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E-Article

A Toad More Traveled: The Heterogeneous Invasion Dynamics of Cane Toads in Australia

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abstract: To predict the spread of invasive species, we need to understand the mechanisms that underlie their range expansion. Assuming random diffusion through homogeneous environments, invasions are expected to progress at a constant rate. However, environmental heterogeneity is expected to alter diffusion rates, especially by slowing invasions as populations encounter suboptimal environmental conditions. Here, we examine how environmental and landscape factors affect the local invasion speeds of cane toads (*Chaunus* [*Bufo*] *marinus*) in Australia. Using high-resolution cane toad data, we demonstrate heterogeneous regional invasion dynamics that include both decelerating and accelerating range expansions. Toad invasion speed increased in regions characterized by high temperatures, heterogeneous topography, low elevations, dense road networks, and high patch connectivity. Regional increases in the toad invasion rate might be caused by environmental conditions that facilitate toad reproduction and movement, by the evolution of long-distance dispersal ability, or by some combination of these factors. In any case, theoretical predictions that neglect environmental influences on dispersal at multiple spatial scales may prove to be inaccurate. Early predictions of cane toad range expansion rates that assumed constant diffusion across homogeneous landscapes already have been proved wrong. Future attempts to predict range dynamics for invasive species should consider heterogeneity in (1) the environmental factors that determine dispersal rates and (2) the mobility of invasive populations because dispersal-relevant traits can evolve in exotic habitats. As an invasive species spreads, it is likely to encounter conditions that influence dispersal rates via one or both of these mechanisms.

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Invasive species pose critical threats to native biological diversity and impose a substantial financial burden on economies throughout the world (Wilcove et al. 1998; Pimentel et al. 2005). Despite the global significance of invasive species, our ability to predict their spread remains limited (Holt et al. 2005). Improved understanding of the mechanisms underlying rates of range expansion by introduced species can serve to clarify why some species spread rapidly across novel environments while others only incrementally expand their range or fail to spread at all. In this way, invasive species offer a window into the general mechanisms that underlie the range dynamics of all species (Elton 1958; Holt et al. 2005), a topic of clear relevance as species shift their ranges because of climate change (Parmesan 2006). Here, we use data from one of the best-documented invasions in natural history, the cane toad's (*Chaunus* [*Bufo*] *marinus*) continuing colonization of Australia, to evaluate regional heterogeneities in the speed of its range expansion and then to relate these patterns to environmental variation.

Historically, invasion has been modeled as a simple random-diffusion process. Assuming random and localized dispersal through homogeneous environments, the radial ($\text{area}^{1/2}$) range of an invading species is expected to increase linearly with time (Fisher 1937; Skellam 1951). In many cases, such as the muskrat in Europe (Skellam 1951), the sea otter in California (Lubina and Levin 1988), and the coypu in Great Britain (Reeves and Usher 1989), predictions based on linear diffusion perform well. However, in other cases, accelerating invasion dynamics have been described (Andow et al. 1990; Shigesada et al. 1995; Silva et al. 2002; Liebhold and Tobin 2006). Accelerating range expansions often are attributed to a nonzero probability of long-distance dispersal that generates a "fat-tailed" dispersal kernel (where the dispersal kernel is the probability density function describing the displacement of individuals from a point over time; Kot et al. 1996; Caswell et al. 2003; Clark et al. 2003). Fat-tailed dispersal

kernels can lead to a rapid acceleration of invasion dynamics as long-distance dispersers form multiple satellite populations that then coalesce into an ever-widening range (Shigesada et al. 1995).

An alternative and perhaps complementary reason for accelerating or decelerating invasion patterns involves the effect of environmental conditions on a species' movement and demography. Underlying landscape heterogeneity in factors such as climate, resources, or habitat connectivity may give rise to strongly differing expansion rates across space (Lubina and Levin 1988; Grosholz 1996; Smith et al. 2002). These differing expansion rates can occur simply because species-specific movement behavior or fitness covaries with the underlying environment and landscape matrix (With 2002). In such cases, separate regions of the invasion will likely be characterized by different dynamics (e.g., linear, decelerating, or accelerating). In addition, we can expect that as an organism realizes the spatial limits of its niche, suboptimal environments will curb the forward progress of an invasion and demarcate a stable range boundary (Shigesada et al. 1995; Wangen and Webster 2006).

Thus far, most proposed mechanisms of variable range expansion have been based on the assumption that the dispersal kernel or the environmental dependence of the dispersal kernel remains constant over time and space (reviewed by Hastings et al. [2005]). This assumption of kernel constancy is likely to be violated when evolution modifies either the kernel or its relationship to environmental variables. Such evolution can occur when landscape heterogeneity creates regions of variable natural selection and lowered gene flow. Under these circumstances, natural selection may change dispersal rates across an invasive species' expanding range in response to local environmental conditions. Evolution may also drive an increase in dispersal ability through simple spatial assortment by dispersal ability on the invasion front. Simulations and empirical data suggest the possible evolution of higher dispersal rates at the edges of expanding populations (Travis and Dytham 2002; Simmons and Thomas 2004; Phillips et al. 2006, 2008). Spatial variability in demographic or dispersal rates could thus interact with evolutionary shifts in the organism to generate divergent invasion trajectories that include heterogeneous accelerations of advance.

Discriminating among divergent patterns of spatial spread by invasive species can generate insights into the mechanisms underlying range expansion and can identify regions for intensive control efforts (Shigesada et al. 1995). Although more sophisticated theoretical frameworks are beginning to incorporate heterogeneous environmental conditions in order to predict rates of range expansion (reviewed by Shigesada and Kawasaki [1997]; Hastings et al. [2005]), rarely have ecological and landscape variables been linked explicitly with observed invasion rates. The few attempts at evaluating the relationship between local invasion speed and environmental heterogeneity have generally been limited to assessments of expansions across separate geographic regions (e.g., regions with either high or low minimum temperatures; Liebhold et al. 1992), indirect analyses of the probability of patch colonization over time (Silva et al. 2002; Smith et al. 2002), or a post hoc explanation for divergent invasion rates along two transects (Lubina and Levin 1988). Few studies have analyzed the environmental determinants of invasion speed because such analyses require large data sets that document invasions over a long enough time period to allow for accurate estimates of speed and acceleration. Fortuitously, concern for the effect of cane toads on native Australian wildlife has prompted an expansive and enduring effort to catalog its spread. This attention has resulted in the documentation of cane toad invasion dynamics by 1,911 unique spatially and temporally referenced occurrence records beginning with their introduction and continuing to the present. We used this data set to examine patterns of range expansion through time in populations of the invasive cane toad to evaluate their rates of spread into diverse geographic and climatic regions within Australia.

Cane toads are considered to be one of the world's worst invasive species, reflecting their multiple introductions to islands and continents (from the Caribbean Sea to the Indian Ocean) and their deleterious effects on local wildlife (IUCN 2001; Lever 2001; Phillips and Shine 2004). Since their introduction along a 1,200-km stretch of the northeastern Australian coast in 1935–1937, cane toads have expanded their range to more than 1.2 million km^2 of northeastern Australia (Urban et al. 2007). Further range expansion is expected because of an increasing breadth of habitat suitability in regions of both colder and warmer temperatures than forecast from their ancestral range in Central and South America (Sutherst et al. 1996; Urban et al. 2007). Moreover, range expansion rates have increased in the Northern Territory of Australia, and the evolution of enhanced dispersal ability has been implicated in these accelerated invasion dynamics (Phillips et al. 2006). However, the question remains, are these accelerated dynamics restricted to only one region, or do they represent a continent-wide pattern?

To answer this question, we assessed range expansion dynamics of cane toads throughout their invasive range, including three regions characterized by different environments. We analyzed each invasion trajectory to determine whether range expansion has accelerated, decelerated, or proceeded in a linear fashion, as predicted by random diffusion models. We then explored the hypothesis that invasion speed is influenced by conditions that likely

affect cane toad population growth and dispersal, including favorable climates, anthropogenic environments, long-distance dispersal corridors (roads), and landscape connectivity. Unlike prior researchers, we evaluated the correspondence between invasion speed and environmental factors by fitting a data-driven model of localized Laplacian approximations to point data in order to highlight spatial differences in invasion speeds. We then analyzed the residuals from the environment-speed relationship to identify regions where predictor variables did a relatively poor job of predicting invasion speed and thus may require additional explanation. We expected that invasion dynamics should at first occur linearly and then saturate as toads reached the edge of their native niche envelope, where low fitness, combined with disruptive gene flow from dense core populations, would limit future expansion (Kirkpatrick and Barton 1997).

Material and Methods

Natural History and Distribution

The cane toad is a large anuran (up to 24 cm in snout-vent length and 2.8 kg in weight, although rarely exceeding 14 cm and 0.7 kg, respectively; Lever 2001; B. L. Phillips, unpublished data) that is native to tropical and subtropical regions of Central and South America (Lever 2001). The cane toad inhabits a variety of habitats but reaches its highest densities in open grassland and disturbed habitats (Zug and Zug 1979; Brown et al. 2006). Females lay their eggs in temporary or permanent water bodies. Aquatic tadpoles metamorphose into terrestrial juveniles after 1–2 months of development (Zug and Zug 1979). On the northern expansion front, adult toads can move up to 22 km in a single month, a distance greater than that reported for most other amphibians (Phillips et al. 2007).

The cane toad was introduced from 1935 to 1937 to multiple locations spanning 1,200 km of coastal Queensland, Australia, in an ill-fated attempt to control sugar cane pests. Since that time, the cane toad has expanded its range to 1.2 million km^2 (Urban et al. 2007). Across its invasive range in Australia, the toxic and often competitively superior cane toad has initiated declines in native species, and further declines may occur as it expands into new regions (Phillips et al. 2003; Murray and Hose 2005). The distribution of cane toads is constrained by extreme maximum and minimum temperatures, precipitation, evaporation, and the availability of open habitats in their native ranges (Zug and Zug 1979; Sutherst et al. 1996). However, cane toads in Australia increasingly are found colonizing regions of more extreme maximum and minimum temperatures and drier conditions in different parts of Australia (Urban et al. 2007).

Toad Distribution and Colonization Data

More than 2,500 records of toad locality (latitude and longitude) and observation year were assembled from the Queensland Museum, published sources (Floyd et al. 1981; Sabath et al. 1981; Easteal et al. 1985; Estoup et al. 2004; Phillips and Shine 2004; Phillips et al. 2007; Urban et al. 2007), and new records collected in the Northern Territory (http://www.frogwatch.org.au/canetoads/default.cfm). These records include data associated with museum specimens, the results of systematic postal surveys (Sabath et al. 1981; Easteal et al. 1985), ongoing regional surveys of the expanding invasion front (Estoup et al. 2004; Phillips et al. 2007), and continued management efforts to track the spread of cane toads into new territories. Past work has used these data to map the continuing spread of cane toads in Australia (Sabath et al. 1981; Easteal et al. 1985) and to evaluate the relationship between environmental variables and toad colonization probability (Urban et al. 2007). Redundant samples from the same grid locations (minute-by-minute grids) were removed from analysis. Eleven points were eliminated from consideration either because they represented island populations (north of the Cape York Peninsula) that were not representative of the toad's continental expansion or because they constituted human-aided introductions that have not resulted in establishment (south of Port Macquarie, New South Wales). This reduced data set yielded 1,911 unique toad presences recorded from the date of the toads' introduction in 1935 until 2006. Data density increased through time, with about 50 records available during the late 1930s and more than 400 records available during the first half of the 2000s. However, the number of records per year was not significantly correlated with an increase in expansion rates (see "Results"), suggesting that the bias introduced by differential observation intensity was minimal in our analyses.

Toad Ranges

Cane toad range boundaries were estimated annually from 1935 through 2006. The range boundary was determined using the method of α-hull polygons in a program written in MATLAB, version 7.1, with the Mapping Toolbox 2.2 (MathWorks, Natick, MA). We chose the α-hull approach over standard minimum convex polygons because the latter approach can be biased toward larger ranges when species distributions follow nonconvex patterns (Burgman and Fox 2003). The α-hull algorithm first creates a Delaunay triangulation of all the toad presences recorded up to a given year. A Delaunay triangulation connects all the points in a data set subject to the constraint that a circle passing through any three connected points does not in-

clude any other points (Legendre and Legendre 1998). The outermost line segments from this Delaunay triangulation form the minimum convex hull that is commonly used in species range determinations. However, in the α-hull approach, all of the line segments that surpass a predetermined limit (α) to the average length of all triangle sides are removed from further analysis. In this way, the α-hull eliminates long segments that span across empty concavities or that connect isolated island populations and is thus more conservative than a standard minimum convex hull. We decided on the α value by iteratively finding the value that reproduced the contiguous toad distribution found along coastal Australia and determined by other methods (Urban et al. 2007). We calculated toad ranges for each year from 1935 until 2006 to form 72 range hulls.

We extracted the radial invasion range at time t,

$$r_t = \sqrt{\frac{2 \cdot \text{area}_t}{\pi}},$$

as an estimate of the idealized radial expansion of a semicircle originating from a single introduction point (Shigesada and Kawasaki 1997). Clearly, given the multiple introductions of toads that occurred along the Queensland coast (Sabath et al. 1981), this approach is a simplification; thus, we also measured radial expansion rates as the annual progression of range distance from the perimeter of the original introduction region for three superimposed transects (e.g., Andow et al. 1990). These transects originate at specific introduction points and traverse divergent geographic and climatic regions of toad range expansion: the Gordonvale–Timber Creek transect (from an original introduction point in Gordonvale northwest to Normanton and west to Timber Creek); Mackay West transect (from a central introduction point west to the interior range limit); and the Isis–Brisbane–Port Macquarie transect (south from the southernmost introduction point to Brisbane and then to Port Macquarie).

To discriminate among possible invasion patterns through time, we estimated the power exponent of the nonlinear regression ($y = \alpha + \beta x^b + \varepsilon$) of radial toad range versus time since introduction. A linear relationship was not rejected if the 95% confidence intervals of the estimated exponent included 1. An exponent that was significantly greater than 1 indicated an accelerating function; an exponent less than 1 denoted a decelerating function. Confidence intervals for regression coefficients were estimated using 10,000 bootstrapped samples in a program written in MATLAB, version 7.1.

Invasion Speed

Estimating invasion speed requires information on both toad arrival dates and the spatial distribution of those arrival dates. We first constructed a grid surface indicating the locally averaged time since colonization of toads and then derived from this grid a second surface estimating invasion speed. An averaged invasion surface, as opposed to an interpolated surface, was used to control for the nonsystematic effort by which most toad presences were recorded over the years. Beginning with the latest and ending with the earliest range estimate, we deleted new records embedded in the hulls of previous time periods. Thus, only data points located on the edge of estimated range boundaries were used to calculate invasion speed. We also bordered our analysis by our previous prediction of the toads' potential range (Urban et al. 2007), a process that leads to more conservative estimates of range expansion by excluding rare, highly isolated, and possibly nonpersistent toad populations.

We used the MATLAB "gridfit" program (D'Errico 2006) to construct the surface of time since colonization. In gridfit, a bilinear interpolation was fitted to each data point. Then a finite difference approximation to the Laplacian operator was used to smooth the interpolated surface. The balance between interpolation and estimation was determined by an adjustable smoothing factor. We objectively determined the smoothing factor by finding the model with a minimal likelihood cross-validation criterion (CVC), a model fit parameter analogous to the Akaike Information Criterion (Horne and Garton 2006). The CVC estimates the Kullback-Leibler distance by measuring the sum of the negative log likelihoods between partitions of the data set into training and prediction subsets. We calculated the CVC across a range of smoothing parameter values (0.1 : 0.1 : 1, 10 : 10 : 1,200) after applying a 10-fold partition of the data set (van der Laan et al. 2004). For our data, CVC values quickly reached an asymptote. Therefore, we chose the smoothing factor that produced a model with a CVC that approached this asymptote. In practice, we chose the model with a CVC that was 99.9% of the asymptotic value estimated from an exponential asymptotic nonlinear regression (Crawley 2002). Further increases in fit after this point were marginal, and this model retained known regional heterogeneities in toad invasions. The final invasion surface was constructed at a resolution of one-fifth of a degree to facilitate manageable run times of the difference equations.

Finally, we calculated invasion speed as the inverse of the change in time since colonization versus distance and converted it to kilometers per year, using a latitude-dependent grid cell-to-area correction factor. This map

was then linearly interpolated to a minute-by-minute grid to match the finer-scale resolution of toad data.

The Effect of Environmental and Landscape Factors on Invasion Speed

We restricted predictors to a set of environmental variables based on prior knowledge of cane toad physiology and habitat (Zug and Zug 1979; Sutherst et al. 1996; Lever 2001). These variables, the expected directions of their effects, and relevant citations can be found in table A1. We predicted that annual temperature (minimum and maximum and their squared terms), annual precipitation, elevation, topographical heterogeneity, and proportional road and developed land cover would affect cane toad range expansion speeds. Details on the derivation of these variables can be found in Urban et al. (2007).

In addition to environmental variables, we also evaluated the relationship between invasion speed and the landscape connectivity of predicted habitat patches. The connectivity of suitable habitat was measured in two ways: patch density and patch connectivity (*C* index; Hanski 1994; Vos et al. 2001). The two statistics differ in that the first measures the simple density of patches per defined landscape, whereas the second incorporates the total area of surrounding patches weighted by their distance from the focal patch. We measured patch density in FRAGSTATS (McGarigal et al. 2002) in a 55-km-radius moving window, which corresponds to the maximum observed annual invasion speed of cane toads. The patch connectivity index takes the sum of surrounding patch area weighted as a decaying exponential function of distance. We modified this algorithm somewhat by assuming that each grid cell of suitable habitat was a patch and making it a relative measure by dividing it by the total possible value ($C_{\max}$) for each estimated region. We calculated the metric within the same 55-km-radius moving window used for the patch density statistic in a program written in MATLAB. The species-specific α parameter (different from the α parameter used in hull construction) was estimated via maximum likelihood as the probability that observed toad displacements from a radiotracking survey (Phillips et al. 2007) fell into one of 13 binned distances. Because these displacements were collected over variable periods of time, they were first standardized to reflect a 100-day wet season (the period during which the majority of annual movement occurs; Phillips et al. 2007).

We modeled invasion speed in relation to environmental and landscape factors. Maximum and minimum temperatures were centered, and squared terms were calculated after centering to eliminate inherent colinearity between squared terms and their roots (Legendre and Legendre 1998). Subsequent colinearity among variables was low (mean variance inflation factor [VIF] = 2.1, maximum VIF = 5.4; Hall et al. 1999). The Akaike Information Criterion (AIC) was used to select the best (minimal AIC) model (Burnham and Anderson 2002). Six other models were detected with AIC values close to that of the best model ($\leq$2.0; Burnham and Anderson 2002). These models retained the same variables as the minimum-AIC model, except that they also retained precipitation, developed area, or patch density. Because including these variables resulted in little difference in variation explained (<0.001) and no difference in the sign of parameter estimates, we interpreted results from the minimum-AIC model.

The contribution of spatial autocorrelation to invasion speed was assessed by fitting a cubic trend surface to the data (Legendre and Legendre 1998). The spatial variables for describing the invasion surface were selected on the basis of those retained by the minimum-AIC model. The same technique was used to select variables used in the full model, which included both spatial and environmental variables. The variation attributed to environmental and spatial variables alone and their interaction were determined by a standard partitioning of the explained variation (Legendre and Legendre 1998).

Results

Toad Range Size

By 2006, cane toads were reported about 300 km north of Sydney (Port Macquarie, New South Wales) and as far west as Timber Creek and Darwin in the Northern Territory (fig. 1). Much of the recent expansion in toad range has occurred along the western invasion front in the Northern Territory and, to a lesser degree, south along the coast in New South Wales.

After the period of the initial multiple introductions (1935–1937), total radial toad range [$(2 \cdot \text{area}_{\text{total}}/\pi)^{1/2}$] increased rapidly at first and then entered a slower stage of expansion (fig. 2; table 1), suggesting a decelerating pattern over the entire time period. However, this saturating pattern can be decomposed into two accelerating phases, occurring at different initial velocities but with similar accelerations, that characterize expansion dynamics before and after the colonization of the Northern Territory in the 1970s (table 1). If the observed increase in range expansion rates could be attributed to increases in the detection of toads as surveys became better or more intensive in later years, then we would expect to a see a positive relationship between the number of records in a year and the absolute increase in total range area. However, we found that this relationship was not significant ($F = 0.6$, df = 1, 70, $P = .452$).

Within specific regions, toad range expansion rates de-

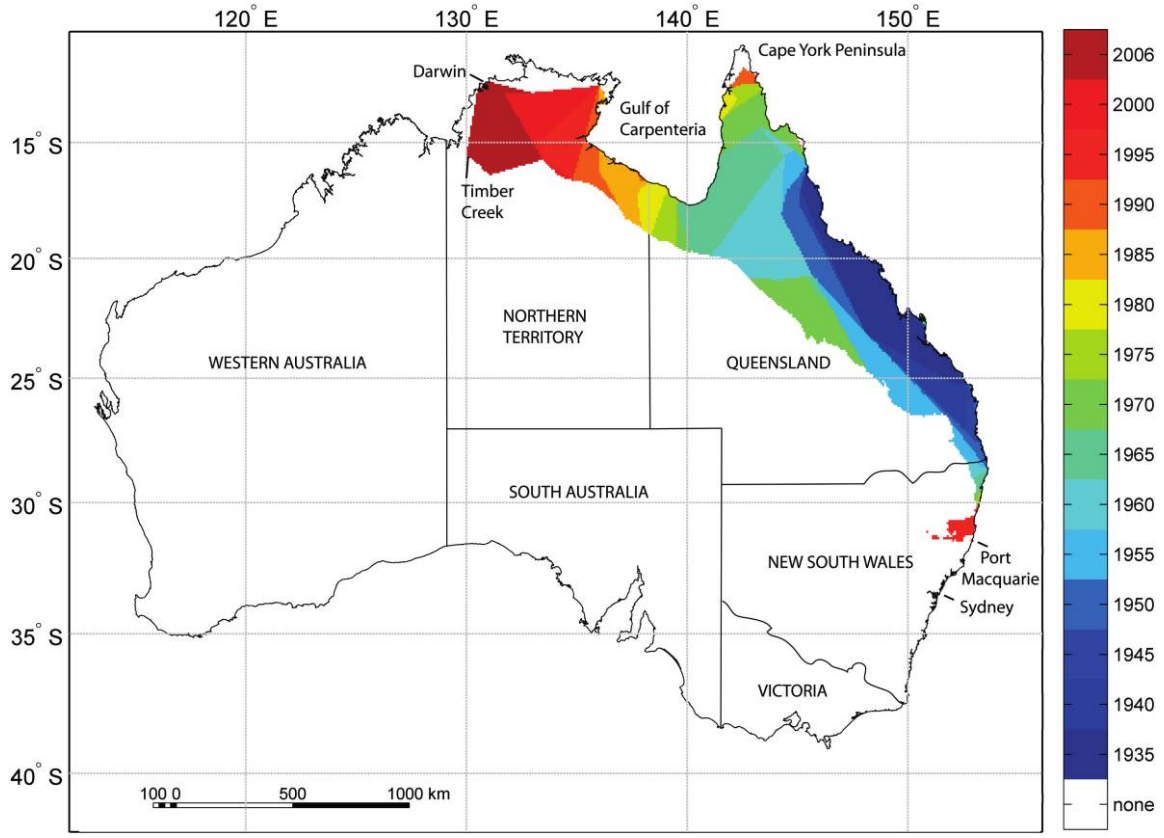

Figure 1: Map of Australia depicting the α-hull representations of cane toad range in 5-year increments (6 years for the latest estimate). Invasion hulls are shown only for the area of estimated suitable habitat (isolated interior populations are not plotted). Key cities and geographic features are indicated.

celerated as toads moved west from Mackay into the hotter and drier climate of interior Australia (fig. 2). In a similar way, toad expansion has slowed as toads moved south along the eastern Australian coast toward Sydney along the Isis–Brisbane–Port Macquarie transect (table 1). Note that both of these decelerating range dynamics still demonstrated a decelerating pattern when range boundaries were not limited to suitable habitat, suggesting that these patterns are not due to this constraint. In contrast to these decelerating patterns, toad range expansion has accelerated as toads moved northwest along the Gulf of Carpenteria and into the Northern Territory.

Invasion Speed

Invasion proceeded at a rate of 10–15 km/year along the east coast of Australia during the initial phase of colonization (fig. 3). However, invasion speeds accelerated up to 30 km/year as toads expanded their range along the Gulf of Carpenteria in northern Australia. These rates continued to accelerate as toads colonized areas in northern Australia. This includes hot, dry inland areas that were previously expected to be of low suitability for cane toads because of native habitat conditions (Sutherst et al. 1996). As toads approached the western part of the Northern Territory, their invasion speed increased up to a maximum rate of 60 km/year.

We next turned to an evaluation of the climate and landscape factors associated with cane toad invasion speed. We predicted that invasion speed would decrease as toads approached less hospitable areas of hotter and drier conditions in interior regions and more fragmented potential habitat. The minimum-AIC regression model of invasion speed retained maximum and minimum temperature plus their squared terms, precipitation × topographical heterogeneity, elevation, proportional road area, and patch connectivity (table 2). The variables in this model significantly predicted toad invasion speed ($F = 365.5$, df = 8, 1,064, $P < .001$) and accounted for 73.3% of its variation. The relationships between invasion speed and each re-

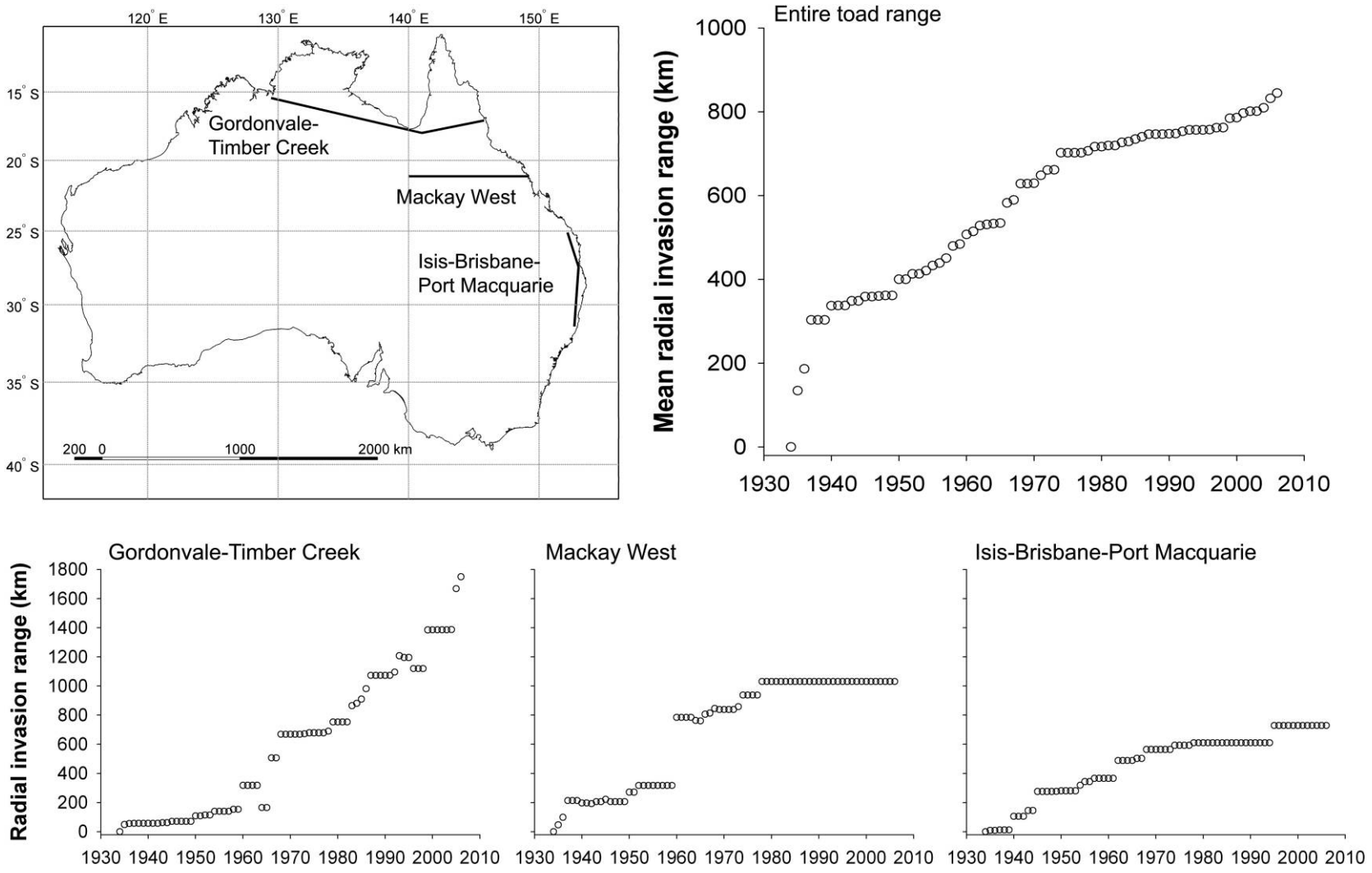

Figure 2: Radial range size for cane toads by year for the entire range and for three separate transects (map at top left) that represent different environmental regions. The Gordonvale–Timber Creek transect intersects a region of hot tropical savanna, the Mackay West transect begins in moist tropical forest and ends in dry desert interior, and the Isis–Brisbane–Port Macquarie transect follows the general contours of the coastline into cooler regions of southeastern Australia.

Table 1: Power regressions of radial cane toad range expansion through time for the entire range and for separate transects through different geographic regions

Range	Estimated power exponent (b)	95% bootstrapped CIs (lower, upper)	Suggested relationship
Entire toad range (1937–2006)	.73	.57, .82	Decelerating
Initial expansion (1937–1973)	1.54	1.43, 1.71	Accelerating
Beginning with northwestern expansion (1974–2006)	1.72	1.18, 2.41	Accelerating
Gordonvale–Timber Creek	1.63	1.50, 1.76	Accelerating
Mackay West	.72	.64, .81	Decelerating
Isis–Brisbane–Port Macquarie	.66	.61, .71	Decelerating

Note: The power regression function used in these analyses took the form $y = \alpha + \beta x^b + \varepsilon$. The intercept ($\alpha$) in this regression model was set to 0 in models that were evaluated at the beginning of the cane toad invasion. The power exponents were estimated in a nonlinear regression model, and their upper and lower ninety-fifth-percentile confidence intervals (CIs) were estimated with 10,000 bootstrap samples (including the original estimate). A coefficient of 1 indicates a linear relationship between toad radial range and time. A coefficient significantly greater than 1 signifies an accelerating relationship; a coefficient significantly less than 1 signifies a decelerating relationship. The entire toad range was evaluated during two periods: from the end of the consolidation of initial introductions until 1973, when the westward expansion began across coastal Northern Territory, and after that period until 2006.

tained variable were in the directions expected, with the exceptions of squared maximum and minimum temperatures. In contrast to predictions, the estimated relationships between squared maximum and minimum temperature and invasion speed were positive, indicating a general pattern of increasing invasion speed with increasing temperatures.

We plotted residuals from the regression model to evaluate the spatial distribution of departures (>5 km/year) from expectations developed in the previous regression (fig. 4). This analysis of residuals can suggest regions where toad invasion speeds are disconnected from environmental variation and thus may represent regions where cane toad populations differ in traits related to their spread. The residuals analysis demonstrated three broad areas where invasion speeds diverged from model predictions. The toads moved more quickly than expected along the coast in the region of their introduction. This rapid early expansion can be attributed to the consolidation of multiple introductions along the coast. Relatively slower invasion rates were associated with their northern expansion into the Cape York Peninsula and their northwestern expansion along the Gulf of Carpenteria. Faster rates were associated with recent expansions into the Northern Territory. The overall message from this analysis is that toads have invaded different regions at divergent rates even after key underlying environmental variables were taken into account.

We next looked at the contribution of spatial autocorrelation in environmental variables to patterns of invasion speed. To do this, we estimated a regression model of invasion speed based on spatial variables from a trend surface analysis and a regression model of both spatial and environmental variables and then evaluated the variance explained independently by the environment, space, and the interaction between environment and space. All spatial variables were retained in the minimum-AIC spatial trend model. This spatial trend model explained 99.5% of the variation (table A2). Note, however, that we expect a high degree of variance explained because spatial variables are being used to predict a smoothed surface. All variables except squared maximum temperature, latitude × longitude, and cubed latitude were retained in the global model with both spatial and environmental variables. The global model explained 99.6% of the variation in invasion speed. By far the most variation in the invasion surface was explained by the interaction between spatial and environmental factors (73.2%), suggesting that environmental variation contributes to differences in invasion speed but that these contributions differ, depending on region. Environment and space alone explained 0.1% and 26.3% of the variation, respectively.

Discussion

Understanding the spread dynamics of invasions can provide insights into the basic mechanisms underlying range expansion and can inform efforts to control invasive species (Elton 1958; Andow et al. 1990; Holt et al. 2005). Practical limitations meant that early predictions from invasion theory depended on the assumptions that invasion rates remained constant over time, environments were homogeneous, and dispersal occurred as a local diffusion process. Under these assumptions, invasions were expected to progress at constant linear rates. However, empirical studies suggest that invasion dynamics can be characterized by accelerating (Kot et al. 1996; Caswell et al. 2003; Clark et al. 2003), decelerating (Silva et al. 2002), or environment-dependent linear range expansions (Lubina and Levin 1988; Andow et al. 1990; Grosholz 1996). By relaxing these restrictive assumptions, more recent theory

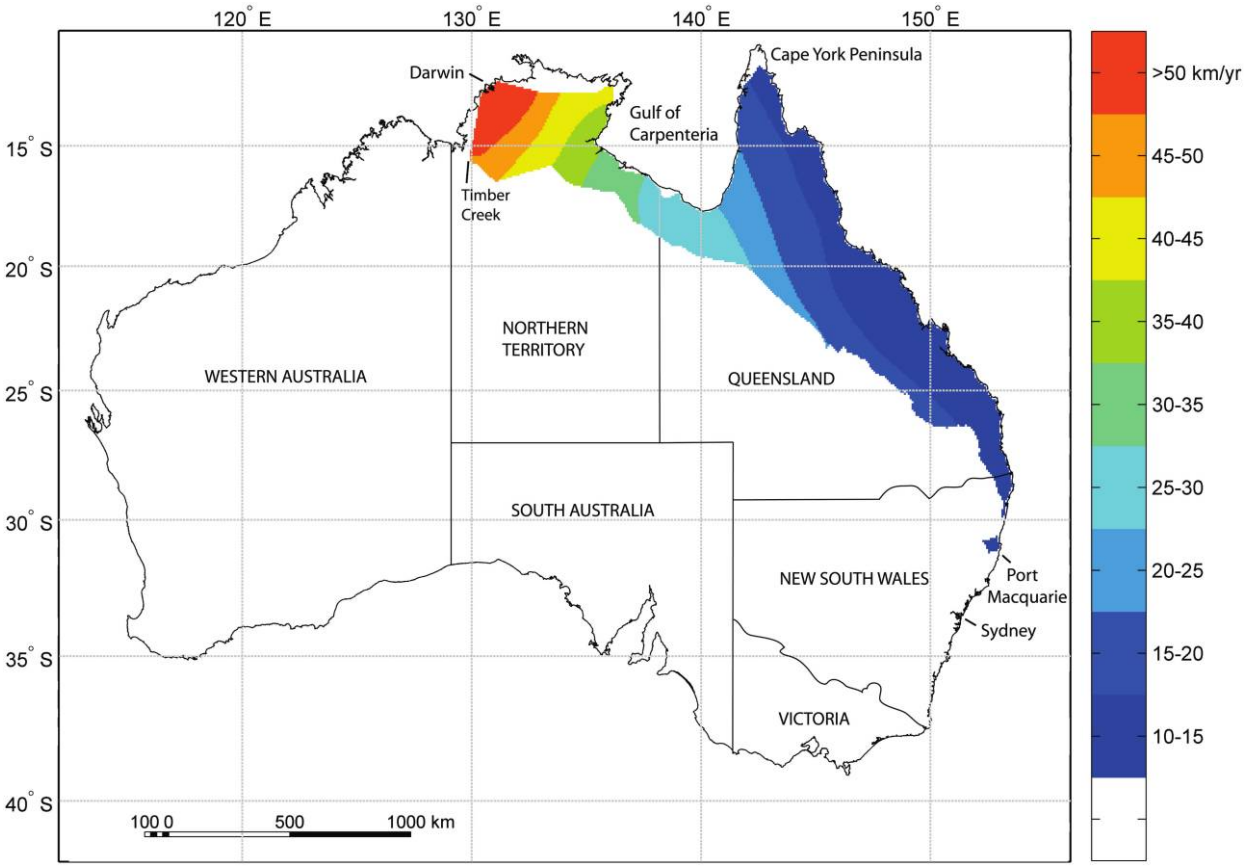

Figure 3: Cane toad invasion speed (km/year) in areas of suitable habitat. The map was generated by smoothing a bilinear interpolation of the arrival times of cane toads and taking the derivative at each grid point. The color ramp from dark blue to red illustrates increasing range expansion rates.

predicts a wide range of possible dynamics (Hastings et al. 2005). In particular, jump dispersal provides one potentially important explanation for findings of accelerating dynamics (Kot et al. 1996). However, strong Allee effects, such as might characterize sexual organisms like toads, can severely restrict the establishment of peripheral populations outside range boundaries and thus can prevent jump dispersal from generating accelerating dynamics (Lewis 1997). An alternative explanation involves interactions between dispersal, demography, and the environment.

Clearly, invasions usually proceed across heterogeneous landscapes, and environmental variation can affect the spread of invasive species (With 2002; Hastings et al. 2005). For instance, the invasion rates calculated for the invasive European green crab (*Carcinus maenas*) in California poorly predicted green crab invasion rates in Maine and South Africa (Grosholz 1996). Therefore, invasion speed may be affected directly by environmental (e.g., distribution of habitats) and spatial (e.g., fragmentation) heterogeneity or in more complex ways as niches or dispersal abilities evolve (Garcia-Ramos and Rodriguez 2002; Simmons and Thomas 2004; Holt et al. 2005). To some degree, environmental variation should play a role in all invasions, if only to limit a species' further range expansion once it encounters the spatial limits of its conserved niche (Kirkpatrick and Barton 1997; Wiens and Graham 2005). Therefore, a comprehensive theory of species invasions requires a reconciliation of existing theory with a niche-based perspective on the limits to a species' range. The success of this integration depends on a better understanding of how environmental variation interacts with spatial position to determine interregional variation in population demography and the distribution of dispersal abilities.

Cane Toad Invasion Rates across Regions

Cane toads offer an exceptional model system to study invasion dynamics across heterogeneous environments.

Table 2: Regression results for environmental and landscape variables retained in the minimum-AIC model of invasion speed

Variable	Partial regression coefficients (β_k)[a]	Standardized regression coefficients (β'_k)	t (df = 1, 1,064)	P
Maximum temperature	1.62	.42	14.83	<.001
Maximum temperature^2	.46	.42	17.01	<.001
Minimum temperature	.37	.10	4.59	<.001
Minimum temperature^2	.28	.27	13.51	<.001
Annual precipitation	…			
Topographic variation × precipitation	1.11^{-5}	.04	1.97	.049
Elevation	-1.22^{-2}	−.17	−9.35	<.001
Percent built-up area	…			
Road density	54.39	.05	2.58	.010
Patch density	…			
Patch connectivity	26.61	.03	1.91	.057

Note: The magnitude of standardized regression coefficients can be interpreted as the relative importance of variables in determining invasion speed.

[a] Ellipses indicate variables that were not selected via the method of minimum Akaike Information Criterion (AIC).

Their invasion has been well documented, and their introduced range now encompasses more than a million square kilometers, including diverse ecological zones of tropical rain forest, tropical grasslands, and subtropical savanna. We found that the total radial range of cane toads in Australia has decelerated over time as the result of two distinct periods of expansion, with the later period characterized by a slower initial velocity but the same acceleration. However, this overall decelerating pattern disguises highly divergent invasion dynamics that are unique to different geographic regions. Range expansion has been slow in hot, dry regions of interior Australia and in cooler regions in the southern part of the range. In these regions, the cane toads' southward and westward expansion rates rarely exceeded 20 km/year, and the decelerating power exponents estimated for invasions in these regions suggest that cane toads may be reaching their niche-determined range limits. In contrast, cane toads in the Northern Territory have dramatically accelerated their invasion rates. At the leading edge of the invasion, cane toads are expanding their range at up to 60 km/year.

To estimate these invasion speeds, we applied a data-driven method of choosing the smoothing factor for the invasion surface. Ultimately, the best model fit was obtained for a highly smoothed invasion surface. Hence, we caution that our interpretations reflect this broader scale of inquiry. However, it is encouraging that our model predicted relationships between environmental variables and invasion speed similar to those determined by ground-based monitoring of radio-tracked toads (Phillips et al. 2007; for details see "The Role of the Environment"). We also cannot exclude the possibility that changes in climate and anthropogenic development over time have increased the suitability of different regions to cane toad invasion. Future research will be needed to address the confluence of spatiotemporal environmental changes and cane toad range expansion rates.

Explaining Divergent Invasion Rates

What differentiates the cane toad's accelerating invasion of the Northern Territory from its expansion into other parts of its range? Two scenarios might give rise to an accelerating dynamic. The populations at the current invasion front might be producing a greater proportion of long-distance "jump" dispersers. Species that sometimes disperse great distances can accelerate their range expansion by forming multiple nuclei outside of the main range body, which then coalesce into an ever-widening range (Andow et al. 1990; Shigesada et al. 1995; Silva et al. 2002). Alternatively, median dispersal rates might increase as the environment becomes progressively more conducive to movement, the environment provides a greater advantage to long-distance dispersal (e.g., finding scarce resources in a resource-limited environment), or the traits that determine dispersal distance evolve. Hence, a species' invasion rate may accelerate as a collection of piecewise linear expansions without a change in the proportion of long-distance jump dispersers.

Several pieces of evidence suggest that accelerated dynamics of toads in the Northern Territory reflect an increase in overall dispersal distances rather than a proportional increase in long-distance dispersers. The median displacement distances of populations at the Northern Territory invasion front were more than 13 times the median displacement distances of populations at sites colonized

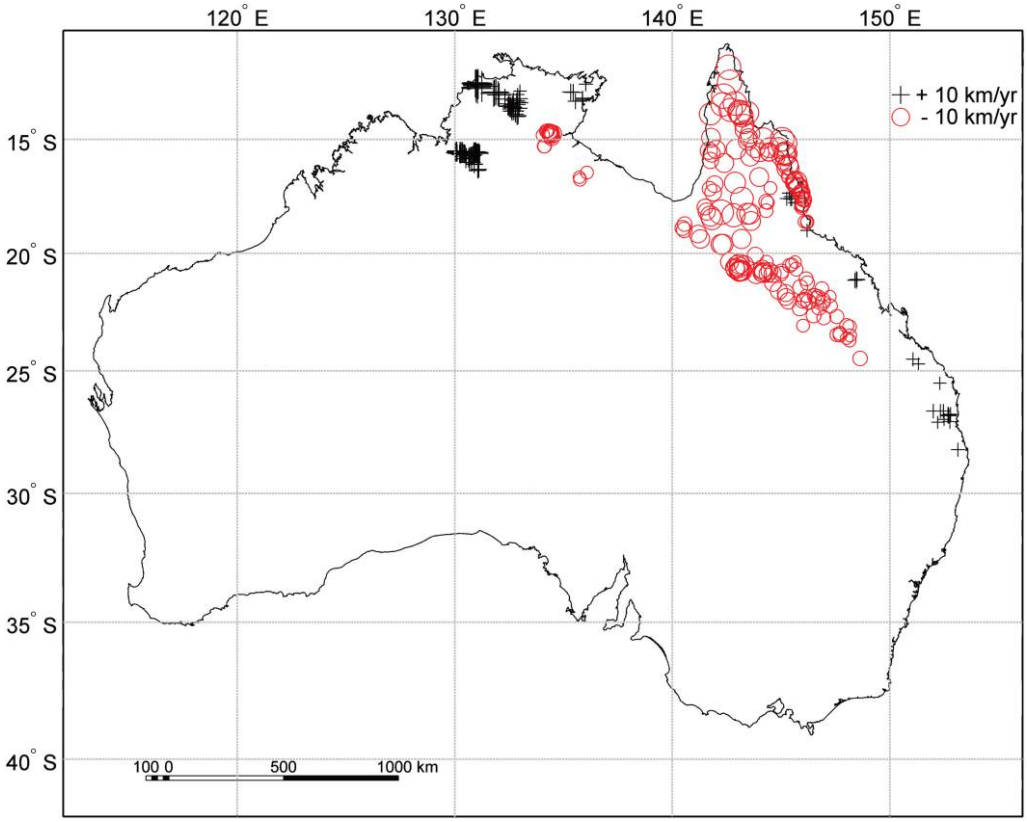

Figure 4: Residuals of invasion speed versus the predictions generated by the regression of invasion speed on environment. Absolute residuals less than 5 km/year were excluded. Remaining symbols indicate whether the invasion speed was higher (*plus signs*) or lower (*circles*) than that predicted in the regression. Symbol size is proportional to absolute residual size (see key). Regions characterized by large residuals indicate where toads moved slower or faster than expected by the model developed in this article for toad invasion speed based on underlying environmental variables.

50 years before the year of sampling (Schwarzkopf and Alford 2002; Phillips et al. 2007). Intensive field surveys conducted during the toad's 2004–2005 wet-season range expansion in the Northern Territory showed little evidence for jump dispersal during the time window evaluated (Phillips et al. 2007). Instead, toads moved westward at a constant rate. Also, preliminary evidence suggests that kurtosis in dispersal kernels, an indicator of a high proportion of long-distance dispersers, has declined in populations from the current Northern Territory front (2.2) relative to long-established populations (4.3–8.1; Phillips et al. 2008; R. A. Alford, G. P. Brown, L. Schwarzkopf, B. L. Phillips, and R. Shine, unpublished data). These data suggest that the extent and perhaps even the shape of the dispersal kernel differ, depending on population and location. However, we cannot discount a general influence of jump dispersal on cane toad dynamics, considering that kurtosis estimates are generally positive and that several cases of long-distance introduction by humans have been documented. Rather, environmental heterogeneity may affect both median dispersal distances and the proportion of long-distance dispersers.

The Role of the Environment

Our analyses suggest that the tropical environment of the Northern Territory may facilitate toad dispersal. Toads moved faster in regions characterized by hot weather, abundant water bodies suitable for breeding (topographical complexity × precipitation), low elevation, and high road density. These results accord with field observations of radio-tracked cane toads that moved farther on warm, wet, humid, and windy nights in open habitats and along roadways (Schwarzkopf and Alford 2002; Brown et al. 2006; Phillips et al. 2007). The environmental conditions in the Northern Territory may facilitate higher reproductive rates or enhanced movement rates. Warmer temperatures might allow for an increased number of reproductive events per year or facilitate sustained locomotion in ectothermic toads (Phillips et al. 2007). Alternatively, unfavorable environ-

mental conditions might also lead to increased dispersal by promoting the fitness advantages of locating new and unexploited habitat patches (e.g., breeding pools) or scarce food resources in a meager environment.

The Potential Role of Evolution

The evolution of higher dispersal or reproductive rates also could explain part of the observed increase in toad expansion rates in the Northern Territory. The specific environmental context in this region might select for higher rates of reproduction or of dispersal. Higher reproductive rates are expected to evolve in invasive species if tradeoffs between reproduction and enemy defenses no longer operate because of an absence of natural enemies in the novel environment (Wolfe 2002; Blair and Wolfe 2004). Faster dispersal also might evolve in toads at the invasion front either because selection favors movement to locate unoccupied or high-quality habitat in a low-quality landscape (i.e., higher fitness of dispersers; Lubina and Levin 1988; Pulliam 1988; McPeek and Holt 1992; Winker et al. 1995) or because of spatial assortment by dispersal ability during range expansion (irrespective of fitness; Travis and Dytham 2002; Phillips et al. 2006, 2008). However, our data suggest that differences in the environment or the population genetics of toads in the Northern Territory play some role in the toad's accelerating dynamics. Otherwise, we would expect to see increasing invasion rates at all edges of the toad's range, and this was not the case.

The environment of the Northern Territory may have influenced toad dispersal rates in two ways: directly, by facilitating toad movement, and indirectly, by imposing selection on those dispersal rates. While both ecological and evolutionary mechanisms likely have interacted to accelerate invasion speeds, available data do not yet allow us to distinguish between ecological and evolutionary mechanisms of range expansion. However, research suggests that cane toads at the invasion front have longer limbs and altered behavior, which may have evolved to support longer-distance dispersal (Phillips et al. 2006, 2008). Besides the alteration of morphology, we expect that behavioral traits should evolve, such as the decisions to leave shelter sites or to continue moving. Common-garden experiments are currently under way to determine whether a genetic basis underlies these dispersal-related traits in populations at the invasion front.

Conclusions

Cane toads reached the western Northern Territory in 2006, a full 21 years before a 1985 forecast that assumed constant expansion rates predicted their arrival (Freeland and Martin 1985). The failure to predict the accelerated range expansion of cane toads in Australia suggests that invasion dynamics may have to be considered at multiple spatial scales and in the context of environmental heterogeneity and evolutionary dynamics. This may be particularly true for invasive species that have expanded across a large geographic region characterized by heterogeneous environments and variable selection regimes. Future work will benefit from measuring relationships between dispersal rates and environment gradients and incorporating these parameter dependencies into predictive models. Along these lines, invasion models are beginning to incorporate spatial heterogeneity in environments by including context-dependent diffusion rates or biased movement in gravity models or by simulating dispersal on spatially explicit landscapes (reviewed by Hastings et al. [2005]). In addition, we need to understand the conditions that generate natural selection for enhanced dispersal at the leading edge of an invasion and how selection changes a population's dispersal kernel. Ultimately, knowing the specific mechanisms responsible for invasion speed will be critical for applying the limited funds available for invasive species control and, more generally, for understanding the processes by which species expand their ranges under altered conditions.

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APPENDIX

Choice of Predictor Variables and Results from the Spatial Trend Model

Table A1: A priori choice of model variables and their assumed relationship with cane toad performance and invasion speed

Variable	Relationship[a]	Justification	References
Minimum annual temperature (squared term)	Positive (negative)	Poor larval and adult performance at low temperature (~6°–17°C); requires sufficient number of degree days for development	Zug and Zug 1979; Floyd 1985; Sutherst et al. 1996
Maximum annual temperature (squared term)	Positive (negative)	Poor larval performance at high temperature (38°–43°C)	Floyd 1985; Sutherst et al. 1996
Annual precipitation	Positive	Requires moist conditions and wetlands for breeding	Zug and Zug 1979; Sutherst et al. 1996
Elevation	Negative	Native range generally occurs at low altitude	Zug and Zug 1979
Topographical variation × annual precipitation	Positive	Likelihood of breeding pools increases with topographical relief and precipitation	Sutherst et al. 1996
Road density	Positive	Accidental human transport- or disturbance-mediated effects on invader success	Estoup et al. 2004
Percent built-up area	Positive	Accidental human transport- or disturbance-mediated effects on invader success	Estoup et al. 2004
Patch density	Positive	Higher patch density is expected to be associated with higher persistence	Hanski 1999
Patch connectivity index	Positive	Higher patch connectivity is expected to be associated with higher persistence	Hanski 1994

[a] Assumed relationship with toad performance and invasion speed.

Table A2: Results from the regression of invasion speed on spatial variables

Variable	Partial regression coefficients (β_k)	t (df = 1, 1,063)	P
Latitude	−92.39	−2.2	.030
Longitude	−103.69	−2.8	.006
Latitude^2	4.92	6.7	<.001
Longitude^2	.81	2.9	.004
Latitude × longitude	2.93	3.5	<.001
Latitude^2 × longitude	-3.91^{-2}	−6.4	<.001
Latitude × longitude^2	-1.60^{-2}	−4.4	<.001
Latitude^3	-1.22^{-2}	−4.2	<.001
Longitude^3	-2.59^{-3}	−3.3	<.001

Note: Model residual standard error was 0.90 with 1,063 degrees of freedom, and model R^2 was 99.5.

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