree.2004.05.002

Radmacher S, Strohm E. 2011. Effects of constant and fluctuating temperatures on the development of the solitary bee *Osmia bicornis* (Hymenoptera: Megachilidae). Apidologie 42(6):711–720. https://doi.org/10.1007/s13592-011-0078-9

Russo L. 2016. Positive and negative impacts of non-native bee species around the world. Insects 7(4):69. https://doi.org/10.3390/insects7040069

Russo L, De Keyzer CW, Harmon-Threatt AN, et al. 2021. The managed-to-invasive species continuum in social and solitary bees and impacts on native bee conservation. Curr. Opin. Insect Sci. 46:43–49. https://doi.org/10.1016/j.cois.2021.01.001

Rust RW. 1974. The sytematics and biology of the genus *Osmia*, subgenera Osmia, Chalcosmia, and Cephalosmia (Hymenoptera: Megachilidae). Wasmann J. Biol. 32(1):1–93.

Rust RW. 1990. Spatial and temporal heterogeneity of pollen foraging in *Osmia lignaria propinqua* (Hymenoptera: Megachilidae). Environ. Entomol. 19(2):332–338. https://doi.org/10.1093/ee/19.2.332

Sedivy C, Dorn S. 2014. Towards a sustainable management of bees of the subgenus *Osmia* (Megachilidae; *Osmia*) as fruit tree pollinators. Apidologie 45:88–105. https://doi.org/10.3929/ETHZ-B-000078283

Silva DP, Vilela B, De Marco P, et al. 2014. Using ecological niche models and niche analyses to understand speciation patterns: the case of sister neotropical orchid bees. Chaline N, editor. PLoS One 9(11):e113246. https://doi.org/10.1371/journal.pone.0113246

Stout JC, Morales CL. 2009. Ecological impacts of invasive alien species on bees. Apidologie 40(3):388–409. https://doi.org/10.1051/apido/2009023

Thomson D. 2004. Competitive interactions between the invasive European honey bee and native bumble bees. Ecology 85(2):458–470. https://doi.org/10.1890/02-0626

Torchio PF, Asensio E. 1985. The introduction of the European bee, *Osmia cornuta* Latr., into the U.S. as a potential pollinator of orchard crops, and a comparison of its manageability with *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae). J. Kans. Entomol. Soc. 58(1):42–52.

Torchio PF, Asensio E, Thorp RW. 1987. Introduction of the European Bee, *Osmia cornuta*, into California almond orchards (Hymenoptera: Megachilidae). Environ. Entomol. 16(3):664–667. https://doi.org/10.1093/ee/16.3.664

USDA. 2018. 7 C.F.R. Part 322 [accessed 1 July 2023].

Vicens N, Bosch J. 2000. Pollinating efficacy of *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae, Apidae) on 'Red Delicious' apple. Environ. Entomol. 29(2):235–240. https://doi.org/10.1093/ee/29.2.235

Westreich LR, Westreich ST, Tobin PC. 2023. Native solitary bee reproductive success depends on early season precipitation and host plant richness. Oecologia 201(4):965–978. https://doi.org/10.1007/s00442-023-05354-5

White J, Son Y, Park Y-L. 2009. Temperature-dependent emergence of *Osmia cornifrons* (Hymenoptera: Megachilidae) adults. J. Econ. Entomol. 102(6):2026–2032. https://doi.org/10.1603/029.102.0602

Wittmann K, Gamal Ibrahim M, Straw AD, et al. 2024. Monitoring fast-moving animals—Building a customized camera system and evaluation toolset. Methods Ecol. Evol. 15(5):836–842. https://doi.org/10.1111/2041-210X.14322

Zhu G, Gutierrez Illan J, Looney C, et al. 2020. Assessing the ecological niche and invasion potential of the Asian giant hornet. Proc. Natl. Acad. Sci. U.S.A. 117(40):24646–24648. https://doi.org/10.1073/pnas.2011441117

Downloaded from academic.oup.com/ee/article/53/6/1147/7828291 by guest on 14 November 2026