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Contextualized niche shifts upon independent invasions by the dung beetle *Onthophagus taurus*

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Abstract The historical contingencies of biological invasions may have important consequences for final invasion outcomes. Here, we characterize the variations in the realized niche during the invasions of the bull-headed dung beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae) from its native Mediterranean range following accidental (Eastern North America) as well as deliberate (Western North America, Western Australia, and Eastern Australia) releases into novel, exotic ranges approximately 50 years ago.

Specifically, we examined whether the climatic responses of exotic *O. taurus* have diverged from those characterizing their native range, and if so, to what degree and in what dimensions. We found that when compared to the native range, all exotic populations exhibited similar overlap proportions regardless of invasion history. However, more detailed analysis of climatic niche features showed that all three deliberately established populations were characterized by overall similar climatic niche features, whereas the accidentally-established Eastern North American populations have undergone significant changes in their climatic niche. Specifically, when

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analog climates were considered on the background of each pairwise range comparison, accidentally-established Eastern North American populations showed a different climatic niche expansion than their deliberately introduced Australian or Western North American counterparts, in particular towards colder and more humid climates. We discuss our results in the context of the widely divergent introduction histories of *O. taurus* in Australia and North America, and highlight the possible roles of contrasting propagule sizes, disparate genetic profiles and variances, adaptive processes and invadable landscapes in shaping invasion outcomes in the different exotic ranges.

Introduction

A species' range can be defined by the intersection of the suitable biotic and abiotic conditions accessible to its populations through migration (Soberón and Peterson 2005; Soberón 2007). Here, climatic conditions are generally considered the most important determinants of species ranges (Soberón and Nakamura 2009; Soberón 2010; Guisan et al. 2014; Lenoir and Svenning 2014), after accounting for the effect of historical processes that restrict the presence of the species to certain regions (Jiménez-Valverde et al. 2008; Hortal et al. 2012). The same factors delineate the outcome of invasion events, except that in such cases the limitations normally imposed on natural migration are reduced or eliminated via direct human-mediated dispersal and/or elimination of dispersal boundaries (Soberón 2007; Jiménez-Valverde et al. 2011; Guisan et al. 2014). Furthermore, pre-adaptions to the environmental conditions available in potential exotic ranges, and the ability to rapidly evolve or otherwise adjust following initial colonization further impact a species' success during the occupation of new ranges (Sakai et al. 2001; Müller-Schärer and Steinger 2004; Müller-Schärer et al. 2004; Sax et al. 2007).

Current availability of species occurrences and climatological data (Graham et al. 2004; Hijmans et al. 2005) allowed species distribution models (SDMs from here on) to be widely used to test for climatic niche evolution in invasion events (Fitzpatrick et al. 2007; Bradley et al. 2010; Da Mata et al. 2010; Araújo and Peterson 2012; but see Jiménez-Valverde et al. 2011). This practice, however, has recently come under criticism (Jiménez-Valverde et al. 2011; Peterson et al. 2011; Soberón and Peterson 2011; Barve et al. 2011). More specifically, SDMs rely on climatic niche conservation between native and exotic ranges (Pearman et al. 2008; Colwell and Rangel 2009; Peterson 2011), an assumption only partly supported by existing data (Hortal et al. 2012; Guisan et al. 2014). Different SDMs also differ in how they weigh and emphasize the climatic variables used to model species' potential distributions, thereby risking the eventual elimination of important determinants of the distribution of the target organism (Broennimann et al. 2012).

Since occurrence records constitute the main source of data used to describe species' potential distributions, optimal and suboptimal locations are pooled together as equally relevant under the "presence" category. This complicates quantifying a species' true climatic niche, because sink populations are not distinguishable from those inhabiting suitable conditions (see Soberón and Nakamura 2009). Additionally, using SDMs to test for climatic niche shifts in an invasive species requires accepting the assumption of equilibrium of its native distribution with the climatic conditions, which is often not true (Araújo and Pearson 2005; Colwell and Rangel 2009; McInerny and Etienne 2012a), especially in invasive species (Jiménez-Valverde et al. 2011). Finally, comparisons restricted only to the geographic projections generated by SDMs may also vary depending, for instance, on the distribution of climatic gradients in the study area (Broennimann et al. 2012). Given these constraints, there can be uncertainty about whether a calculated distribution truly corresponds to the one occupied by a given exotic species, thereby limiting the confidence with which climatic niche shifts can be assessed (Jiménez-Valverde et al. 2011; Araújo and Peterson 2012).

Even though it remains affected by some of these issues, the ordination method proposed by Broennimann et al. (2012) reduces the impact of these shortcomings by equally weighting all environmental variables thought to be important in determining the

climatic niche features of the target species, optimizing the description of the species' geographic and environmental spaces. Moreover, this method also accounts for sampling biases in the occurrence data (from unsystematic sampling designs) and corrects the densities of known species occurrences considering the environmental space available for the species. Finally, the method relies solely on the species' environmental space, without generating projections onto geographic space. Taken together, these characteristics allow us to evaluate climatic niche features of invasive species currently occupying new ranges while avoiding many of the shortcomings of traditional SDM approaches, and put us in a position to utilize species invasions as "natural experiments" to gain insights into the evolutionary ecology of niche differentiation (Sax et al. 2007; Prentis et al. 2008). Here we utilize this approach to evaluate and contrast post-invasion niche shifts across diverse populations of the bull-headed dung beetle *O. taurus* (Coleoptera: Scarabaeidae) during their invasions of both Australia and North America.

Onthophagus taurus originally exhibited a Mediterranean distribution (Balthasar 1964; Fig. 1a). However, following a series of accidental and deliberate releases, it is now well established in both Eastern and Western portions of Australia (Fig. 1b), as well as parts of the Eastern and Western US (Fig. 1c). The introduction to the Eastern US is believed to have occurred accidentally via a single and small founding population of unknown Mediterranean origin, first discovered in Northern Florida in 1971 (Fincher and Woodruff 1975; Hoebeke and Beuchke 1997). Following its initial detection in the Florida panhandle, the species has spread rather rapidly north- and westward, though no deliberate redistribution efforts have been recorded. In contrast, *O. taurus* was released deliberately, and around the same time, into Eastern and Western Australia (Fig. 1c), as well as the Western US, to help control cow dung and dung-breeding flies (Waterhouse 1974; Tyndale-Biscoe 1990; Doube et al. 1991; Hoebeke and Beuchke 1997; Anderson and Loomis 1998; Evans and Hogue 2004). All three planned introductions are well documented and derive from the same source populations collected originally in Spain, Greece, and Turkey, which were combined and bred collectively in quarantine facilities of the *Commonwealth Scientific Research Organization (CSIRO)* of Australia (AMRC
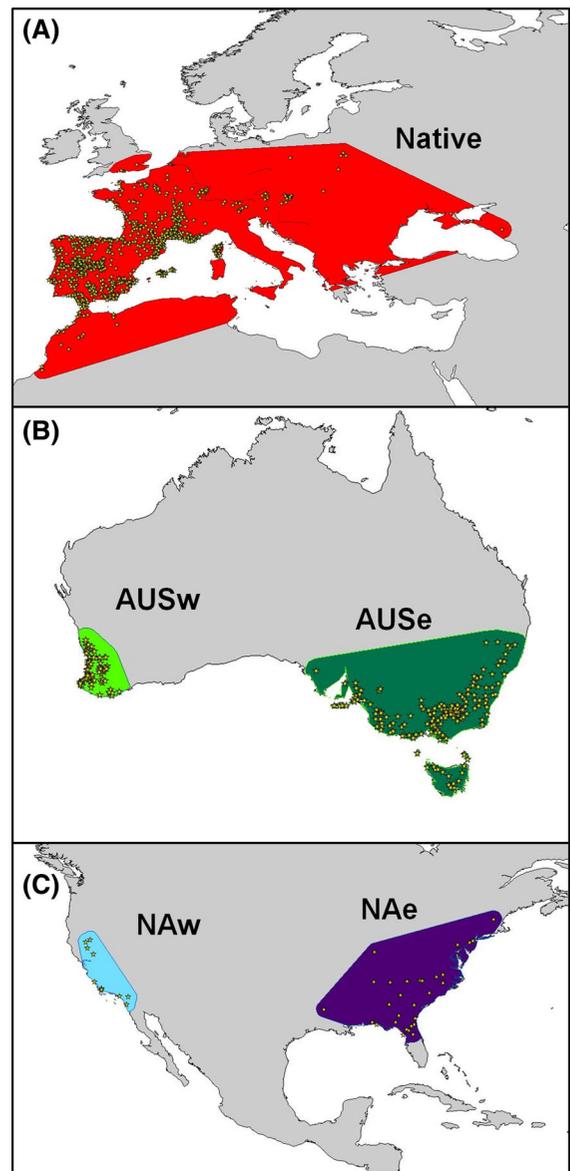
Fig. 1 Geographic distribution of the dung beetle *Onthophagus taurus*. *Stars* represent the occurrence data gathered for each of the geographical backgrounds considered in (**a**) its Native Mediterranean Range—Native (*red*); (**b**) Western (*light green*) and Eastern Australian (*dark green*) exotic ranges (AUSw and AUSe, respectively); and (**c**) Western (*light blue*) and Eastern North American (*purple*) exotic ranges (NAw and NAe, respectively)

1982; Tyndale-Biscoe 1990, 1996), with the resulting offspring being used to fuel individual releases in all three regions.

For Eastern and Western Australia, at least 36 releases with 500–1800 individuals per release were

recorded to have taken place between 1969 and 1983 (Tyndale-Biscoe 1996). No deliberate re-distributions of *O. taurus* from Eastern to Western Australia or vice versa have been documented, and natural migration is likely to be minimal or absent given the vast expanses of arid environment separating both Australian ranges. Lastly, in the Western US *O. taurus* was released in California, beginning in 1973 as part of a collaboration between state agricultural authorities, the University of California at Davis, the US Department of Agriculture, and the CSIRO, which provided the initial breeding stock of *O. taurus* (Hoebeke and Beuchke 1997; Anderson and Loomis 1998; Evans and Hogue 2004). Releases involved up to four different species depending on year including *O. taurus*, and totaled an estimated 680,000 beetles from 1974 to 1977, after which the program was terminated (Anderson and Loomis 1998; Evans and Hogue 2004). In summary, a single and small introduction event in the early 1970s is believed to have initiated *O. taurus'* introduction to the Eastern US, whereas three roughly simultaneously conducted deliberate introduction programs utilizing the same Mediterranean source populations were responsible for the introductions of *O. taurus* to the Eastern US, Eastern Australia, and Western Australia.

Here, we use these similarities and differences in introduction histories to examine the potential influences of invasion mode on realized niches and potential niche differentiation. Specifically, we predict that the single and accidental introduction of *O. taurus* into the Eastern US would have resulted in a strong founder effect and the likely failure to representatively capture the genetic diversity present within the native range. Consequently, the realized niche of North American *O. taurus'* populations may be predicted to either represent a fraction of that of the populations in the native Mediterranean range (reflecting the fraction of the native genetic diversity retained in this population) or, alternatively, depart altogether from the native realized climatic niche (due to founder effect-mediated rapid evolution). In contrast, the planned and repeated introduction of a genetically diverse pool of *O. taurus* individuals into Eastern and Western Australia as well as the Western US should have reduced the probability of founder effects, causing the realized climatic niche of these populations to resemble more closely that of the species' native range.

Methods

We gathered occurrence data records for *O. taurus* from: (1) the Global Biodiversity Information Facility and related institutions (GBIF; http://www.gbif.org; see additional list); (2) the BANDASCA database (Lobo and Martín-Piera 1991); (3) literature records (Supplementary Information); (4) confirmed identified photographs with a minimum of nearest city as geographic reference information from BugGuide.net (http://www.bugguide.net); (5) records from A. Moczek's, K. Floate's, and J. Ridsdill-Smith's personal collections; and (6) Published literature papers. A full list of all studies used to obtain records of *O. taurus*, as well as entomological collections that provided occurrences to the GBIF database, are found in the Supplementary Files. We used Google Earth (Google Inc 2015) and Global Gazetteer version 2.2 (http://www.fallingrain.com) to obtain proxy coordinates from the city halls for records with city/county lacking geographic coordinates. We assembled 1272 records for *O. taurus*. We applied a 10 km buffer around each one to minimize geographical sampling biases, using the spThin R package (Aiello-Lammens et al. 2015), which resulted in 1058 geographically unique occurrences considering the thinning distance applied in our analyses. Then, we considered a minimum convex polygon around the occurrences and the estimated annual dispersal rates for *O. taurus* (130–200 km; Hanski and Cambefort 1991) to define five different geographical backgrounds, as the region defined by a buffer of one degree width around the occurrences in each separate region. Considering the wide niche breadth of this species (Martin-Piera and Lobo 1996), which as a generalist dung beetle is able to consume a variety of dung types, we assumed that species dispersal was not limited by dung availability. The five geographical backgrounds considered (Fig. 1) were: (1) Native Mediterranean Range (hereafter just referred as Native; $n = 785$), (2) Eastern Australian Range (AUSe; $n = 164$), (3) Western Australian Range (AUSw; $n = 69$), (4) Eastern North American Range (NAe; $n = 29$), and (5) Western North American Range (NAw; $n = 11$).

We considered a grid of cells of $0.16°$ size in all analyses. We gathered 19 environmental variables from WorldClim (http://www.worldclim.org) and cropped them according to the above mentioned background regions. Considering the methods

proposed by Broennimann et al. (2012), we evaluated *O. taurus* climatic niche features among all of its five occupied ranges calibrated on each available geographical background.

We used the methods developed by Broennimann et al. (2012) to assess whether the environmental niche of this dung beetle species changed when it dispersed from its Native range into the four other ranges it currently occupies. We chose the PCA-env approach outlined by Broennimann et al. (2012) to consider all ranges occupied by *O. taurus* simultaneously. As a first step, this method considers the density of occurrences of the species, using a smooth kernel density function to correct for potential sampling biases (Broennimann et al. 2012). Second, it considers the environmental variables available within the entire background defined by the species annual dispersal rates. Next, this method transforms the correlated environmental variables into orthogonal (independent) new principal components, thereby allowing the comparison between the environmental spaces available for the species in the different biogeographic regions it occupies. The first two axes from the PCA-env are later considered as the available environmental space for the species to disperse, while the known occurrences for the beetles are used to generate the conditions occupied by the species in each invaded range alongside the environmental niche overlap between them. Finally, the analysis executes pairwise comparisons of all five different ranges occupied by the species.

We compared the environmental conditions available for the species within each of the four exotic ranges (AUSe, AUSw, NAe, and NAw) to those found within the Native range as well as between each pair of exotic ranges. In these comparisons, our approach generated occurrence density models, while correcting for the environmental conditions available in the spatial scale for the analyzed species, and calculated observed niche overlap scores using Schoener's D (Schoener 1970; Broennimann et al. 2012), which varies from 0 (complete dissimilarity between the compared environmental niches) to 1 (complete overlap). We then tested for niche equivalency between the compared ranges by randomizing the occurrence records in both backgrounds and recalculating Schoener's D 100 times in order to produce a null distribution of overlap scores, which we then compared to the observed value, as proposed by Warren et al. (2008).

An observed overlap score that is significantly smaller than one obtained with the null distribution of overlap scores suggests that the focus species is occupying different environmental spaces in the considered ranges. We thus measured niche similarity between each pair of ranges by comparing the overlap of one range with randomized occurrences on the background conditions of the other ($1 \rightarrow 2$), keeping the original number of occurrences, and vice versa ($1 \leftarrow 2$). We repeated this process 100 times in order to produce a null distribution of overlap scores, which was then compared to the observed value. Significantly higher overlap scores indicate more similar environmental conditions across two occupied ranges than expected by chance (Broennimann et al. 2012), whereas significantly lower overlap scores denote more dissimilar environmental niches and the use of unique environmental space across two occupied ranges. We used the package *ecospat* (Broennimann et al. 2014) in R (R Development Core Team 2015) to obtain the proportion of climatic niche in each comparison that was either in expansion, stabilized, or unfilled, following analyses proposed by Guisan et al. (2014). Despite the overwhelming amount of results that can be generated in this kind of analyses, here we will only discuss the differences between the climatic niche of *O. taurus* in its native range and that observed in the exotic ranges after the invasion events (direction $1 \rightarrow 2$, considering only the comparisons of the native vs. the exotic ranges).

The rationale for this method is based on comparisons between both native and invaded ranges and comparisons of all the climatic conditions available and occupied by the species in both ranges. Considering environmental conditions found in both ranges, if the overlap of the occupied conditions is considerable, the climatic niche of the populations in the invaded range would be considered as stabilized. If the overlap of available conditions in both ranges is small, but all environmental conditions in the invaded range overlap with those of the native one, the niche of the species in the invaded range is considered unfilled, when compared to the native one. On both of these scenarios, no niche shift is expected to have occurred during the invasion process. Finally, still considering only the similar conditions available in both ranges, if the overlap between the pair of occupied ranges that is compared is very small or inexistent, then it can be assumed that there was a niche expansion in the

populations of the invaded range in comparison to the native one. Throughout the text, we depict the Native range of *O. taurus* in red and the invaded ranges in Western Australia (AUSw), Eastern Australia (AUSe), Western North America (NAw), and the Eastern North America (NAe) in light green, dark green, light blue, and purple, respectively. A file including a detailed description of our methods and analyses, including all R code used to generate the results, is available in the Supplementary Files.

Results

The first two PCA axes generated in our multivariate analyses combined explain 64.47 % of the original environmental variation (41.41 % for the first and 23.06 % for the second one; Figure S1A). The most important variables according to our density plots were annual mean temperature (bio 1), mean temperature of the coldest quarter (bio 11), mean temperature of warmest quarter (bio 10), maximum temperature of warmest period (bio 5), and mean diurnal range (bio 2). The contributions of each variable to each of the two PCA axes are shown in Figure S1B-C. All pairwise comparisons between the five *O. taurus* ranges yielded variable proportions of overlap, ranging from 0.161 to 0.442 (Table 1; Table S1–S2; Figure S1). When compared only to the Native range, the accidental NAe range exhibited the smallest overlap proportion (0.180), followed by all three deliberately established exotic ranges: AUSw (0.182),

AUSe (0.299), and finally NAw (0.442). In general, while the planned introductions (AUSw, AUSe, and NAw) resulted in populations occupying slightly more humid climatic conditions than those found in the Native range, populations in the accidental NAe range occupied areas that were considerably colder and more humid (Fig. 2). Furthermore, both AUSw and NAw ranges exhibited realized climatic niches that were significantly more similar to the Native range than expected by chance (assuming an alpha of 0.05 in the niche stability test, keeping the native range fixed and randomizing the invaded range), whereas the climatic conditions inhabited by *O. taurus* within the NAe and AUSe ranges did not exhibit high similarity to the Native range (Table 1). Figure 3 illustrates the proportion of overlap among all ranges considered in this analysis.

Lastly, the climatic niches of the invaded ranges of *O. taurus* showed high degrees of filling of the niche space (Native [1] → invaded ranges [2]; Table 1) and niche expansion (Table 1) when compared to the Native range. At the same time, environmental niche stability with the Native range was high in all comparisons to exotic *O. taurus* ranges (Table 1; Table S3–S5). Still, the niche similarity of the native range was statistically significant to that observed in both NAw and AUSw ranges, while it was not in the comparisons between the native range and NAe and AUSe. The lack of similarity between native and NAe ranges conforms with the notion that this exotic range is showing different environmental features than that observed in the native one (Table S2).

Table 1 Pairwise comparisons of niche overlap (D), niche similarity, niche unfilling (i.e., lack of filling the available climatic space), niche stability, and niche expansion between each one of the invaded ranges of *Onthophagus taurus* when compared to its native range, according to the framework of Broennimann et al. (2012)

IRs	Overlap (D)	Similarity test Native → IRs *p* values	Niche unfilling Native → IRs	Niche stability Native → IRs	Niche expansion Native → IRs
NAw	0.442	**0.050**	0.000	0.931	0.069
NAe	0.180	0.119	0.000	0.948	0.052
AUSw	0.182	**0.020**	0.022	0.963	0.037
AUSe	0.299	0.317	0.016	0.980	0.020

Note that the niche similarity test verifies whether the niche overlap between two ranges is greater than expected by chance

Native Native Mediterranean Range, *AUSe* Eastern Australian Range, *AUSw* Western Australian Range, *NAe* Eastern North American Range, *NAw* Western North American Range, *IRs* Invaded Ranges

Bold values represent significant *p* values ($\alpha = 0.05$)
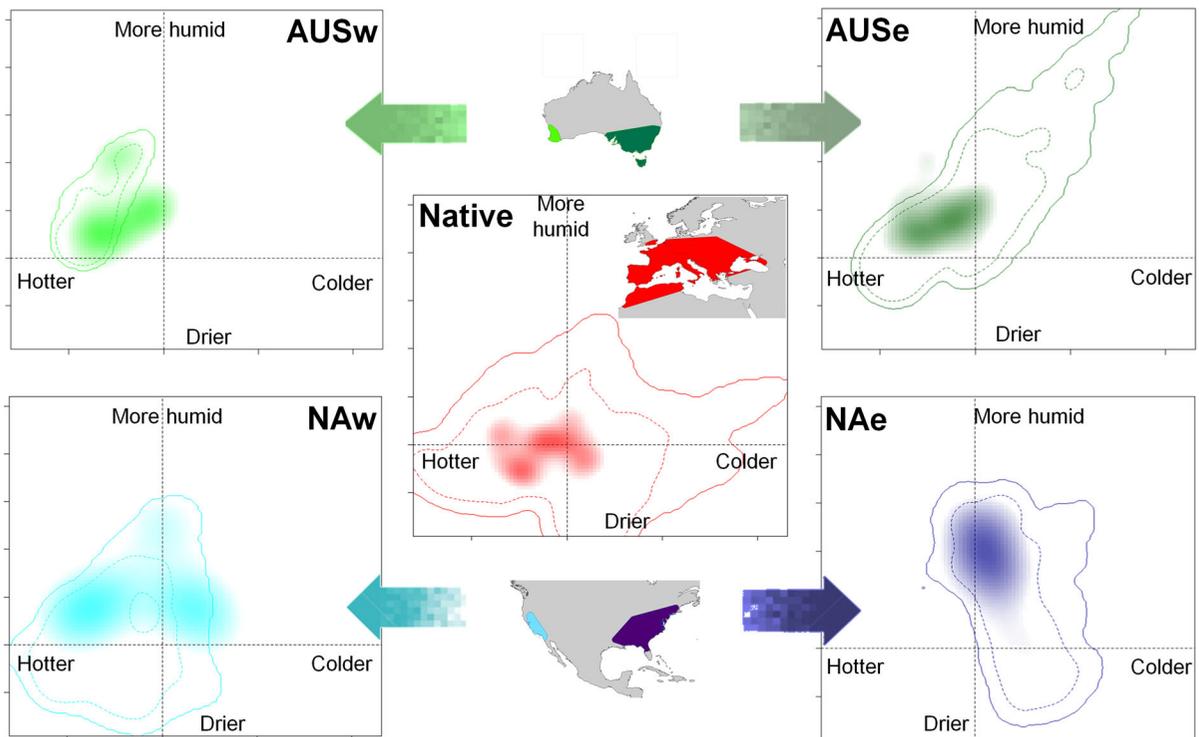
Fig. 2 Climatic conditions occupied by *Onthophagus taurus* in all of its known distributional ranges, showing the results obtained from the environmental niche analysis. The *solid* and the *dashed lines* illustrate, respectively, 100 and 50 % of the available (background) climate for *O. taurus* in each one of its ranges. The *shading* follows the same scheme used in Fig. 1, where the Native range is represented in *red*, Western Austalia (AUSw) is in *light green*, Eastern Australia (AUSe) is in *dark green*, Western North America (NAw) is in *light blue*, and Eastern North America (NAe) is in *purple*

Although a D value of 0.299 was found between the native range and AUSe, the lack of similarity indicates that this value is not different from what would be expected from a random invasion process. Therefore, such overlap may be explained by the similar climate conditions available on AUSe when compared to the native range.

Discussion

Our results show that the independent invasions of *O. taurus* resulted in significantly different realized niches, possibly due to the particular invasion context in each of its ranges. Specifically, both Australian (AUSw and AUSe) and North American (NAw and NAe) populations expanded their environmental niches beyond the climatic boundaries of the species' within its native Mediterranean range. Furthermore,

and consistent with our initial predictions, both Western Australian and Western North American populations exhibit a similar realized niche to that observed for the original Mediterranean range of *O. taurus*. Eastern Australian populations failed to yield a significant similarity test with the native range, yet examination of their respective climatic niche breadths nevertheless supports the existence of significant similarities and overlap in realized niches between Eastern Australian and native *O. taurus* populations.

In contrast, despite similar overlapping proportions, the accidentally established NAe population expanded towards colder and more humid climates not occupied in any of the other region, consequently showing a greater niche divergence than all the other studied ranges. Differences between the climatic space occupied by Mediterranean, Australian, and Western North American populations could be partially
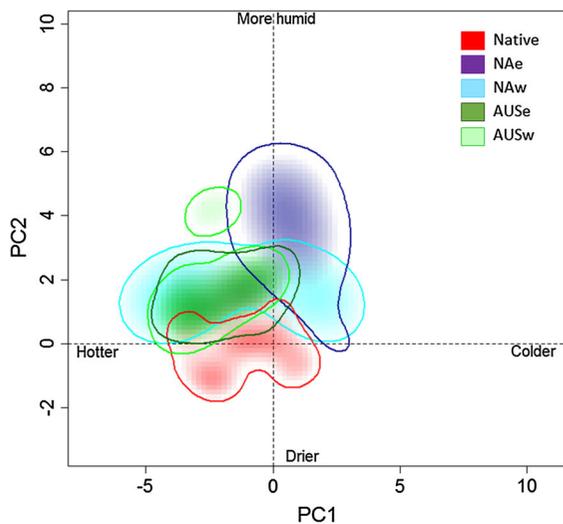
Fig. 3 Overlap of the realized climatic niches of *Onthophagus taurus* in all its considered (native and invaded) ranges. Native: *red*; Western North America (NAw): *light blue*; Eastern North America (NAe): *purple*; Western Australia (AUSw): *light green*; Eastern Australia (AUSe): *dark green*. The *solid line* represents 10 % of the occurrence density

attributed to small differences in the available climates in both continents (as in Gouveia et al. 2014), since some of the climatic domains occupied by *O. taurus* populations in the Mediterranean range are simply not available in these exotic regions. Although some areas in the NAe range have environmental features very similar to those found in the native range of *O. taurus*, in the former there is also a wide availability of new environmental conditions that do not occur in the latter. Therefore, differences in the realized niche between the deliberate releases (AUSe, AUSw, NAw) and the accidental one (NAe) when compared to the native range may be attributed by the lack of adequate climates for the species in the NAe range.

The limited influence of climate availability on niche expansion raises the possibility that differences in the realized niche may be due to the different histories of colonization in Australia and North America. While both Australian as well as the Western North American introductions involved numerous releases of large numbers of genetically heterogeneous individuals from different Mediterranean source populations, the Eastern North American introduction was seeded by a single event of a modest number of individuals from a single Mediterranean source population. Previous work has shown that the number of

introduced individuals and the frequency of introductions are key factors for the success of invasive species when expanding into new ranges (Lockwood et al. 2005; Drake et al. 2005; Simberloff 2009; Deacon et al. 2011; Forsman 2014). Invasions involving large numbers of individuals, diverse original populations and/or high frequency of introductions ($\approx$ smaller propagule pressure) are generally more resistant to stochastic events and produce more genetically and phenotypically diverse populations. This could in turn enable more significant niche evolution following initial colonization (Simberloff 2009; Deacon et al. 2011). However, invasions with higher propagule pressure and low individual abundances may result in Allee effects and genetic disruptions that, when transcended, may result in even more pronounced genetic differences between native and introduced populations (Courchamp et al. 1999; Kanarek and Webb 2010). This could also increase the probability of fixing adaptive genetic variants conducive to using new niche space after colonization. It is thus conceivable that the divergent introduction histories of *O. taurus* in North America and Australia may have led to the emergence of different realized niches for *O. taurus* in both exotic ranges.

Alternatively, or in addition, pre-existing ecological differences between Australian and North American ranges may have shaped differential niche evolution in both ranges. Prior to the introduction of *O. taurus* in North America, cow dung was already used by many native *Onthophagus* and other dung beetle species, which in turn provided an important resource for specialized dung beetle predators, parasitoids, and brood parasites (Davis 1958; Kohlmann 1991). Pre-existing competitors, predators, and parasites may therefore have both reduced the accessibility of available niche space in Eastern North America and generated selection pressure on invading *O. taurus* to diversify into novel niche ranges. In contrast, for both Western and Eastern Australian populations, cow dung is as exotic a resource as is *O. taurus* as a dung beetle (Bornemissza 1976). Even though more than 200 *Onthophagus* species are native to Australia (Matthews 1972; Storey and Weir 1988, 1990), nearly all are specialized to feed and breed on marsupial dung and for the most part do not use cow dung as a resource (Matthews 1972; Moczek 2003). As a consequence, *O. taurus* released into Australia were likely to have encountered an ecological space rich in resources but

largely free of native competitors, predators, parasites, or other biotic pressures that otherwise would have forced a more significant niche expansion. That said, *O. taurus* was one of ultimately 52 species of dung beetles introduced into Australia between 1969 and 1984 to help control cattle dung abundances (Bornemissza 1976; Tyndale-Biscoe 1996; Duncan et al. 2009). Even though many of these introductions failed (Duncan et al. 2009), those that led to established heterospecific populations could have exerted at least some competitive pressure on *O. taurus* in selected locations. Differences in the type and densities of large herbivore communities in North America (hoofed mammals) and Australia (dominated by marsupials) may have further contributed to providing different opportunities for niche expansion in different exotic ranges.

Finally, it is worth noting that while the smoothed kernel method utilized in this study constitutes a useful approach, in part due to its ability to allow for the comparison of "entities" (*sensu* Broennimann et al. 2012) from different taxonomic, geographic or temporal perspectives, it also suffers from significant limitations, such as a strong dependency on occurrence data and the diverse biases inherent to surveys (Reddy and Davalos 2003; Sastre and Lobo 2009; Pyke and Ehrlich 2010; Newbold 2010). Consequently, the observed ranges and/or environmental conditions defining the distribution of a species provide a likely incomplete estimation of its true realized niche (Broennimann et al. 2012). For invasive species, as is the case of *O. taurus*, the reality is possibly even more complex, because such species are likely not in equilibrium with the environmental conditions of their newly invaded range (Araújo and Pearson 2005; Colwell and Rangel 2009; McInerny and Etienne 2012a). In this study, however, the range with the smallest number of occurrences, and thus the greatest probability of sampling bias, was NAw ($n = 11$), followed by NAe ($n = 29$), followed lastly by both Australian ranges (more than 50 occurrences each). Despite the small amount of occurrences for NAw, this range emerged as very similar to both the native and the Australian ranges. In constrast, NAe—with almost three times the number of occurrences than NAw, differed significantly from all other ranges, whether inhabited by native and deliberate released

populations. Thus, we would expect our results to be robust even if more occurrences are sampled in future studies.

Concluding remarks

Our results illustrate that an evaluation of niche evolution that is based on approaches that only consider a species' known occurrences and realized niche are prone to disregard biological processes (e.g. competition, mutualisms, predation, parasitism) that may have shaped a species' realized niche (Soberón 2007, 2010; Hortal et al. 2012; McInerny and Etienne 2012a, b, c; Guisan et al. 2014). Without being able to fully consider the fundamental niche of an invasive species, a meaningful assessment of the causes of invasion success or failure thus remains difficult (Soberón and Peterson 2005; Soberón 2007; Jiménez-Valverde et al. 2011; Araújo and Peterson 2012; Guisan et al. 2014). With the increasing availability of occurrence records, many studies have attempted to substantiate niche evolution using SDMs and multivariate analyses (Fitzpatrick et al. 2007; Petitpierre et al. 2012; Strubbe et al. 2013, 2015; Higgins and Richardson 2014). However, the available evidence suggests that the majority of invasive species considered in these studies may in fact be failing to fill the climatic space available in their native ranges, rather than exhibiting true niche shifts in the exotic ones (e.g. plants: Petitpierre et al. 2012; Faleiro et al. 2015; birds: Strubbe et al. 2013; Strubbe and Matthysen 2014, mammals: Strubbe et al. 2015; but see Ancillotto et al. 2015).

This is particularly important when we consider the North American populations of *O. taurus*: without knowing their precise origin and how their abundances may have oscillated through time and space, it is impossible to fully determine the climatic requirements that regulate their densities. Therefore, additional data and physiological experiments involving sample populations from all five ranges (Native and all four exotic ones), are necessary to better evaluate the species' physiological responses within each particular range (Tingley et al. 2014). Such experiments would be especially useful in order to predict the behavior of *O. taurus* in yet another and very recently established new range: New Zealand (Dymock 1993).

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