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High potential subsidy of dry-season aquatic fauna to consumers in riparian zones of wet–dry tropical rivers

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Abstract

Aquatic fauna provide an important subsidy to terrestrial consumers. In the wet–dry tropics, important subsidies from rivers to riparian-zone consumers are expected in the dry season but may vary depending on riparian zone condition. We investigated the potential subsidy of aquatic fauna to consumers in riparian zones in 2 highly seasonal rivers in Australia's wet–dry tropics. Stable carbon and nitrogen isotopes of invertebrate predators in riparian zones were closely aligned with aquatic invertebrates and emergent adult insects. Further, a considerable proportion (40–50%) of the observed vertebrate fauna in riparian zones were consumers of aquatic fauna, which included fish, crustaceans, invertebrates, and flying adult insects with aquatic larval stages. For hydrologically disconnected waterbodies, estimates of potential insect emergence and the proportion of vertebrate species (in riparian zones) that consume these insects both increased as indicators of riparian plant regeneration and condition improved. Our findings suggest that aquatic fauna provide important subsidies to terrestrial-zone consumers (both invertebrates and vertebrates) during the dry season, and that these transfers can be moderated by riparian zone condition. The wide home and foraging ranges of some consumers also suggest that the importance of these subsidies may extend far beyond the waterbody of origin. Human activities and climate-driven alteration of flow regimes and riparian zones that reduce the availability of dry-season waterbodies or degrade their riparian zones are likely to have negative impacts on aquatic–terrestrial linkages in these systems.

Key words: emergence, food webs, hydrological connectivity, resource subsidies, riparian predators, temporary rivers, terrestrial vertebrates

Introduction

Transfer of biomass, nutrients, and energy between aquatic and terrestrial ecosystems, including riparian zones, is a 2-way process, creating fuzzy boundaries (Polis et al. 1997, Richardson et al. 2010). Transfers from the aquatic zone provide subsidies to terrestrial consumers, with evidence of their reliance on aquatic food sources coming from biomass and biodiversity studies (e.g., Lynch et al. 2002, Allen et al. 2012) and natural isotope studies

that show incorporation of aquatic signals into riparian food webs (e.g., Collier et al. 2002). This subsidy can be substantial (e.g., Fausch et al. 2010) and plays an important role in the food web structure and dynamics of both ecosystems (Nakano and Murakami 2001, Baxter et al. 2005).

Floods and drying events may instigate changes in the availability of aquatic food sources to riparian consumers (Greenwood and McIntosh 2008, 2010). In regions where seasonal cycles of flooding and drying occur each year,

the temporal and spatial variation in the flux of organic material between aquatic and terrestrial zones is therefore likely to be high. During the dry season in wet–dry tropical rivers, for example, higher aerial insect densities are observed near streams rather than farther into the terrestrial landscape (Lynch et al. 2002), leading to the proposition that aquatic insects emerging this time of year constitute an important resource for riparian zone consumers, including terrestrial vertebrates (Lynch et al. 2002). Observations such as this have influenced the development of general principles about riverine food webs in the wet–dry tropics, in particular that aquatic–terrestrial subsidies are linked closely to river flow regimes and the strong seasonal variation in hydrological connectivity that exists in the region (Douglas et al. 2005).

Riparian zone characteristics also affect the transfer and importance of subsidies between aquatic and terrestrial zones, although our understanding of these effects draws more heavily on studies of terrestrial contributions to aquatic consumers (e.g., England and Rosemond 2004) than exchanges in the opposite direction. This is true for the wet–dry tropics, where riparian zone integrity and species composition plays an important role in structuring riverine food webs through supply of terrestrial inputs (e.g., leaves, fruits, invertebrates; Pusey and Arthington 2003, Davis et al. 2010). Pettit et al. (2012a) also showed that while the importance of dry-season leaf litter subsidies to macroinvertebrates differed between 2 nearby rivers of contrasting seasonal hydrology (perennial vs. intermittent), the difference could also be attributed to the rivers' contrasting characteristics in riparian cover and species composition; however, the role played by riparian zone characteristics in moderating the potential subsidy of aquatic-derived material to terrestrial consumers in this region is unclear.

In this study, we assessed the potential subsidy to terrestrial consumers from aquatic invertebrates of dry-season waterbodies in wet–dry tropical rivers, and the effect of riparian zone condition on this subsidy, using multiple lines of enquiry: stable carbon (C) and nitrogen (N) isotopes of aquatic and riparian invertebrates, emergent insect flux estimates, surveys of terrestrial vertebrates, and riparian zone characteristics. We used these data to extend the understanding of directional subsidies from the aquatic to terrestrial zone in these systems beyond that based on observations of aerial insect densities (e.g., Lynch et al. 2002). We hypothesized that the potential subsidy of aquatic fauna to terrestrial zone consumers in the riparian zones around dry-season waterbodies would be (1) high, as evidenced by close coupling between stable isotope values of aquatic invertebrates (including emergent insects) and riparian predatory invertebrates, and by high proportions of terrestrial

vertebrate species that consume aquatic fauna; and (2) moderated by riparian zone characteristics, as evidenced by association between measures of riparian condition and estimates of aquatic invertebrates, insect emergence, and terrestrial vertebrates.

Study sites

Four waterbodies in the wet–dry tropics of northern Australia were examined during the dry season in September 2006. In northern Australia, the dry season occurs between approximately May and October each year, with the majority of the total annual discharge occurring in the wet season (~Nov–Apr) owing to heavy rainfall during the austral summer. The flow regimes and general characteristics of the 4 waterbodies have been detailed previously (Leigh and Sheldon 2008, 2009, Leigh et al. 2010). Two sites were isolated waterholes in the lower Flinders River catchment, approximately 3 km apart, one on the Cloncurry River main channel (FMiso) and one on an anabranch (FAiso), a distributary that rejoins the main channel. The 2 other sites were in the lower Gregory River catchment, one on a flowing reach of the perennial Gregory River (GM), and one approximately 4.5 km away on an anabranch that disconnects during the dry season to form an isolated waterhole (GAiso). These 4 sites were referred to as FUm, FUo, GUm, and GUo, respectively, in Leigh and Sheldon (2009) and Leigh et al. (2010). For each site, spatial dimensions (wettered width and length) were estimated from aerial imagery (Google Earth) and ground-truthed in the field.

Methods

Riparian condition

Riparian condition was assessed using the Tropical Rapid Appraisal of Riparian Condition (TRARC) protocol (Dixon et al. 2006), a visual assessment method specific to the Australian savannah. The sampling unit (riparian zone transect) at each site, defined according to the protocol, was 100 m in length parallel to the waterbody channel and between 5 and 20 m wide depending on the riparian zone width of each site (defined in the protocol from the channel edge laterally to where a distinct change occurs in vegetation and landform type). Riparian condition is based on 4 indices: Plant Cover is the amount of cover by all vegetation; Regeneration is the extent of native plant regeneration (based on plant size classes and abundances); Erosion is the extent of bank erosion; and Weeds is the relative cover of exotic to locally native plants, which we identified using Thorp and Lynch (2000), Brock (2001), Fox et al. (2001), and Smith (2002). The indices can range

between 0 (worst score) and 25 (best score), which when summed give the overall Condition score. For Erosion and Weeds scores, this means that sites with higher scores have less erosion and lower weed to native species ratios, respectively. For reporting, we multiplied each index score by 4 to give comparable ranges with the Condition score (0–100) and canopy cover over the water surface (0–100%). Canopy cover was measured at each site at 2 locations approximately halfway between the upstream and downstream ends of waterbodies. At each location, we calculated the average of 4 hand-held densiometer readings (north, south, east, and west). The resultant values from the 2 locations were then averaged to give one canopy cover value per site.

Aquatic and riparian invertebrates

Benthic macroinvertebrates, emergent insects, and predatory invertebrates in the riparian zone were collected from each site for stable C and N isotope analysis. Collection of benthic macroinvertebrates followed methods in Leigh et al. (2010). A 500 μm mesh dip net was swept proportionally over each habitat present around the edges of each waterbody (snags, leaf packs, aquatic macrophytes, algal mats, and bare regions) for at least 20 s, and the contents were emptied into sorting trays. Invertebrates were picked from trays by gloved hand; organisms included individuals from the Crustacea (aquatic decapods), larval and adult life-stages of aquatic insects (Coleoptera, Diptera, Ephemeroptera, Odonata, Trichoptera and some Hemiptera), and surface-dwelling insects (some Hemiptera).

Four floating traps were also placed around the shoreline of each waterbody for 48 h to collect emerging aquatic insects. Traps were cubes (side length = 0.38 m) enclosed in mesh (0.5 mm) except for the one open side in contact with the water surface. One edge of the open side was secured with tent pegs parallel to the shoreline and the other 3 edges were buoyed over the water with floats. Insects, which included winged Diptera and Ephemeroptera, were collected from traps with an aspirator after 24 and 48 h. Predatory invertebrates were collected opportunistically from riparian zones: odonates with a butterfly net (2 mm mesh size) and spiders by gloved hand from webs or the ground. Nonpredatory invertebrates (potential prey items of predatory riparian invertebrates), including Hemiptera and Hymenoptera, were also collected opportunistically from the riparian zone with the net or by gloved hand. All invertebrates were kept alive in shade (with predators separated from each other and from non-predators) for ~24 h before being frozen.

In the laboratory and in preparation for stable isotopes analysis, individuals were rinsed with distilled water to

remove any foreign material and identified to the lowest taxonomic resolution practicable under a dissecting microscope. Carapaces and portable cases were then removed from all Decapoda and Trichoptera. For each category of invertebrate (benthic macroinvertebrates, emergent insects, and riparian invertebrates), individuals were grouped into similar size classes within each taxon. To obtain the required mass for analysis, groups contained up to 26 individuals (but most often only 1–4). Each group was then treated as a separate sample for analysis. When numbers of individuals were sufficient, we prepared more than one sample per taxon. Samples were then dried (60 °C for at least 24 h) and ground using a mortar and pestle before analysis for stable isotope ratios ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) via combustion and mass spectrometry using a Eurovector EA 3000 (Milan, Italy) inlet with a GV Isoprime (Manchester, UK) mass spectrometer. Stable isotope values of samples ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) were calculated as parts per thousand (‰) relative to the Vienna Pee Dee Belemnite standard for C and air for N. Machine precision was within 0.1‰ for $\delta^{13}\text{C}$ and 0.2‰ for $\delta^{15}\text{N}$, and the mean difference between sample duplicates within runs was 0.8‰ for $\delta^{13}\text{C}$ and 0.4‰ for $\delta^{15}\text{N}$ ($n = 14$).

Stable isotope-based studies of food webs in Australian rivers suggest that trophic fractionation in aquatic invertebrates between primary- and secondary-consumer levels is low (e.g., $0.6 \pm 2.0\text{‰}$ for $\delta^{13}\text{C}$ according to SE Bunn, C Leigh, and TD Jardine, unpubl. data; and $1.2 \pm 1.3\text{‰}$ for $\delta^{15}\text{N}$ according to Bunn et al. 2013), but fractionation between aquatic and terrestrial invertebrates is uncertain. Given this, and taking into account the error in stable isotope values due to machine error and natural variation in sample duplicates, we considered that assimilation of potential prey items by riparian predators (spiders and odonates) was likely if $\delta^{13}\text{C}$ values of prey and predators overlapped (within about $\pm 2\text{‰}$) and $\delta^{15}\text{N}$ values of prey were lower than predators, with the prey therefore constituting an important food source for the predators. We did not rule out the possibility that prey with higher $\delta^{15}\text{N}$ values were potentially being consumed by predators if other prey were available with sufficiently low $\delta^{15}\text{N}$ to match the predator $\delta^{15}\text{N}$, given trophic fractionation and the mixed assimilation of both prey types.

For each site, biplots of $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ values of aquatic decapods, aquatic larval insects, aquatic adult insects, water surface dwellers, emergent insects, non-predatory riparian invertebrates, riparian odonates, and riparian spiders were examined to assess potential prey and predator coupling, based on the above *a priori* criteria. While quantitative methods of examining stable isotopes data (e.g., Layman et al. 2012) offer an alternative to visual assessment methods, the data input requirements (e.g., fractionation values in mixing models) and

assumption criteria (e.g., that samples represent the full suite of potential prey types available to predators) of quantitative methods made them a less suitable choice for our study. At GAiso, for example, no nonpredatory riparian invertebrates were captured, but their absence from the riparian zone and hence unavailability as a potential prey was unlikely.

Benthic macroinvertebrate and emergent insect count data were used as complementary estimates of potential insect emergence from sites (Wesner 2012). We collected 3 additional samples of benthic macroinvertebrates from each site, which were preserved in 70% aqueous methanol and later identified in the laboratory to the lowest taxonomic level practicable (following methods outlined in Leigh and Sheldon 2009). For each site, we then calculated the mean abundance and richness of larval insect taxa that have flying adult life stages. Wetted width (w) of waterbodies and the numbers of individuals collected from emergence traps were used to estimate potential number of emerging insects (E , ind. $m^{-2} d^{-1}$), following the equation of Gratton and Vander Zanden (2009):

$$F = E (w/2),$$

where F is emergent insect flux (ind. m shoreline $^{-1} d^{-1}$). For example, if 10 insects were collected in 48 h from 4 traps, each with a 0.38×0.38 m surface area, in a waterbody 15 m wide, then

$$E = 10 / (4 \times 0.38 \times 0.38 \times 2) = 8.7 \text{ ind. } m^{-2} d^{-1}$$

$$F = 8.7 \times (15 / 2) = 65.2 \text{ ind. } m^{-1} d^{-1}.$$

Terrestrial vertebrates

Observational surveys of vertebrate fauna (mammals, birds, and reptiles) were conducted in riparian zones during daylight hours. Birds were surveyed within a transect that encompassed the width of each waterbody, extending approximately 50 m up- and down-stream from the observer, including 20 m into the riparian zone on one bank, and up to the height of the canopy. Presence of birds and mammals (identified to species) was detected by sound or movement and recorded. Presence of reptiles (identified to species) was recorded during noninvasive searches within the riparian zone of each bird transect. Information on the dietary guilds and feeding habits of all species identified was then collated from several sources (Marchant and Higgins 1990, 1993, Ehmann 1992, Higgins and Davies 1996, Higgins 1999, Higgins et al. 2001, 2006, Higgins and Peter 2002), which allowed us to categorise each species as a potential consumer (or not) of different types of freshwater fauna: fish, crustaceans, invertebrates, and flying adults insects with aquatic larval

stages. Proportions of vertebrate fauna observed at study sites that feed (exclusively or otherwise) on aquatic fauna were then calculated.

Results

Riparian zone condition: canopy cover and TRARC scores

Canopy cover over surface water was greatest at GM, the perennially flowing site (Fig. 1). Among isolated waterbodies, canopy cover showed similar patterns to plant cover and composition in the riparian zone; overall plant cover increased with canopy cover, and this plant cover was associated more with native species (Fig. 1). TRARC Condition scores followed the same pattern as Regeneration scores, decreasing in value from GM to GAiso to FAiso and finally to FMiso (Fig. 1).

Potential aquatic subsidy to the terrestrial zone

Stable isotope values of riparian predatory invertebrates (spiders and odonates) were closely aligned among and within sites (Fig. 2 and 3). Across all sites, mean $\delta^{13}C$ was $-22.0 \pm 2.6\text{‰}$ for odonates and $-22.6 \pm 3.6\text{‰}$ for spiders; mean $\delta^{15}N$ was $7.8 \pm 0.7\text{‰}$ for odonates and $6.7 \pm 1.0\text{‰}$ for spiders. Emergent insect signatures overlapped those of aquatic larval and adult insects within sites (Fig. 2 and 3). Nonpredator isotopic signatures from the riparian zone were either too N-enriched (e.g., at FAiso) or C-depleted (e.g., at FMiso) compared with the predatory riparian invertebrates for the nonpredators to be considered the major source of N and C assimilated by the predators, at least for sites in the Flinders catchment. In contrast, riparian predators were well aligned with aquatic invertebrate signatures. Larval and adult life-stages of aquatic insects, along with the emergent insects, tended to have ranges of $\delta^{13}C$ values that overlapped those of the riparian predators and $\delta^{15}N$ values that were lower than the riparian predators (Fig. 2 and 3). Aquatic decapods were collected at GM and FMiso only, but their signatures were too N-enriched for these fauna to be likely prey items of the collected riparian predators, unless trophic fractionation was exceptionally low and the predators were also targeting aquatic invertebrates with very low $\delta^{15}N$ (Fig. 2 and 3). Water surface dweller $\delta^{15}N$ tended to be comparable with $\delta^{15}N$ of riparian predators, reducing the likelihood that the surface dwellers were a major source of food for these consumers (Fig. 2 and 3).

Fewer emergent aquatic insects were caught in traps over a 48 h period from sites in the Flinders catchment (3 chironomids at FMiso; 1 ephydrid and 9 chironomids at FAiso) than the Gregory catchment (4 baetids and 9

Table 1. Feeding habits^a and potential proportional reliance on aquatic fauna as a food source for vertebrate fauna^b observed in the riparian zones of waterbodies.

Fauna group	GM	GAiso	FMiso	FAiso	Total
<i>Number of species observed</i>					
Mammals	1	1	1	0	1
Birds	27	31	42	15	64
Terrestrial reptiles	2	1	2	0	4
Total	30	33	45	15	69
<i>Number of species within feeding habit groups (% of total number of species)</i>					
Consumers of freshwater fish	6 (20.0)	8 (24.2)	12 (26.7)	3 (20.0)	13 (18.8)
Consumers of freshwater crustaceans	6 (20.0)	5 (15.2)	9 (20.0)	3 (20.0)	13 (18.8)
Consumers of freshwater invertebrates	2 (6.7)	5 (15.2)	6 (13.3)	2 (13.3)	9 (13.0)
Consumers of flying adult insects with aquatic larval stages	7 (23.3)	10 (30.3)	11 (24.4)	4 (26.7)	12 (17.4)
Consumers of aquatic fauna (any of the above groups)	13 (43.3)	14 (42.4)	22 (48.9)	7 (46.7)	26 (37.7)

^a Feeding habits of vertebrate fauna may be exclusive or otherwise regarding their consumption of aquatic fauna

^b See Appendix A for the full list of vertebrate species observed in the study region

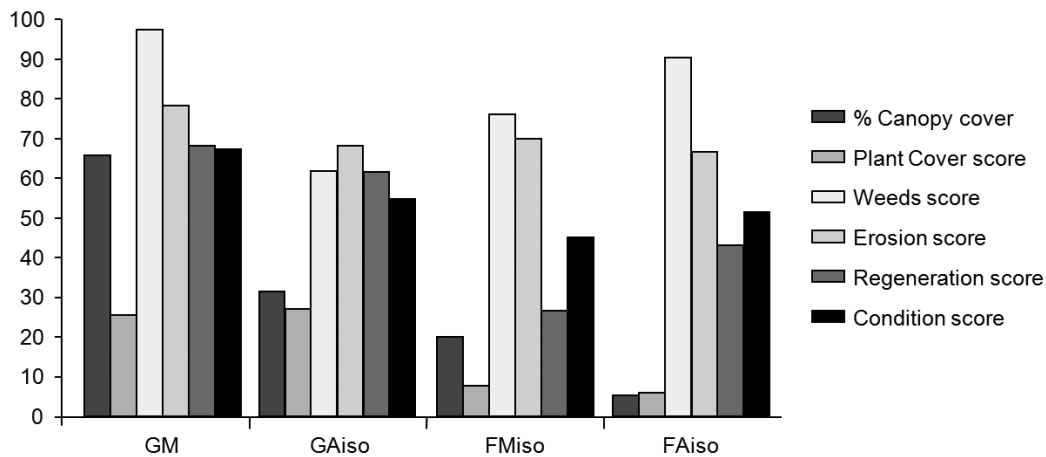


Fig. 1. Patterns in riparian condition among sites, as indicated by TRARC scores and percent canopy cover over the water surface.

chironomids at GM; 8 baetids, 15 chironomids, 5 tabanids, and 1 ephydrid at GAiso). These catches equated to daily areal emergences (E , ind. $m^{-2} d^{-1}$) of 2.6, 8.7, 11.2, and 25.1 for FMiso, FAiso, GM, and GAiso, respectively. Flux estimates (F , ind. $m^{-1} d^{-1}$) reflected the same pattern of increase across the same order of sites: 32.5, 65.2, 84.0, and 251. Similar patterns of potential emergence across sites were also provided by the site means of abundance and richness of aquatic larval insect taxa with flying adult life stages, even considering the wide variation in abundances among site replicates; FMiso had the lowest estimates (98 ± 82 individuals and 8.3 ± 0.6 taxa), followed by FAiso (193 ± 130 individuals and 8.3 ± 0.6 taxa), then GM (371 ± 186 individuals and 24.0 ± 1.0

taxa) and GAiso (687 ± 113 individuals and 13.7 ± 1.2 taxa). Among the isolated waterbodies (FMiso, FAiso, and GAiso), consistent patterns were also found between the emergence estimates and riparian condition. As TRARC Regeneration and Condition scores improved, potential emergence from these waterbodies (estimated as E , F , or as based on abundance and richness of aquatic larval insects) increased (Fig 4).

We observed 69 total vertebrate species (mainly birds) in the riparian zones of sites; the most at any one site was 45 species at FMiso (Table 1; Appendix A). Known consumers of aquatic fauna (fish, crustaceans, invertebrates, and flying adult insects with aquatic larval stages) made up a reasonable proportion (37.7%) of the total vertebrate

species and indicated an important potential subsidy from the aquatic to terrestrial zone (Table 1). Proportions at individual sites were even higher, such that between 42.4 and 48.9% of species at any one site consumed aquatic fauna. Similar to the patterns seen in potential emergence estimates, there was a consistent pattern among isolated waterbodies of greater potential subsidy from the aquatic to terrestrial zone associated with changes in riparian condition; higher TRARC Regeneration and Condition scores were associated with higher proportions of the riparian vertebrate fauna that consume flying adult insects with aquatic larval stages (Fig. 4). These proportions were also higher than the proportion observed at the hydrologically connected site, GM (Table 1).

Discussion

Multiple lines of evidence showed that the potential subsidy of aquatic food sources to consumers in riparian zones of our study region was substantial and moderated by riparian zone condition. Stable isotopes values of aquatic insects were more closely aligned than nonpredatory riparian insects with predatory riparian invertebrates (spiders and adult odonates), suggesting that the predators relied on aquatic more than terrestrial food sources. Spider and adult odonate signatures were also well aligned, providing further evidence that the predatory spiders were reflecting an aquatic isotope signature. In addition, close to 50% of the terrestrial vertebrate species we observed in

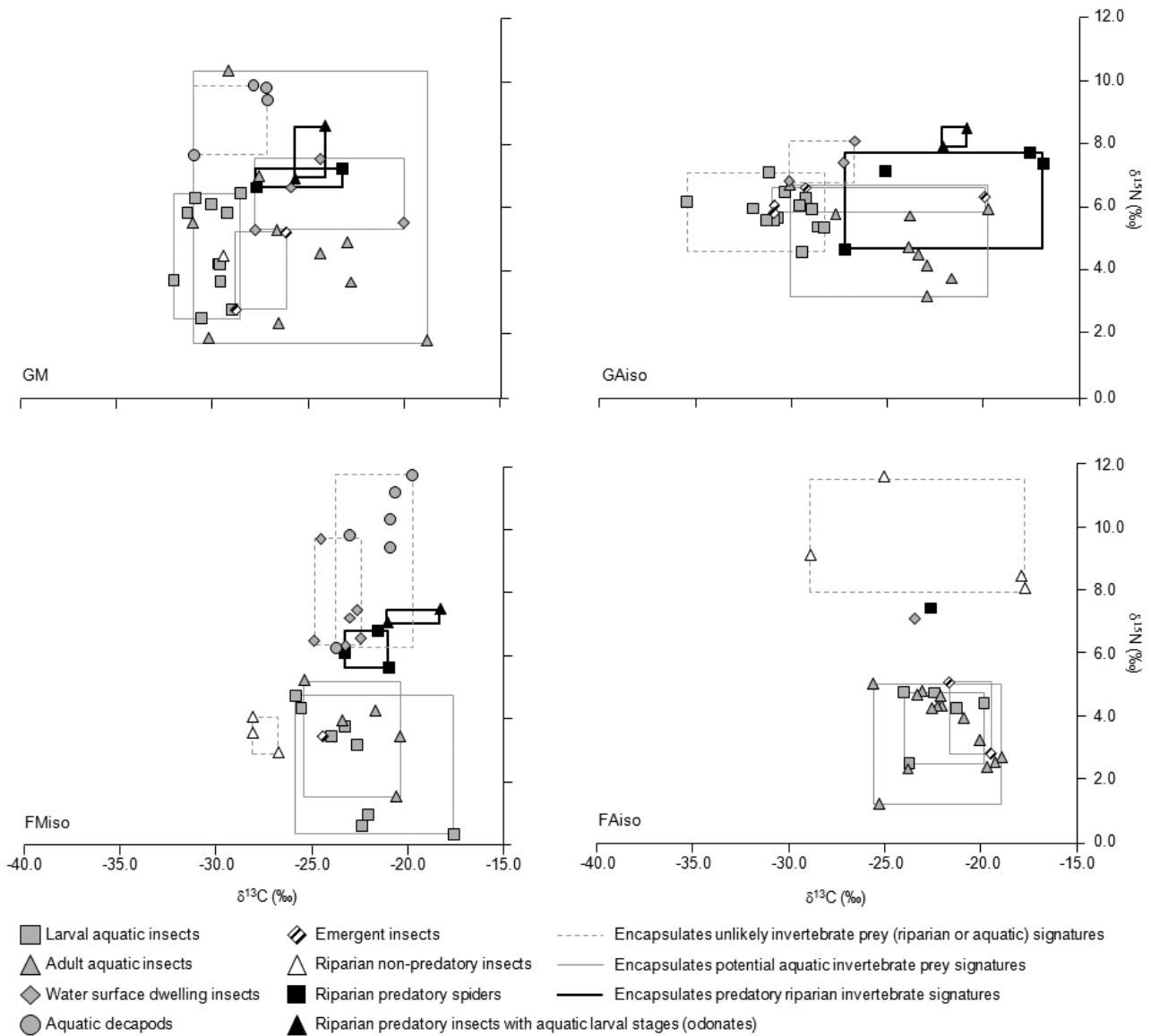


Fig. 2. Stable C and N isotope biplots for each waterbody.

riparian zones consume aquatic fauna, and ~25% consume flying adult insects with aquatic larval stages. Aquatic subsidies, such as emergent insects, from the dry-season waterbodies therefore likely play an important role in the riparian invertebrate and vertebrate food webs. Further, in the hydrologically disconnected waterbodies, potential emergence of aquatic insects and the proportional subsidy of this aquatic-derived material to riparian vertebrate fauna increased as the condition of riparian zones improved. These findings were based on data collected from 4 sites sampled during one dry-season period only, and therefore may be viewed as tentative; however, the combined use of stable isotopes, benthic assemblage, insect emergence, and terrestrial survey data add strength to our conclusions.

The mechanisms driving the greater benthic insect abundance and emergence in isolated waterbodies with

higher riparian zone condition scores are at this stage unclear but can be postulated. First, aquatic-derived carbon, rather than leaf litter and terrestrial-derived carbon, is the major source of organic matter assimilated by benthic invertebrates in these waterbodies (Leigh et al. 2010). Rather than acting directly as a food resource, inputs of leaf litter from intact riparian zones may instead provide suitable aquatic habitat that supports high abundances of benthic invertebrates and therefore high emergence. For these waterbodies, the proportion of leaf litter substrate follows the same pattern of increase from FMiso to FAiso to GAiso (Leigh 2008) as found in this study for insect abundances, emergence, and riparian condition scores. High quality riparian zones may also provide emergent insects with suitable terrestrial habitat in which to complete their adult life stages and reproduce

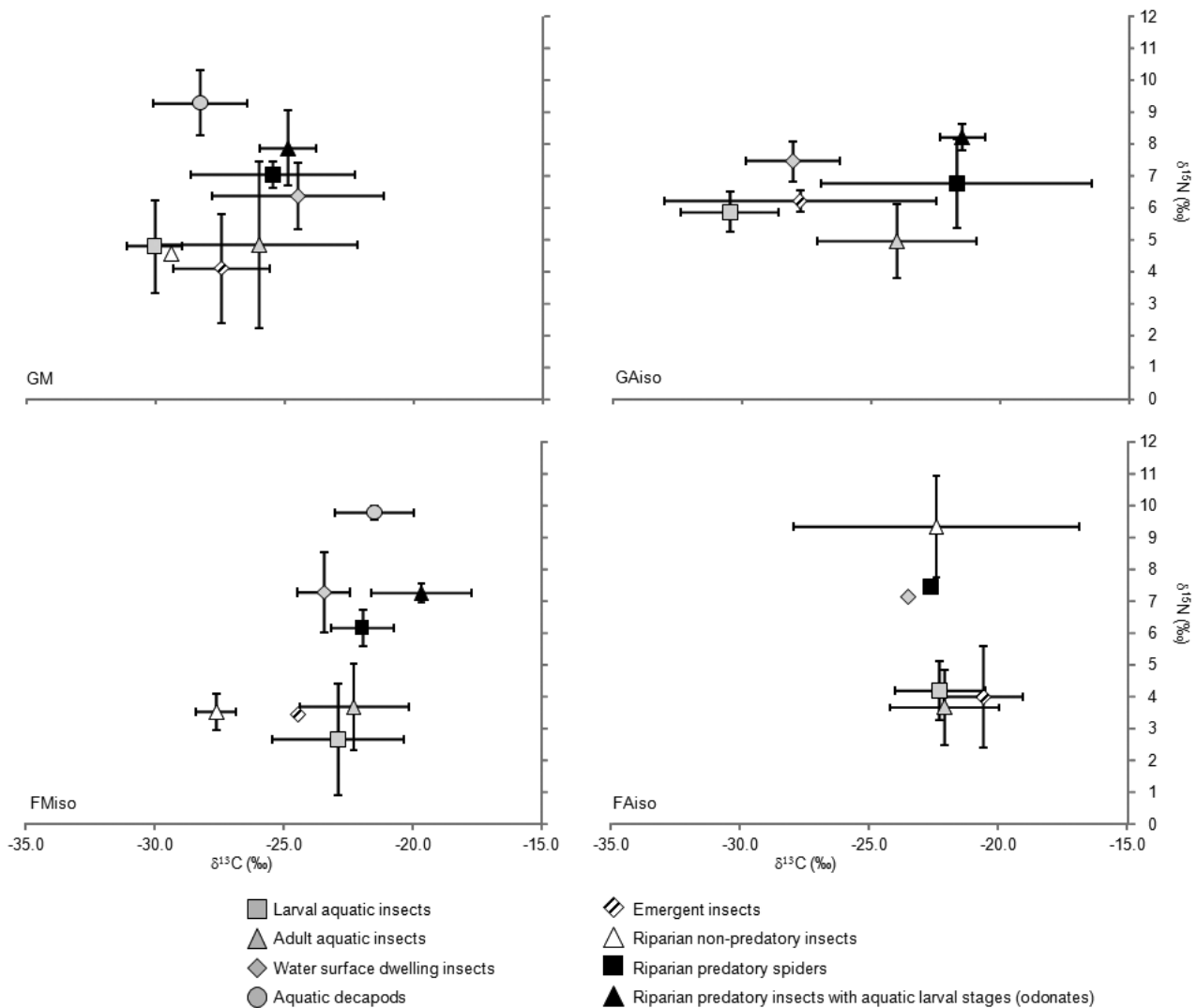


Fig. 3. Stable C and N isotope biplots for each waterbody based on trophic group means (± 1 standard deviation).

(Ballinger and Lake 2006). In turn, we postulate that the importance of emergent insects in the diets of terrestrial vertebrates was the primary driver of the pattern we observed in the terrestrial consumer communities of isolated waterbodies. This hypothesis is based on the positive relationship we found between riparian condition and the proportion of vertebrate species that consume emergent insects, not with the total number of vertebrate species (riparian condition was not associated with higher absolute numbers of species). As such, we propose that riparian condition positively influences emergence, and emergence then positively influences the vertebrate fauna that consume emergent insects.

The relationships we observed between riparian zone characteristics and emergence estimates therefore suggest

that riparian zone degradation, in terms of plant regeneration and overall condition, could affect linkages between aquatic and terrestrial food webs in the region, particularly those associated with dry-season waterholes. Riparian zones in the wet–dry tropics are vulnerable to disturbance from stocked animals (e.g., cattle) via trampling and overgrazing (Bengsen and Pearson 2006, Woinarski et al. 2007), which may intensify during the dry season when water becomes scarce (e.g., Pettit et al. 2012b). Extreme weather events, such as severe tropical cyclones, are also a potential threat to the condition of riparian zones in the wet–dry tropics. Climate projections for northern Australia suggest that although these events may become less frequent, the cyclones that do occur may be more intense (CSIRO 2007). Tropical cyclones can severely damage

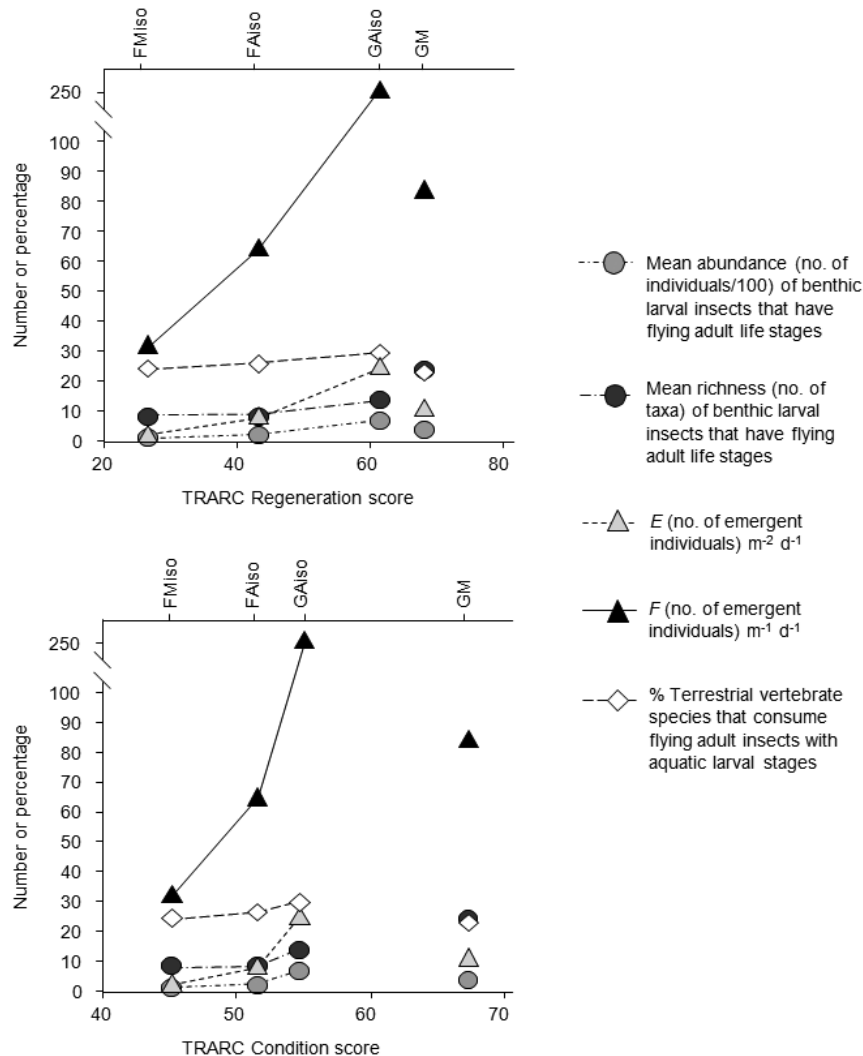


Fig. 4. Relationships between site riparian condition (TRARC Regeneration and Condition scores) and estimates of potential aquatic subsidy to the terrestrial zone. Dashed and solid lines highlight the consistent trend observed only among isolated waterbodies, whereby potential subsidy increases as TRARC scores improve. The trend does not extend to include the hydrologically connected site, GM.

riparian plants, particularly pioneer species important for plant regeneration and succession, and have been associated with substantial uprooting of stream-side vegetation (Bruce et al. 2008, Pohlman et al. 2008, Turton 2012). Potential impacts of both cattle grazing and future climate on the integrity of riparian zones are therefore of concern for the integrity of trophic linkages between the region's aquatic and terrestrial zones. Our findings suggest that this may be particularly relevant around isolated waterbodies during the dry season.

Aquatic ecosystems can provide a substantial subsidy by way of food resources to consumers in terrestrial zones (Polis et al. 1997, Collier et al. 2002), and our study provides further evidence that aquatic ecosystems in the wet–dry tropics are no exception (Lynch et al. 2002). Here, not only does aquatic production fuel aquatic food webs (Leigh et al. 2010, Hunt et al. 2012, Jardine et al. 2013), it also provides an important food source for terrestrial consumers. Further, many of the terrestrial vertebrate species we observed that consume aquatic fauna have wide home and foraging ranges (e.g., the white-bellied sea-eagle, *Haliaeetus leucogaster*, may forage over a 100 km² zone) and can travel large distances during seasonal migrations (e.g., the whistling kite, *Haliastur sphenurus*, has been observed to travel 2400 km; Marchant and Higgins 1993). The importance of aquatic subsidies from these wet–dry tropical systems to the terrestrial zone may therefore extend far beyond the waterbody of origin (Jonsson et al. 2013). Our findings do not, however, negate or downplay the importance of reciprocal subsidies from the terrestrial zone to aquatic food webs (Davis et al. 2010), or the importance of intact flow regimes in underpinning these exchanges (Douglas et al. 2005). Maintaining flow regimes that preserve spatially and temporally dynamic aquatic–terrestrial ecosystems and riparian zones of high quality and functionality will therefore support both aquatic and terrestrial food webs, maintaining their interconnectivity across the landscape.

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Supplementary Material

Supplementary Material is available for download via the Inland Waters website, <https://www.fba.org.uk/journals/index.php/IW>:

Appendix A: Vertebrate species observed (‘o’) in riparian zones of sites during the 2006 dry season: main dietary guild classification and their potential aquatic food sources (‘yes’), as detailed in Marchant and Higgins (1990, 1993), Ehmann (1992), Higgins (1999), Higgins and Davies (1996), Higgins et al. (2001, 2006) and Higgins and Peter (2002).