Forecasting the spatiotemporal pattern of the cane toad invasion into northwestern Australia

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Running head: Predicting cane toad invasion patterns

Abstract

Context: The toxic cane toad (*Rhinella marina*) has invaded over 50 countries and is a serious conservation issue in Australia. Because the cane toad invasion has taken several decades to colonize northern Australia due to the large size of the continent and the east-west invasion axis, there is scope for making testable predictions, prior to invasion, about how toads will invade new areas. The western toad invasion front is far from linear, providing clear evidence for heterogeneity in invasion speed.

Aims: A number of *ad hoc* hypotheses have been offered to explain this heterogeneity, including the evolution of traits that could facilitate dispersal, and spatial heterogeneity in climate patterns. Here we offer an alternative hypothesis, and generate a prediction for the spatiotemporal pattern of invasion into the Kimberley Region – the next frontier for the invading toads in Australia.

Methods: Using observations of spatiotemporal patterns of cane toad colonization in northern Australia over the last 15 years, we offer a conceptual model based on the orientation of wet season river flows relative to the invasion axis, and toad rafting/floating behavior during the wet season.

Key results: Our model predicts that toads will invade southern areas prior to northern areas; an alternative model based on rainfall amounts makes the opposite prediction. The models can now be tested by monitoring the spread of invasion front over the next 5-10 years.

Implications: Although control of cane toads has largely proved ineffective, knowledge of the spatiotemporal pattern of the toad invasion in the Kimberley could (i) facilitate potential

management tools for slowing the spread of toads; (ii) inform stakeholders in the local planning for the invasion; (iii) provide researchers with a temporal context for quantifying toad impacts on animal communities; and (iv) reveal the mechanism(s) causing the heterogeneity in invasion speed.

Key Words: Colonisation, wet season, river flow, amphibian, *Rhinella marina*

Introduction

Many plants and animals use linear habitats, often termed corridors, for dispersal and movements. Some animal species are restricted to corridors, but corridors can also be important to species using the larger landscape matrix (e.g., (Arnold *et al.* 1991; Rosenberg *et al.* 1998; Sutcliffe and Thomas 1996). Linear habitats may thus have positive effects on the persistence of populations and metapopulations, although in the case of invasive species the use of linear habitat could facilitate unwanted dispersal (Tikka *et al.* 2001). Regardless of context, determining the most probable route of dispersal can be useful for both ecologists and conservationists.

A key question in invasive species biology and management is predicting how invasive organisms will spread through a landscape. Three factors are involved in the dispersal of invasive species: direction, distance and speed (Lockwood *et al.* 2013). While it is often assumed that dispersal will be isotropic, i.e. that dispersal occurs at equal speeds in all directions and for equal distances, this may rarely hold true. For example, species that disperse via river or wind currents will move in directions and at greater speeds and distances favoured by those currents, and disperse more slowly in directions opposite these forces (Byers and Pringle 2006; Grosholz 1996). Moreover, species can disperse faster along watercourses, regardless of direction of flow; for example, muskrats (*Ondatra zibethicus*) dispersed up to four times faster along waterways than in landward directions in the Czech Republic (Andow *et al.* 1990).

The toxic cane toad (*Rhinella marinus*) has invaded over 50 countries, mostly Pacific and Caribbean islands (Lever 2001). Its invasion into Australia, however, is unique in two major ways; first, the cane toad has caused demonstrable and severe impacts on animal communities via lethal toxic ingestion and associated cascading effects, especially on reptiles (Doody *et al.* 2013; Doody *et al.* 2009; Doody *et al.* 2014; Doody *et al.* 2017; Doody *et al.* 2015b; Letnic *et al.* 2008; Shine 2010), making the cane toad invasion a serious conservation issue. Second, the cane toad has taken several decades to colonize northern Australia due to the large size of the Australian continent and the east-west invasion axis (Kolbe *et al.* 2010; Sabath *et al.* 1981; Sutherst *et al.* 1995; Urban *et al.* 2007). These two facts warrant efforts to understand toad invasion dynamics and allow us to make testable predictions prior to toad invasion, respectively. Attempts to predict range dynamics for toads should consider heterogeneity in the environmental factors that determine dispersal rates and habitat occupancy (Letnic *et al.* 2014; Urban *et al.* 2007).

Accordingly, on a broad scale, models have been generated to predict the cane toad distribution under future climates (Kearney *et al.* 2008; Kolbe *et al.* 2010; Urban *et al.* 2007). At a more regional scale, the western toad invasion front has been non-linear, providing clear evidence for heterogeneity in invasion speed, and there is evidence that the westward spread of cane toads across the Northern Territory recently accelerated from ~30 km/year in the Gulf Country to perhaps twice that in the Top End (Phillips *et al.* 2007). Several *ad hoc* hypotheses have been offered to explain this acceleration in invasion speed including the evolution of traits affecting dispersal, and heterogeneity in climate (Brown *et al.* 2014; Phillips *et al.* 2007; Phillips *et al.* 2006). However, these hypotheses have limited utility to make predictions of how toads might continue to invade the last toad-free frontier in northwestern Australia – the Kimberley region. For example, we cannot predict whether any evolutionary responses (e.g., increases in leg length or dispersal ability) would continue to evolve, although spatiotemporal variation in those traits could exist along the invasion vanguard (Phillips *et al.* 2006).

Given current invasion speed we would expect cane toads to colonize the remainder of the Kimberley region over the next 5-10 years. How then, in the spatiotemporal sense, will cane toads invade this region? Aside from revealing the cause(s) for the heterogeneity in invasion speed, knowledge of the spatiotemporal pattern of the toad invasion in the Kimberley could (i) facilitate potential management tools for slowing the spread of toads; (ii) inform stakeholders in the local planning for the invasion; and (iii) provide researchers with a temporal context for quantifying toad impacts on animal communities.

Herein we generate an alternative hypothesis for the heterogeneity in invasion speed of cane toads in northern Australia. During the last 15 years we noted, anecdotally, that the acceleration of toad invasion speed was associated with the wet season river flow relative to the orientation of the invasion axis: the invasion vanguard moved faster when rivers flowed ahead of the existing toad front. Accordingly, we also noted rafting/floating behavior of toads during wet season flooding. Our model makes a clear prediction about the future spatiotemporal invasion pattern in cane toads across the Kimberley Region, because the physiography (river catchment flow direction) of the region generates one prediction, while its climate variation generates the opposite prediction (a null model makes a third prediction). Our model, and its alternative, should be readily testable with toad colonization data over the next 5-10 years.

The current and forecasted distribution of cane toads in Australia

The cane toad has spread across most of northern Australia, and currently occupies the eastern third of the Kimberley Region, Western Australia (Fig. 1). It is difficult to define a precise toad 'front'; at any one time there exists a small number of toads ahead of most others, followed by moderate numbers and lastly a breeding front with numbers that are orders of magnitude higher. This 'blurred' front can be tens of kilometers wide (J. S. Doody, pers. obs.). Nevertheless, the best approximation of the current (westward-moving) cane toad front in the east Kimberley region at the submission of this paper is near the Mueller Ranges west of Halls Creek in the south, and near Ellenbrae Station and the eastern edge of Drysdale National Park in the north (Fig. 1). This map of the toad fronts was constructed and is updated by Western Australia Department of Parks and Wildlife (DPAW) (http://www.dpaw.wa.gov.au/pests-diseases/cane-toads) using location records. The location records are anecdotal sightings submitted to DPAW by the public and in particular from community groups (e.g., Kimberley Toad Busters). The fronts are defined by (i) a readily detectable number of individuals having been observed there, and (ii) those individuals not being completely disjunct from toads behind the front. For example, we do not consider 'hitchiker' toads, which start new populations well ahead of the front with human assistance (e.g., in cars, camping gear – see (Phillips *et al.* 2007). There is little doubt that the cane toad will continue to spread into the western Kimberley, very likely reaching the west coast within the next ~10 years (Fig. 1). Although the west Kimberley landscape comprises more gorges and escarpments than the east Kimberley, similar escarpments in the east Kimberley have been readily and rapidly penetrated by cane toads (e.

g., El Questro Wilderness Park, unpubl. data). Although cane toads may move further south across the Great Sandy Desert and into the Pilbara region, we confine our analysis to the Kimberley Region because this area is virtually certain to be occupied by cane toads in the near future, while there is at least some doubt as to the toads' ability to cross into the Great Sandy Desert and Pilbara regions.

Evidence that rivers act as corridors that enhance toad colonization during the wet season

Over the last 15 years, we gathered evidence for spatiotemporal patterns of cane toad colonization and its mechanism in northern Australia. Below we describe three examples of colonization patterns that are consistent with particular rivers enhancing toad invasion speed. We then provide behavioral evidence that toads move down rivers during wet season flooding via rafting and by floating or swimming. Although our evidence is anecdotal, it is nonetheless compelling enough to generate hypotheses for future heterogeneity in dispersal rates.

Case 1: The pattern of spread of cane toads into the Top End region, Northern Territory

There is little doubt that as cane toads crossed the Top End region of the Northern Territory (NT) they did so at an accelerated rate relative to their rate of spread in the previously invaded Gulf Country (Fig. 2). According to Phillips *et al.* (2006), toads moved at a rate of >50km/year in the Top End, compared to 27/km in the Gulf Country (Gulf of Carpentaria, (Freeland and Martin 1985). An initial hypothesis for this acceleration was that toads evolved longer legs which in turn increased their invasion speed (Phillips *et al.* 2006); later, the wetter and hotter conditions of the Top End were said to also contribute to this acceleration (Phillips *et* *al.* 2007), and later still the evolution of the propensity to disperse in straight lines was implicated (Brown *et al.* 2014).

As the toads invaded the Top End, our research group was conducting scientific studies on the Daly River, NT. Seeing the chance to use a before-and-after design to determine the impacts of cane toads on monitor lizards, and discovering that large numbers of these lizards could be counted from a boat, we initiated an impacts study in 2001 that spanned seven years (Doody *et al.* 2009). We desired a study design that would (i) provide multiple pre-toad years (pre-intervention); and (ii) include a control site that would differ in timing of invasion. To accomplish this study design we needed to know when toads would invade our prospective sites. We thus, realized that toads entering the headwaters of the Daly River would, for the first time in decades, encounter a river that flowed ahead of the toad front; the rivers previously encountered by toads in the Gulf Country and eastern Top End flowed northward into the Gulf of Carpentaria (Fig. 2). Thus, we took caution in choosing sites, reasoning that the toad front may move faster once toads reach the Daly River catchment, especially during wet season flooding.

In fact, the toad front moved faster than we even allowed for; they not only arrived earlier at our treatment site than we had predicted but also slightly breached one end of our control site during the same year (Fig. 2). More broadly, toads were not making the same progress in areas farther north where the rivers generally flowed northward (Fig. 2). This heterogeneity in invasion speed resulted in a spatial invasion pattern that surrounded the northwestern Top End (essentially areas surrounding Darwin). Indeed, Darwin, which is not situated on a major freshwater river, was invaded much later than the areas directly to the south and east that fall within the catchments of significant rivers such as the Daly River, Mary River and Alligator Rivers (Fig. 2). The most logical and parsimonious explanation for this heterogeneous invasion pattern would be that the direction of flow of rivers during the wet season enhanced invasion speed of toads via floating or rafting individuals ahead of the toad front (see section below on rafting toads) whereas, to invade Darwin, the toads had to move overland for considerable distances, much as they did in the Gulf country.

Case 2: The spread of cane toads into the Cockburn Ranges, Western Australia

By 2009 the western cane toad front had reached close to Kununurra, Western Australia. Anticipating toad arrival, in 2010 we constructed a toad exclusion fence at the entrance of Emma Gorge, in the Cockburn Ranges, 67 km west of Kununurra (Doody *et al.* 2015a). The 2.7 km-long fence was designed to keep arriving toads out of Emma Gorge (or at least in low numbers), aided by steep vertical cliffs surrounding the Cockburn ranges. El Questro Wilderness Park rangers would then collect any toads that might find their way into the gorge. Although we anticipated that toads would eventually penetrate the gorge from the north where there were gaps in the steep cliffs, we felt we could keep toads out (or in low numbers) for a few years before toads found their way on top of the ranges and over the Emma Gorge waterfall. To our surprise, although the fence was effective as a toad barrier, during 2012-2013, toads began tumbling over the Emma Gorge waterfall essentially as quickly as they arrived at the gorge entrance. Numerous toads were found dead, dying or alive after plunging over the 60 m-high waterfall (we also found toads at the top of the waterfall). This coincidental timing of arrival at both ends of Emma Gorge was puzzling, given that the most probable paths from the north to the waterfall were much longer than the direct westward path to the gorge entrance, and given that sheer cliffs blocked toads from entering the gorge directly from the east. Similar timing of invasion at both ends of the gorge could be explained by heterogeneity in spatiotemporal invasion speed, however. There were three distinct possibilities for the path of toads from Kununurra to the Emma Gorge waterfall. First, toads dispersing due west to the Cockburn Ranges may have climbed the vertical cliffs on the eastern side of the ranges (distance approximately 67 km). This seems unlikely given that the vertical cliffs that are 50-150 m high. A second possibility is that toads moving west from Kununurra moved faster with the northwesterly flow of the Ord River (especially during wet season flooding), and then subsequently turned south along the King River and its tributaries into the Cockburn Ranges and Emma Gorge waterfall (a total distance of approximately 120 km). A final possibility was that toads reaching the Cockburns then dispersed along the cliffs to the north side of the ranges and then climbed onto the top of escarpment through gaps between the cliffs on that side (a distance of 95 km). However, how could toads dispersing 95 km arrive at the same time as other toads dispersing 67 km? The most logical reason for the simultaneous arrival of toads at both ends of the gorge, in our opinion, is that the toads reaching the waterfall from the north were able to travel twice as far as those reaching the gorge entrance because they dispersed faster, facilitated by the Ord River flowing ahead of the invasion front, especially during wet season flooding.

Case 3: The spread of toads into Katherine, Northern Territory

As cane toads moved westward towards Katherine in the Northern Territory in 2001 there were large numbers of roadkills on the Stuart Highway at the King River crossing, 43 km southeast of Katherine. From there, toads moved 75 km downstream along the King River, reaching the Victoria Highway *before* they moved the 43 km along the Stuart Highway to Katherine. These observations were based on roadkills observed in both areas. Toads thus apparently moved roughly twice as fast along the river corridor compared to along the road.

Observations of toads floating or rafting in rivers during flooding

We made a number of observations of floating or rafting toads over the last 15 years, especially during the wet season. In 2003, as toads arrived at our Daly River sites, we documented two toads swimming across the river during late May (dry season) from our boat. Both toads were displaced due to the current, but ended up >100 m downstream from their point of origin. The same year during the wet season (January 2004) from the bank during flood we counted 14 individual toads floating in the river over a period of two days. These included six toads that swam across the river but were displaced downstream 100-300 m as they reached the opposite bank, six individuals that were swimming with the current with outcome unknown, and two toads floating down the river without swimming at all, again with outcome unknown. In 2006, a toad was observed swimming with the current during high flows in the Elizabeth River near Darwin, Northern Territory (I. Morris, pers. comm.). The toad continued swimming for at least 400 m after which it swam out of sight.

In 2011 and 2012 we made observations of rafting of toads in floating chunks of vegetation in the Ord River near Kununurra. In March 2011 the Ord River catchment experienced major flooding (Palmer 2014), although control structures alleviated river levels. During this time, it was particularly common to see rafts of cattails (*Typha domingensis*) floating down the river with the current. These rafts, which ranged in size from 0.3-25 m^2, often provided cover from the sun and predators for small animals. We inspected six such clumps, finding cane toads on four of them (range = 1-7 toads per raft).

During the late wet season in April 2010, we made observations of toads making use of debris rafts on the Victoria River (Table 1). The rafts were comprised of leaves, sticks and logs (Fig. 3). For most of the dry season (April-November), the Victoria River does not flow, but it does flow during the wet season and just after the wet season. During the dry season when the river is not flowing, debris rafts are not present on the river, but form when the river is flowing. During a two week field trip in April 2010 when the river was flowing we observed 6 debris rafts in the upstream freshwater reaches of the Victoria River. The rafts ranged in size from 2-20 m^2. We observed toads on five of the six rafts (Table 1; Fig. 3). The toads ranged in size from 50-100 mm (snout-urostyle length). The rafts provided complex habitat, and we assume because we found the toads on the rafts during the daytime, that the toads were using them as daytime shelter sites and nocturnal foraging sites. It is worth noting that a few of these toads were observed feeding (on insects).

During the wet season of 2004-5 we observed 10 toads on rafts of bamboo floating down the Adelaide River during a flood. Dead fallen stands of the bamboo (*Bambusa arnhemica*) often collect in slack water areas along the riverbanks, where they provide refuges for toads, especially during the dry season. The flood dislodged these into rafts, carrying them down the river. Four cane toads were photographed on a raft of timber, sticks and grasses in the Cambridge Gulf near Wydham, Western Australia in February 2014 (http://www.abc.net.au/news/2014-02-19/rafting-wa-toads/5270188). The raft was moving swiftly in floodwaters after heavy rains and could have originated from any of five rivers that feed the gulf (Ord, King, Pentecost, Durack, Forrest).

What will be the spatial pattern of spread of toads across the Kimberley Region?

In our opinion, the spread of cane toads across the Kimberley region will likely be heterogeneous *along* the invasion vanguard. The geography of river catchments in the Kimberley region – in particular the orientation of river flow – is heterogeneous relative to the orientation of the invasion front. Most of the major rivers flow northward before emptying into the Timor Sea; in contrast, the Fitzroy River flows westward across the south Kimberley before reaching the sea (Fig. 4). Thus far, 'Kimberley' toads have only encountered river catchments that flow to the north, but at our time of writing this article toads in the southern Kimberley are close to the headwaters of the Fitzroy River. Toads moving westward across the northern Kimberley will generally only encounter (cross) rivers flowing northward, while those moving westward across the southern Kimberley will enter the Fitzroy drainage which flows westward – ahead of the toad front (Fig. 4). Based on our observations of toads moving downstream in rivers during wet season flooding, we predict that 'southern' Kimberley toads will reach the west coast (e.g., Derby) well before 'northern' Kimberley toads, because west-flowing rivers will increase westward invasion speed, while north-flowing rivers will not (Fig. 4). Southern and northern Kimberley toads would then surround the northwest corner of the Kimberley (the area near Kuri Bay invaded last), resulting in an invasion pattern that is roughly clockwise (Fig. 4). We term this the 'river flow' model of spatiotemporal invasion pattern.

An alternative model - the ‘rainfall’ model – posits that the major factor influencing the rate of movement and dispersal of toads is the amount of rainfall received and the number of rainy days experienced, because toads tend to disperse during and just after rainy periods (Florance *et al.* 2011; Kearney *et al.* 2008). The rainfall model predicts essentially the opposite spatiotemporal pattern of invasion to the ‘river flow’ model. The rainfall model predicts a counter- or anti-clockwise spatial pattern of invasion (Fig. 4), based on rainfall amounts. The northern and western Kimberley receive 1300-1400 mm of rainfall annually (e.g., Kalumburu, Kuri Bay), compared to 700-800 mm in the southern and eastern Kimberley (e.g., Kununurra, Fitzroy Crossing) (Australian Bureau of Meteorology). In other words, westward-moving northern Kimberley toads would move faster than their southern counterparts due to higher and/or more frequent rainfall, reaching the west coast first, and then move southward to colonize the last remaining Kimberley frontier – the southwest Kimberley (the area near Derby) (Fig. 4). Finally, a third null model predicts that neither the direction of river flow nor rainfall amounts will noticeably or substantially affect the westward spatiotemporal pattern of invasion across the Kimberley (or possibly, river flow direction and rainfall amount offset one another). In the null model, northern and southern toads move at similar rates, arriving on the west coast at similar times. We importantly acknowledge here that heterogeneity in dispersal rates due to stochastic processes alone, could occur, but our null model provides a good comparison for our physical models. We also acknowledge that the river flow model and the rainfall model are not mutually exclusive; their predicted effects could indeed offset one another, resulting in an invasion pattern similar to the null model. Similarly, dispersal patterns that partially match the model predictions could result from effects of both models.

Conclusions and predictions

Urban *et al.* (2008) predicted that toad invasion speed would increase in areas with high temperatures, heterogeneous topography, low elevations, dense road networks, and high patch connectivity. Rivers were not considered. However, Freeland and Martin (1985) noted that cane toad colonized an entire drainage, which is >100 km in length (Settlement Creek, Northern Territory, 1983-84), during the same period in which toads only moved 28 km between catchments. Although the direction of colonization was against the direction of river flow, wet season flooding transforms the catchment into an immense wetland covering >5,000 km^2. Thus, rivers with an axis parallel to the invasion axis may enhance invasion speed, regardless of the direction of river flow. Moreover, toads along perennial rivers in northern Australia can continue to disperse throughout the dry season, while their counterparts in the dry savannah cannot disperse, but must aestivate for the ~6-month dry season.

Our observations of spatiotemporal patterns of toad invasion coupled with those on toad movements during wet season flooding suggest that the direction of river flow indeed plays a role in dispersal and thus the pattern of colonization. As such we predict that cane toads will spread faster in the southern Kimberley than those in the northern Kimberley, by dispersing faster via the Fitzroy River. Alternatively, they may spread faster in the northern Kimberley due to higher rainfall there compared to the southern Kimberley; or, toads will disperse relatively evenly across the Kimberley, due to the opposing forces above or due to our models being in error. Fortunately, our *a priori* predictions are testable via monitoring of the toad front as it moves across the Kimberley. It is our hope that a test of these predictions will inform management of cane toads and other invasive species that are affected by physiography and climate.

Conflicts of interest

The authors declare no conflicts of interest.

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Table 1. Observations made of toads using debris rafts in the upper reaches of the Victoria River during April 2010. Body size of toads was measured as snout-urostyle length (SUL).

Raft size (m^2)	# of toads	Body size in mm (N)
20	15	70 (10), 50 (4), 70 (1), 80 (1)
10	1	60 (1)
2	0	---
20	1	60 (1)
7	2	90 (2)
5	1	100 (1)

Figure Legends

Fig. 1. Overview of study areas, showing major and minor rivers, relief, mean annual rainfall (in mm), and the areas shown in detail in Fig. 2 (blue box) and Fig. 3 (red box).

Fig. 2. The ‘Top End’ of the Northern Territory, showing the approximate distribution of the cane toad in 2002 (and before) and in 2005, and the relationships with the coastline and rivers. Scale bar = 150 km (50 km divisions).

Fig. 3. A cane toad forages on a debris raft in the upper Victoria River during the late wet season in April 2010. The area of the raft was approximately 20m^2. The toad was ~100 mm snout-urostyle length.

Fig. 4. Historical and predicted spread of the cane toad through the Kimberley region of Western Australia. Top: location of ‘toad front’ from 2010-2015 (note there are no data for 2011); data from Department of Parks and Wildlife, Western Australia (dotted lines denote inferred positions). Middle: predicted spread of toads according to the ‘rainfall’ model, where higher levels of rainfall along the northwestern coast (See Fig. 1) allow an accelerated rate of advance. Bottom: predicted spread of toads according to the ‘river flow’ model, where river flow volume and direction and the rafting and floating behavior of toads during wet season flooding causes an accelerated rate of advance. Scale bar = 150 km (50 km divisions).

Figure 1

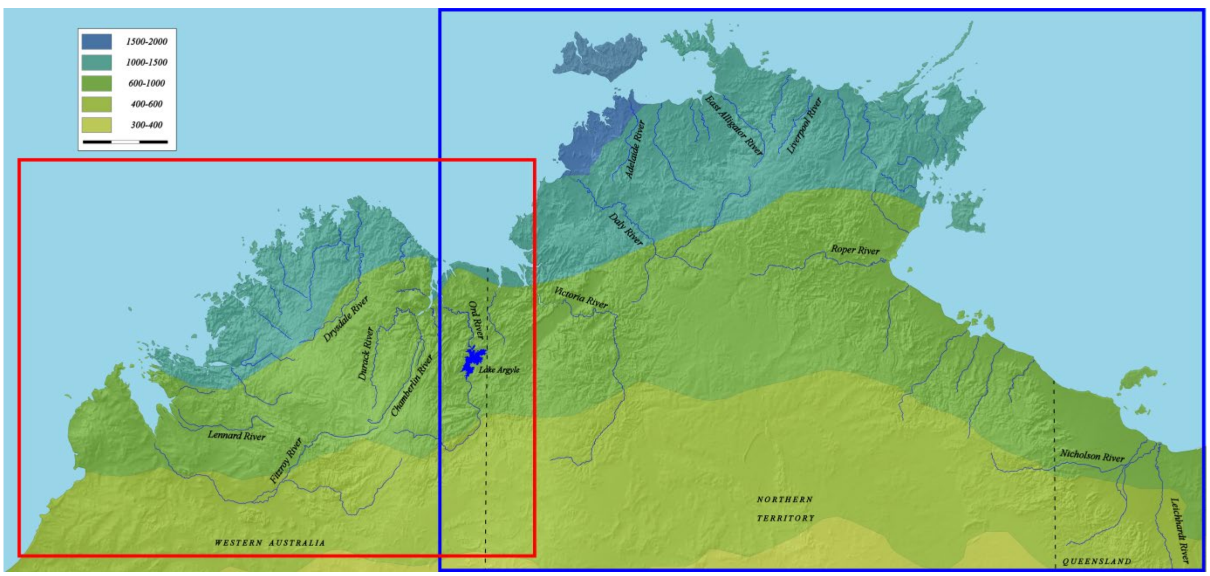

1500-2000
1000-1500
600-1000
400-600
300-400
Adelaide River
East Alligator River
Liverpool River
Daly River
Roper River
Victoria River
Drysdale River
Durack River
Chamberlin River
Ord River
Lake Argyle
Lennard River
Fitzroy River
Nicholson River
Leichhardt River
WESTERN AUSTRALIA
NORTHERN TERRITORY
QUEENSLAND

Figure 2

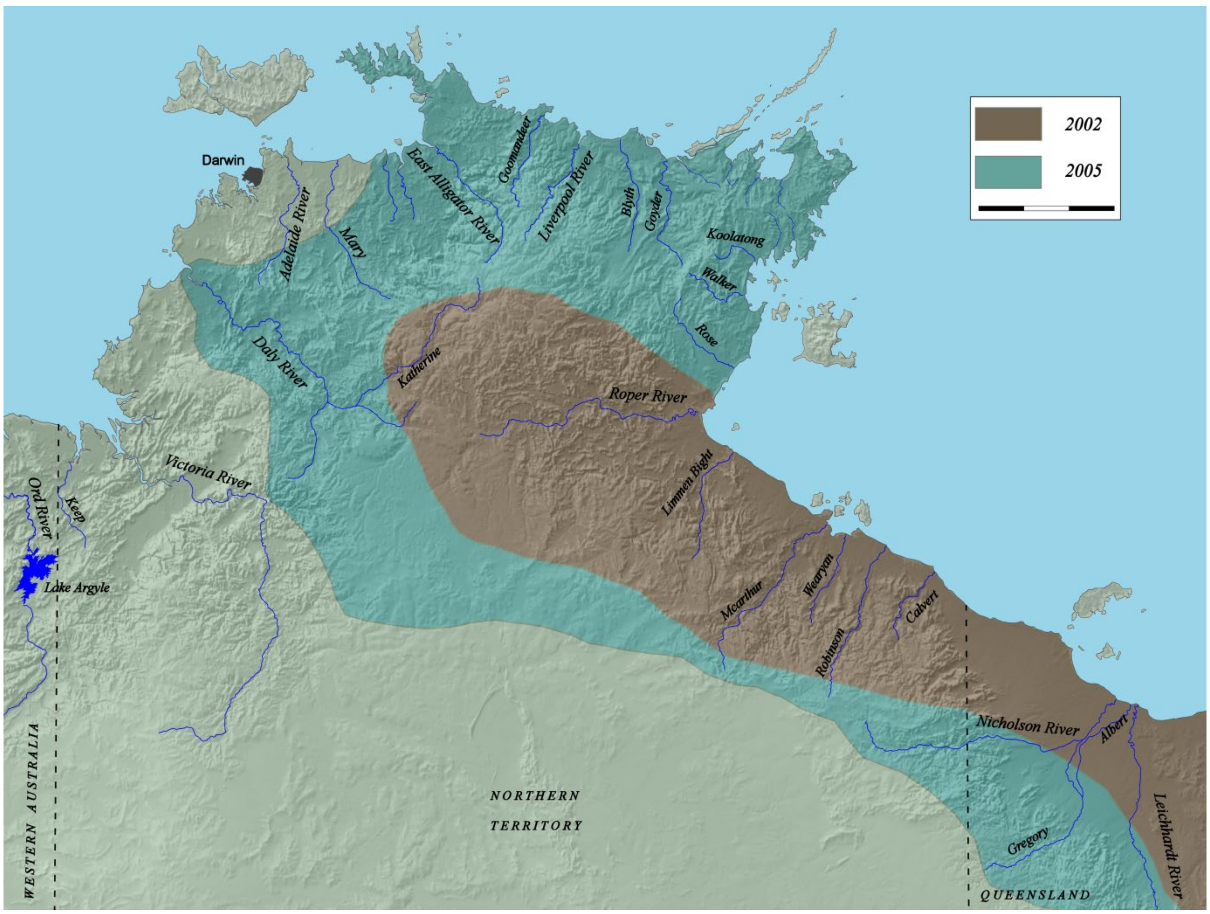
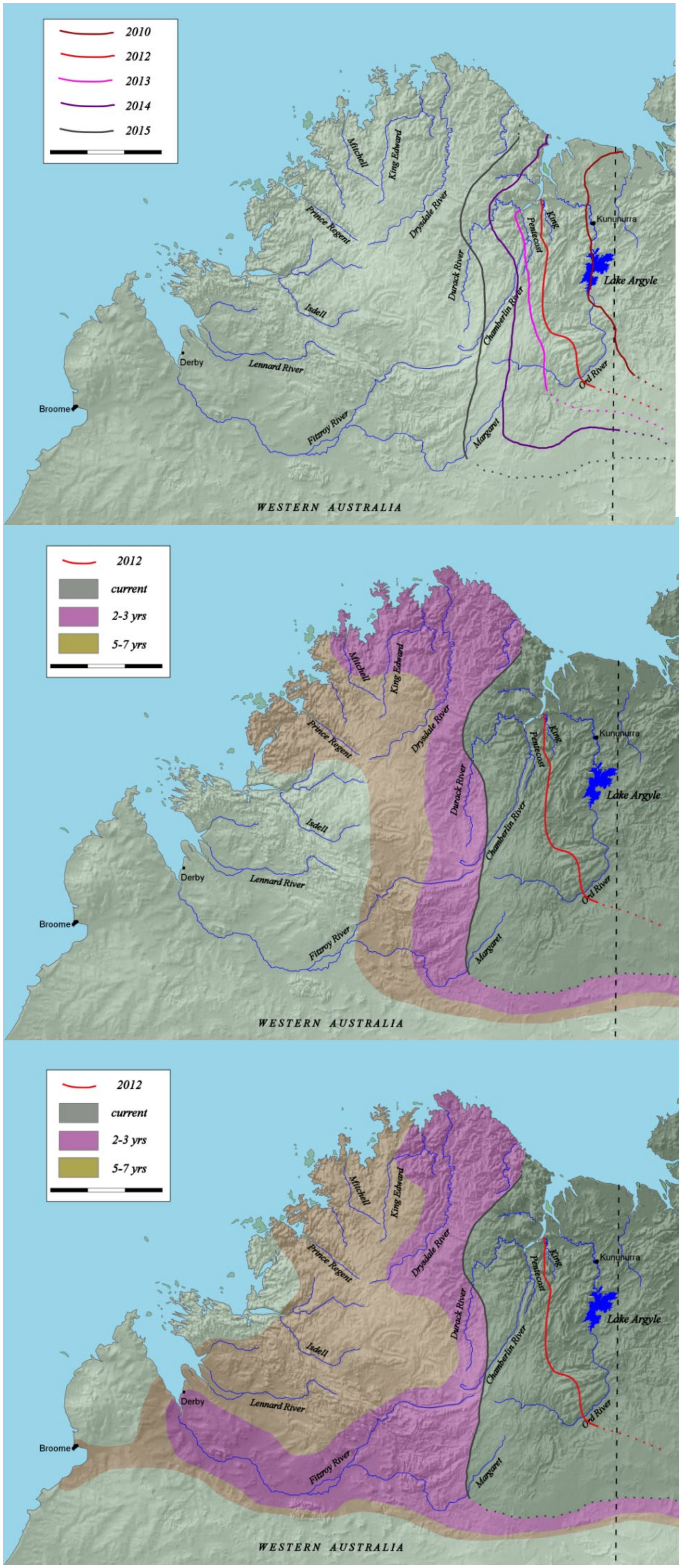

2002
2005
Darwin
Adelaide River
Mary
East Alligator River
Goomadeer
Liverpool River
Blyth
Goyder
Koolatong
Walker
Rose
Daly River
Katherine
Roper River
Victoria River
Ord River
Keep
Lake Argyle
Limmen Bight
Mcarthur
Wearyan
Robinson
Calvert
Nicholson River
Albert
Gregory
Leichhardt River
WESTERN AUSTRALIA
NORTHERN
TERRITORY
QUEENSLAND

Figure 3



2010
2012
2013
2014
2015
Mitchell
King Edward
Prince Regent
Drysdale River
Durack River
Chamberlin River
Pentecost
King
Kununurra
Lake Argyle
Isdell
Derby
Lennard River
Broome
Fitzroy River
Margaret
Ord River
WESTERN AUSTRALIA
2012
current
2-3 yrs
5-7 yrs

Figure 4