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Conserving nature's chorus: Local and landscape features promoting frog species richness in farm dams

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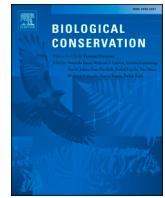
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Conserving nature's chorus: Local and landscape features promoting frog species richness in farm dams

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ABSTRACT

Habitat loss is a key factor in the ongoing freshwater biodiversity crisis. A promising way to help tackle the rapid decline in freshwater biodiversity is to improve the potential for artificial wetlands to provide habitat for aquatic wildlife. Farm dams (also known as agricultural ponds) are among the most abundant waterbodies in agricultural landscapes and can act as “oases” against droughts for many species. Despite their prominent role in agriculture, predictive models to evaluate their ecological potential are yet to emerge. Here we use a continental-scale data set of 104,013 audio recordings from citizen scientists to identify and locate 107 species of frogs near 8800 Australian farm dams. Frog species are among the most threatened taxa on earth and we asked: *What characteristics promote higher frog species richness at farm dams?* We found that the highest values of frog species richness were at old (>20 years) farm dams of intermediate size (0.1 ha in surface area), with small or medium rainfall catchments (<10 ha), and situated near other freshwater systems or conservation sites. The relationships shown here are highly generalisable and applicable on a continental scale. By identifying quantifiable features improving the ecological value of farm dams, we help identify “win-win” outcomes for agricultural productivity and conservation. In the future, “biodiversity credit” policies could incentivise large-scale ecological restoration by rewarding individuals who invest in enhancing their farm dams to support and promote local biodiversity.

1. Introduction

We are amidst a freshwater biodiversity crisis (Harrison et al., 2018). Freshwater environments exhibit higher rates of species extinction among mammals, birds, fishes, crayfish, and amphibians compared to terrestrial or marine habitats (Tisseuil et al., 2013; Albert et al., 2021; Moor et al., 2022). Among the principal causes is the degradation and loss of freshwater habitats (Cushman, 2006; Gallant et al., 2007; Albert et al., 2021), with 70 % of the world's wetlands lost during the 20th century (Davidson, 2014). Amphibian declines are particularly dramatic (Beebe and Griffiths, 2005; Whittaker et al., 2013; Scheele et al., 2019), with nearly half of the species now classified as Threatened or Near Threatened (Button and Borzee, 2021; IUCN, 2022). Maximising the

potential for artificial waterbodies to provide new habitats for local wildlife can help reverse population declines in some species, such as by restoring degraded artificial ponds (Rannap et al., 2009), building new ones (Moor et al., 2022), and establishing natural parks (Knutson et al., 2004; Knapp et al., 2016). Yet, examples of large-scale restoration efforts to support freshwater biodiversity through managing artificial wetlands remain rare (Moor et al., 2022).

In agricultural areas, farm dams (also known as agricultural ponds, impoundments, dugouts, or excavated tanks) are among the most abundant type of waterbodies in rural landscapes and are critical to maintaining water security for livestock and crops (Malerba et al., 2021; Swartz and Miller, 2021). While individual farm dams are generally small (surface area, 10^3 – 10^4 m² or 0.1–1 ha), their cumulative surface

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area surpasses that of lakes and reservoirs in many agricultural regions (Malerba et al., 2021; Swartz and Miller, 2021). The continuous proliferation of farm dams on the landscape is having intensifying effects on biodiversity, affecting species richness (Lewis-Phillips et al., 2019; Reyne et al., 2020), species composition (Hazell et al., 2001), and the risk of biological invasions (Letnic et al., 2015). It is becoming increasingly important to identify management strategies for farm dams to benefit local biodiversity (Chester and Robson, 2013; Chen et al., 2019).

The biodiversity conservation value of a farm dam depends on several characteristics at local and landscape scales. At a local scale, farm dams surrounded by established vegetation offer higher habitat heterogeneity for native wildlife and better protection from predators than bare dams (Hazell et al., 2001; Hamer et al., 2011). Also, reduced plant diversity around dams due to intensive agriculture can drive phylogenetic filtering and community homogenisation (Moreira et al., 2020). Other abiotic features of farm dams have less intuitive effects on species richness. For example, larger and deeper farm dams with greater rainfall catchments offer species more protection against desiccation (Scheele et al., 2016), yet they often have higher predation risks from fish or reptiles (Hamer et al., 2011; Chester and Robson, 2013; Holbrook and Dorn, 2016). At a landscape scale, a network of well-connected water bodies should favour dispersal and colonisation, compared to isolated dams (Faggioni et al., 2021). Similarly, freshwater systems near protected areas or national parks should accumulate more species through spillover than those surrounded by agricultural land with more intense human activities (Zolderdo et al., 2019; Shen et al., 2022). Conversely, roads or railways nearby farm dams may reduce species richness by increasing mortality and reducing wildlife movement (Cosentino et al., 2014; Villaseñor et al., 2017; Hamer, 2018). Finally, the climate is a key determinant of habitat suitability, with hotspots of frog species richness often in tropical and sub-tropical climates with high rainfall and temperatures (Williams and Hero, 2001; Slatyer et al., 2007).

Previous work on the effects of farm dam characteristics on freshwater biodiversity has focused on monitoring programmes targeting specific regions and species (Jansen and Healey, 2003; Hazell et al., 2004; Mahony et al., 2006). However, to understand generalisable characteristics of farm dams that affect wildlife, studies would need to compile data for more species over a broader area. One way to increase the coverage of field studies is to engage with citizen scientists to help collect data at larger temporal and spatial scales (Callaghan et al., 2019; Fritz et al., 2019; Olivier et al., 2020; Rowley et al., 2020). Frog species are highly threatened and an excellent “surrogate” for broader patterns of freshwater biodiversity, as their species richness and endemism patterns have the highest correlations with other freshwater taxa (Tisseuil et al., 2013). Also, there are now several successful citizen-science programmes to track frog species density and diversity, including FrogID (Rowley et al., 2019) and Melbourne Water's Frog Census (Catus-Wood, 2017) in Australia; the Louisiana Amphibian Monitoring Program (Carter et al., 2021) and the North American Amphibian Monitoring Program (Villena et al., 2016) in the USA; and “Toads on Roads” in Great Britain (Petrovan et al., 2020). These programmes mostly rely on smartphone apps to collect georeferenced audio recordings of frog calls that are then validated by experts, enabling the collection of vast and high-quality datasets.

Leveraging five years of validated data, this study combined citizen science with spatial data to offer the first continental-scale assessment of farm dam environmental characteristics influencing frog species richness. The aims of this study are (1) to quantify frog species richness near farm dams and (2) to assess the statistical association between frog species richness and the size, age, or nearby landscape characteristics of farm dams. We hypothesise that the frog species richness at a farm dam depends on local features (e.g., surface area, catchment size, farm dam age), landscape features (e.g., density of other freshwater systems, conservation sites, or roads and railways), and the climate (e.g., average

temperature and precipitation). We sourced 104,013 records of frog calls from citizen scientists to identify 107 species calling from 8800 farm dams across Australia. We then quantified the effects on frog species richness of dam surface area, rainfall catchment area, mean annual temperature, and rainfall, as well as landscape features within 500 m of each dam (presence of other water bodies, protected areas, and roads or railways).

2. Materials and methods

2.1. Farm dam locations and characteristics

We sourced the geographic coordinates and surface areas (m²) of farm dams in Australia from AusDams.org, a platform documenting around 1.7 million such features (Malerba et al., 2021). This dataset included on-stream (connected to existing waterways, such as streams or rivers) and off-stream (separated to waterways and relying mostly on rainfall runoffs) dams for any farming operation, particularly livestock and irrigation. We calculated the rainfall catchment area of each farm dam (i.e., the area of land predicted to collect rainfall) using a digital elevation model at 30 m resolution (Takaku et al., 2020) together with the Flow Modelling tools in Whitebox Geospatial Analysis Tools (Lindsay, 2016). We also determined the year of farm dam construction based on biweekly time series from 1987 to 2011 of water detection using the Landsat-based Water Observations from Space programme (30 m resolution) curated by Geoscience Australia (Mueller et al., 2016). Specifically, the year of farm dam construction was taken as the first year when water was consistently reported in at least 25 % of the farm dam area (see Malerba et al., 2021 for details).

2.2. Frog species richness

To compile a database of frog species richness in Australia, we used data from two citizen-science programmes: FrogID, a nationwide initiative launched by the Australian Museum in 2017 (Rowley et al., 2019; Rowley et al., 2020); and Frog Census, a regional programme maintained by Melbourne Water that covers the state of Victoria, in southeastern Australia (Catus-Wood, 2017). Both programmes rely on participants using a smartphone app to record calling frogs and upload an audio file to the cloud. Each recording is tagged with metadata (e.g., time, date, location) and sent to a management system, where a team of experts listens to the audio to identify the frog species calling. We used audio recordings of frog calls geolocated within 50 m of a farm dam from 10 November 2017 to 1 September 2021 for FrogID ($N = 72,663$), and from 1 September 2016 to 25 June 2021 for Frog Census ($N = 11,562$). We used the date and coordinates to ensure no duplicate entries in our dataset. The two programmes differ in their method of geolocalization of the calls: FrogID is automatic (through the mobile location service), whereas Frog Census requires users to manually specify the location. Also, FrogID users can record up to 1 min, while Frog Census allows up to 5 min. Despite these differences, both programs generate comparable data because they use equivalent techniques to identify species from audio recordings.

We sourced data from FrogID and Frog Census to generate a dataset of 104,013 frog calls from 107 species near 8800 Australian farm dams, spanning 27.75° of latitude (from −43.45° to −15.70°) and 38.87° of longitude (from 114.74° to 153.61°; Fig. 1). For determining species identity, we used the expert identification provided by FrogID and Frog Census at the time of data export. The spatial distribution of our data reflects the density of farm dams in Australia (high in southeastern, eastern, and southwestern Australia; low across semi-arid, arid, and northern Australia), and is biased towards dams near major population centres.

We identified threatened frog species in our dataset using Australia's Environmental Protection of Biological Conservation (EPBC) Act of Threatened Fauna (<https://www.environment.gov.au/cgi-bin/sprat/p>

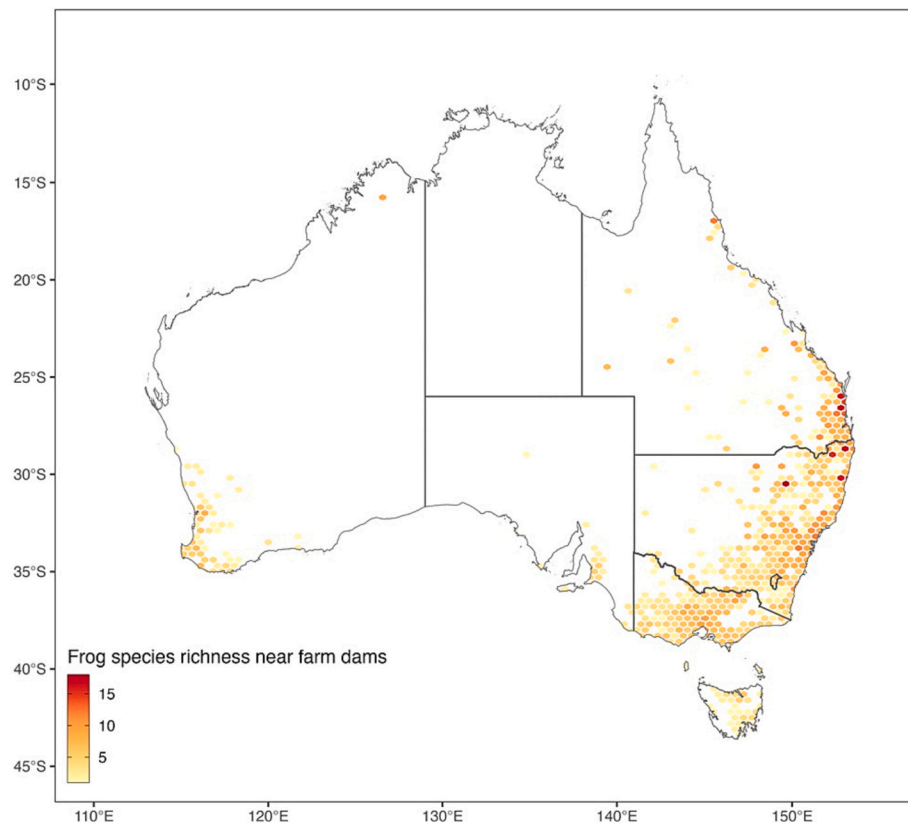


Fig. 1. Number of frog species detected in audio recordings within 50 m of 8800 farm dams across Australia. Each hexagon covers approximately 1000 km², with the colour indicating the density of frog species near dams. Quantiles of species richness: 0 % (minimum) = 1; 25 % = 1; 50 % = 2; 75 % = 4; 100 % (maximum) = 18.

public.ubc.ca/publicthreatenedlist.pl) – sourced on the 23rd Feb 2023.

2.3. Local climate and landscape characteristics

We used ANUclimate (version 2.0) to calculate the average annual temperature (°C) and average total annual rainfall (mm) at each farm dam using monthly values from 1988 to 2020 (Hutchinson et al., 2014). This platform is curated by the Australian National University and covers the country at a 0.01° resolution (Hutchinson and Xu, 2013). Within a circle of 500 m radius around each dam, we used the 2016 Australian Land Use and Management Classification System (ALUM; Dept. of Agriculture and Water Resources, 2016) to quantify the land area occupied by roads and railways (classes 572 and 573: “Road and Railways”), vegetated areas with little human intervention (class 100: “Conservation and natural environments”), and inland water bodies (class 600: “Water”). The inland water bodies included both natural (e.g., lakes, rivers, marshes, wetlands) and artificial (e.g., reservoirs, dams, channels, aqueducts) systems. Finally, we used AusDams.org (see details above) to calculate the density of overlapping farm dams within a 500 m radius as an additional covariate in the model. The choice of a 500 m radius was based on the maximum travelling distances measured for common Australian frogs in agricultural landscapes, which are reportedly up to 719 m (Pulsford et al., 2018).

2.4. Statistical analyses

We fit generalised linear models with Poisson error distribution (with log link) to analyse frog species richness near farm dams. Specifically, the response variable was the number of unique species (species richness) identified across all surveys within 50 m of each farm dam. We detected between 1 and 18 frog species at each dam, with 43.7 % of all dams ($N = 3846$) showing more than two frog species (median = 2

species per dam; Fig. S1 A). However, because many farm dams were associated with multiple audio recordings (up to 460; Fig. S1 B), we included survey effort (number of audio recordings per farm dam) as a polynomial covariate in the model to correct for the increasing likelihood of detecting new species with more surveys up to an expected plateau in richness (Fig. S1 C). We believe this approach is superior to using the mean species per transect because areas of low biodiversity tend to be sampled less often, but at times with peak frog calling (i.e., many species per recording). In contrast, audio recordings in frequently visited areas often have both high and low species richness, and using mean species per survey would risk dampening the biodiversity value by including periods when few species were calling. Nevertheless, total species richness and mean species richness were highly correlated (Pearson $r = 0.73$, $t_{8798} = 100.49$, $p < 0.001$).

The explanatory variables in the fully-parametrised model included the farm dam surface area (\log_{10} ; m²), catchment area (\log_{10} ; m²), average annual temperature (°C), and the average total annual rainfall (\log_{10} ; mm). Additionally, the model quantified the effects of landscape features by including as linear explanatory variables the percentage area within a 500 m radius of each farm dam occupied by freshwater systems ($\log_{10} + 1$; %), conservation and natural environments ($\log_{10} + 1$; %), and roads/railways ($\log_{10} + 1$; %). Finally, we added the density of overlapping farm dams ($\log_{10} + 1$; count) within a 500 m radius as a linear covariate in the model. Semlitsch et al. (2015) showed that an intermediate pond size maximises amphibian species richness, so we included second-degree polynomial functions in our model to describe the effects of farm dam surface area and catchment area on species richness. We also tested polynomial relationships to describe the effects of average annual temperature and rainfall at each site. Finally, the model included a 2D spline smooth of latitude by longitude (argument “s [latitude, by = longitude]” in the R function *gam*; Hastie, 2022) to describe non-linear relationships in spatial data, which serves to account

for spatial autocorrelation in the data (Wood, 2003; Tiedemann et al., 2021).

We used Akaike information criteria (AIC; Burnham and Anderson, 2004) to test all combinations of nested models and identify the best-fitting model, as the one with the lowest number of parameters within two units from the minimum AIC score. For the best-fitting model, we ensured that the standardised residuals showed no systematic patterns with all explanatory variables (i.e., all relationships have non-significant slopes and are centred on zero). Importantly, the model standardised residuals showed no trend with latitude and longitude, indicating that the model could describe patterns across regions and climates equally well.

Our dataset included 8800 Australian farm dams, but we could only determine the year of establishment for 8.3 % (733). The spatial distribution of farm dams with known establishment age overlaps well with the full farm dam distribution. To avoid a substantial decrease in the sample size of the fully parametrised model, we ran a separate analysis using a reduced dataset to investigate the effects of farm dam age on frog species richness. This second model included four parametric coefficients (i.e., the intercept, farm dam age, and a polynomial effect of sampling effort) and the 2D spline smoothing of latitude by longitude (as for the previous model). Using AIC model selection, we tested a 2nd degree polynomial functional response for a saturating effect of farm dam age on species richness, because dams may reach a maximum number of species over time.

To confirm that the model correctly described patterns of frog species richness in areas with different levels of biodiversity, we modelled the effects of farm dam features on relative frog species richness. Specifically, we used the Australian Frog Atlas (Cutajar et al., 2022) to extract the expected total number of frog species richness in the region of each farm dam. We calculated relative frog species richness at each dam as the proportion of observed species relative to the expected total number of frog species. We used beta regressions to analyse the effects of all farm dam properties (i.e., surface area, catchment, the nearby densities of conservation areas, other waterbodies and roads, and year of establishment) on relative frog species (proportion of the expected total species) using the *betareg* package in R (Cribari-Neto and Zeileis, 2010), based on Ferrari and Cribari-Neto (2004) and Simas et al. (2010). This modelling technique can capture heteroskedastic and asymmetric distributions in percentages (bound from 0 to 1) by fitting two separate regressions to describe mean and precision – instead of traditional logistic regressions with a single regression function only for the mean. We also included sampling effort (number of surveys), latitude, and longitude – all as 2nd degree polynomial relationships.

2.5. Model sensitivity

We used a permutation approach to calculate the relative importance of the explanatory variables in the best-fitting model for frog species richness (Niittynen and Luoto, 2018; Virkkala et al., 2021; Malerba et al., 2022b). The approach consisted of permuting each variable in the best-fitting model to remove its explanatory power, and quantifying the decrease in model prediction accuracy compared to the best-fitting model. For each variable (v) in the model (except the smoothing terms and the survey effort), we quantified the relative importance (I_v) by calculating the decrease in the Pearson correlation coefficient (cor) between the predictions of the original data ($Pred$) and the predictions of the model with v permuted ($Pred_v$), as:

$$I_v = 1 - cor(Pred, Pred_v) \quad (1)$$

A higher I_v score indicates greater importance of the variable in the model. We repeated this process 30 times to calculate the mean and 95 % confidence intervals for each variable. Finally, we normalized all coefficients to sum to 100 %.

3. Results

3.1. Frog species richness near farm dams

Our dataset included 107 frog species detected at 8800 farm dams (see Table S1 for the summary table). Most farm dams (56 %) recorded one or two species (median = 2 species per dam; maximum = 18; Fig. S1 A). Nearly half (46 %) of farm dams had only a single frog survey, with just 20 % of locations having more than four surveys (maximum of 460 surveys at an individual dam; Fig. S1 B).

The most represented genera were *Litoria* (39 species), *Limnodynastes* (14), *Crinia* (13), and *Uperoleia* (10). The most common species in the data were *Crinia signifera* ($N = 22,118$), *Litoria peronii* (10,465), *Litoria fallax* (9846), and *Limnodynastes tasmaniensis* (7965).

We found 4846 frog records (4.66 % of the total) of threatened species near 409 farm dams (4.65 % of the total). Specifically, species classified by EPBC as “Vulnerable” are *Litoria raniformis* (3272 records at 315 dams), *Litoria aurea* (7 records at 6 dams), and *Mixophyes iteratus* (36 records at 10 dams). Species classified as “Endangered” are *Crinia sloanei* (1493 records at 74 dams), *Litoria littlejohni* (22 records at 2 dams), and *Uperoleia mahonyi* (16 records at 2 dams).

3.2. Effects of farm dam surface area, rainfall catchment area, and year of establishment on species richness

The fully parametrised model included 15 parametric degrees of freedom and 21.4 estimated degrees of freedom in the latitude by longitude smoothing. However, AIC favoured a model without the density of overlapping farm dams within a 500 m radius, reducing the number of model degrees of freedom to 14 (see Table S2 for AIC table, and Table S3 for the best-fitting model). Also, AIC favoured a Poisson distribution over a negative binomial.

Following the best-fitting model favoured by AIC, farm dams of intermediate sizes (10^3 m^2 or 0.1 ha) had the highest recorded frog species richness (on average, 3.1 frog species per dam; Fig. 2A and Table S3). Smaller dams (50 m^2 or 0.005 ha) had 3.07 species (−1 %), larger ones (10^4 m^2 or 1 ha) recorded 2.8 species (−9.7 %), and very large ones (10^5 m^2 or 10 ha) registered 2.3 species (−25.8 %).

We found a negative effect of large catchment areas on species richness (Fig. 2B and Table S3). Farm dams with small or medium catchment areas ($<10^5 \text{ m}^2$ or 10 ha) recorded a roughly constant 3.1 frog species, against 2.7 species (−12.9 %) in dams with larger catchments (10^7 m^2 or 1000 ha). Also, farm dams showed a positive correlation between their catchment area and surface area ($r = 0.4$, $t_{8798} = 41$, $p < 0.001$).

Finally, we found a positive effect of farm dam age on frog species richness (Fig. 2C and Table S4). Farm dams built before 1990 showed 16.5 % higher species richness than those constructed after 2010 (Fig. 2C). There was no evidence of a deceleration in frog colonisation rate over time, as AIC supported a linear relationship (rather than a polynomial one) to explain the rise in frog species diversity within a dam. Finally, dam age was not statistically correlated with any other explanatory variable (i.e., dam surface area, catchment size, average temperature, average rainfall, total num. of surveys, dam location, and the density of nearby protected area, waterbodies, and roads).

3.3. Effects of local climate on species richness

The highest frog species richness was associated with intermediate temperatures and high rainfall (Fig. 3; Table S3). Locations with mean annual daily temperatures of 15°C had 16.1 % and 19.9 % higher frog species richness compared with cooler (10°C) and warmer (20°C) locations, respectively (Fig. 3A). Similarly, wet areas (1000 mm annual rainfall) had 21.6 % higher species richness than dryer regions (300 mm annual rainfall; Fig. 3B).

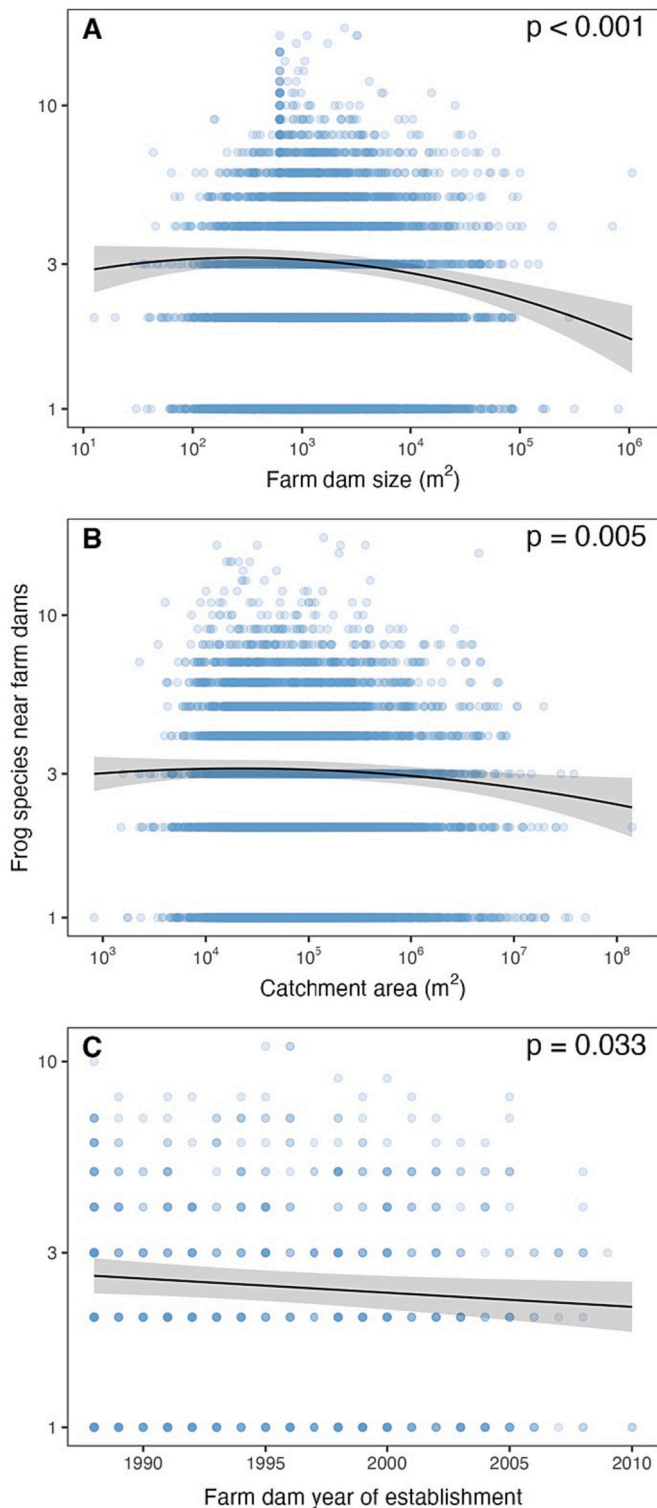


Fig. 2. Effects of farm dam surface area (A), rainfall catchment area (B), and year of establishment (C), on frog species richness. Dots represent farm dams, and the solid lines display the fits of the best-fitting model following AIC (± 95 % confidence intervals). See Tables S1 and S2 for the statistical scores.

3.4. Effects of nearby water bodies, conservation sites, and roads on species richness

The densities of freshwater systems and conservation sites within a 500 m radius from a farm dam were the two most important parametric variables in the model (Fig. 4). Together, these variables contributed

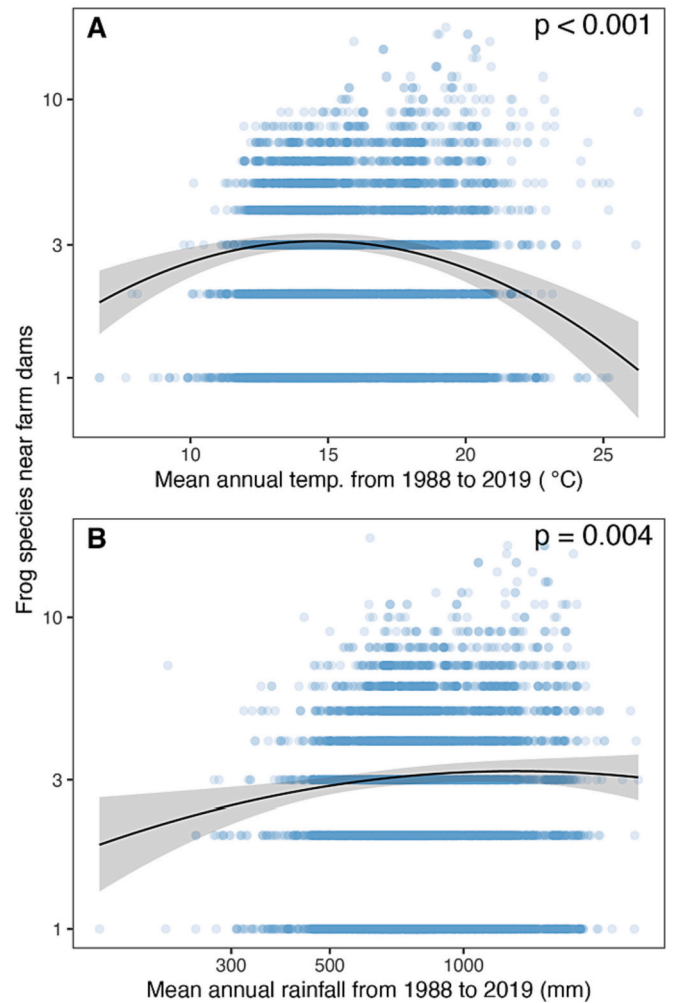


Fig. 3. Effects of average climatic conditions on frog species richness at farm dams, based on annual temperature (A) and annual rainfall (B). Dots represent farm dams, and the solid lines display the fits of the best-fitting model following AIC (± 95 % confidence intervals). See Table S3 for the statistical scores.

59.8 % to the model's explanatory power. For example, farm dams situated near other natural or artificial water bodies had up to 30.3 % more frog species compared with isolated dams (Fig. 5A). Our analysis cannot separate the effects of natural and artificial systems, yet AIC model selection excluded the density of nearby farm dams as an additional covariate in the best-fitting model. This suggests that the benefits of nearby water bodies on frog biodiversity are driven by systems other than farm dams (e.g., lakes, reservoirs, rivers, streams, wetlands, channels). We also found that farm dams surrounded by conservation sites (e.g., national parks) had up to 26 % more frog species per dam than those surrounded by agricultural areas (e.g., crops, paddock; Fig. 5B).

We detected a slight positive association (up to 6.2 %) of roads and railways surrounding a farm dam on the number of detected frog species (Fig. 5C). This parameter had the lowest relative explanatory importance (2.6 %) in the best-fitting model (Fig. 4).

3.5. Effects of farm dam properties on relative frog species richness

The analysis of relative frog species richness (i.e., the number of frog species near farm dams relative to the expected total frog species in the area) revealed virtually identical results to patterns in absolute species richness (Fig. S2). Specifically, old farm dams of intermediate sizes near conservation sites, roads, or other waterbodies showed the highest values of relative species richness. The only difference was for

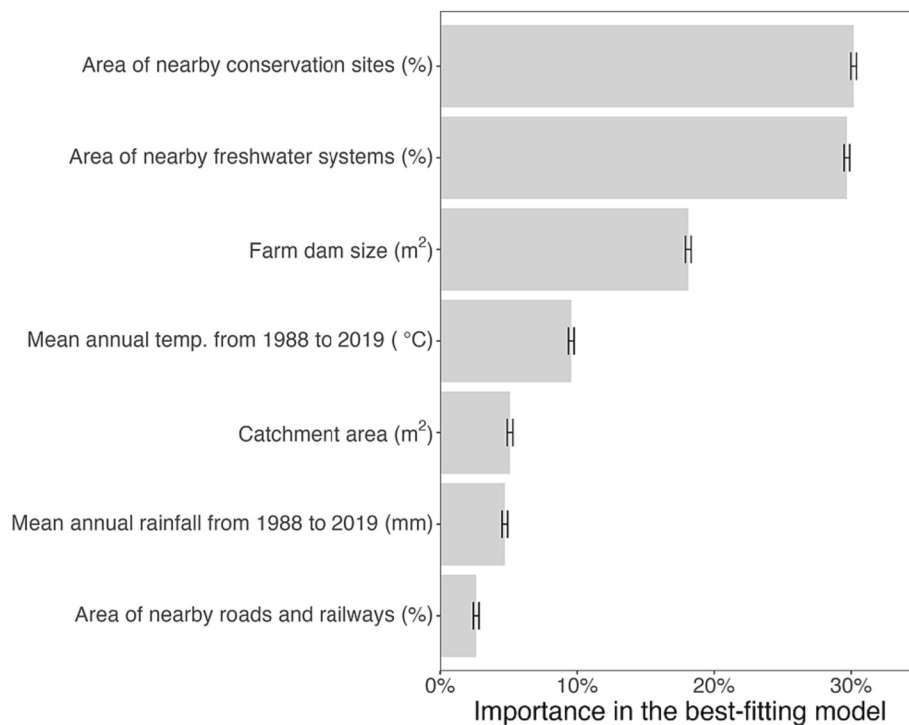


Fig. 4. Relative importance ($\pm 95\%$ confidence intervals) of the explanatory variables in the best-fitting model to explain frog species richness at farm dams (Table S3). Taller bars indicate greater importance in the model's explanatory power (see Eq. 1 in the main text). We used 30 permutations to estimate the uncertainty.

catchment size, which was no longer significant (compare Fig. 2 B with Fig. S2 B). This outcome indicates that the relationships described here are robust and applicable to regions with different frog species richness.

4. Discussion

In this study, we analysed six years of citizen-science data to understand the relationships between frog species richness and local and landscape features of farm dams across Australia. We used over 100,000 audio recordings from citizen scientists at 8800 farm dam sites across Australia to map 107 frog species – nearly half of Australia's 248 described frog species (AmphibiaWeb, 2020; Frost, 2021). The best-fitting model revealed that older farm dams with intermediate surface areas, intermediate rainfall catchment areas, and experiencing annual conditions of high rainfall and intermediate temperatures, recorded the highest values of frog species richness (Table 1, Fig. 6). Species richness was also positively correlated with the density of other nearby freshwater systems and conservation sites, and mildly positively correlated to nearby roads and railways (Table 1, Fig. 6).

The landscape features surrounding a farm dam were the most important variables to explain frog species richness. For example, we found that farm dams near other natural or artificial freshwater systems had higher frog species richness compared with isolated sites. The benefit of nearby aquatic systems on biodiversity is likely because dams in well-connected networks can facilitate the recolonization of ephemeral systems following a drought (Fortuna et al., 2006; Ribeiro et al., 2011), or other causes of local extinction (Gulve, 1994). We also found that farm dams with high densities of nearby conservation areas had greater recorded frog species richness. There are several reasons why conservation sites promote local biodiversity. For example, protected areas have greater canopy cover and habitat heterogeneity to offer refuge for frog populations, while also being immune from the impacts of land-clearing (Marsh and Trenham, 2001; Youngquist and Boone, 2021). Conservation areas also offer frogs more resources during non-breeding seasons, which helps to ensure source populations that can

colonize nearby dams (Mazerolle and Desrochers, 2005). Moreover, our data show that conservation areas are more likely to have additional freshwater systems (Pearson $r = 0.34$, $t_{8799} = 33.7$, $p < 0.001$), providing a further advantage for frog dispersal. Notice however that a minority ($<1\%$) of frog species detected near farm dams are not pond-breeder (e.g., *Assa darlingtoni* is strictly terrestrial breeder (Clulow et al., 2017), *Litoria citropa* is strictly stream breeding (Donnellan et al., 1999)), which suggests that a subset of audio recordings may be detecting frogs in adjacent habitats influencing species richness values at dams near other freshwater habitats.

We found higher frog species richness at farm dams of intermediate sizes (10^3 m² or 0.01 ha), relative to smaller and larger dams. This finding is consistent with previous research on amphibians in the USA (Semlitsch et al., 2015). The proposed explanation is a compromise between two disturbances: smaller ponds are ephemeral and likely to dry out before frogs can complete their aquatic life stages, while larger ponds have higher predation risk from fish populations established in permanent water bodies (Wellborn et al., 1996; Snodgrass et al., 2000; Werner et al., 2007). Another factor explaining this relationship may be the density of frog refuges from fringing vegetation (Boissinot et al., 2019), which is often more significant for small- and medium-sized dams on family-owned farms than for larger dams associated with intensive agricultural operations.

Older farm dams showed higher frog species diversity than more recent ones, indicating that it takes time for frogs to colonize dams (Scheele et al., 2014), and for new dams to develop emergent vegetation that many frogs use as refuge (Swartz and Miller, 2019, 2021). Emergent vegetation can offer breeding sites, protection during calls, and shelter from climatic extremes (Hazell et al., 2001). Interestingly, our results indicate that farm dams accumulate frog species slowly over decades, and there is no indication of saturation, even after 25 years (i.e., AIC rejected a model using a saturating response to describe the accumulation of frog species over time). However, this relationship does not account for the impacts of farm dam dredging to remove accumulated sediments, typically done every decade (Mitsuo et al., 2014; Dabkowski

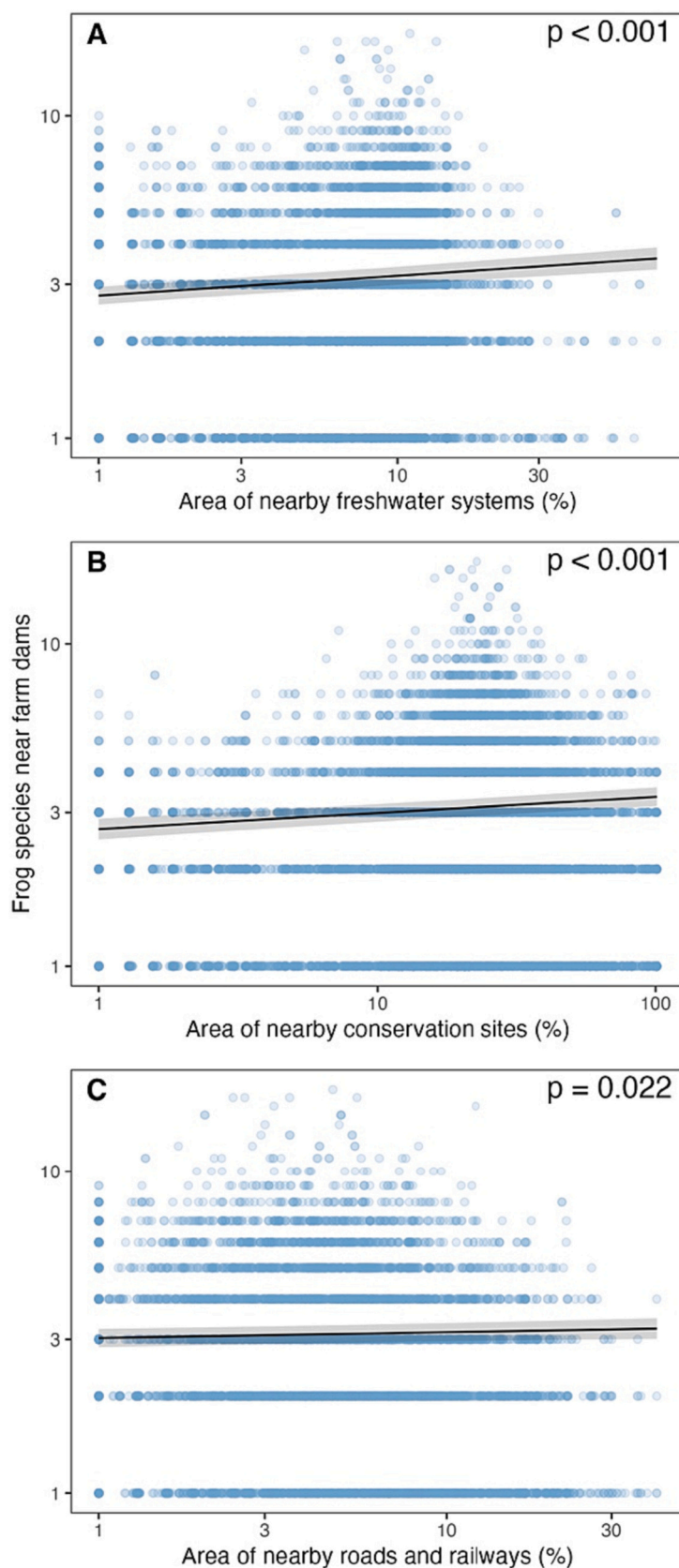


Fig. 5. Effects on frog species richness of freshwater systems (A), conservation sites (B), and roads and railways (C), calculated as the percentage area within a 500 m radius of each farm dam. Dots represent farm dams, and the solid lines display the fits of the best-fitting model following AIC ($\pm 95\%$ confidence intervals). See Table S3 for the statistical scores.

Table 1

Effects of farm dam properties, nearby landscape characteristics, and local climate on frog species richness. For each variable, we reported the range associated with the highest (top 25 %) and lowest (bottom 25 %) quartiles for the average number of frog species per transect following predictions from our best-fitting models. Variables are in order of importance in the model (see Fig. 4). See Figs. 2, 3, and 5 for data and model fits, Fig. 4 for importance scores, Tables S2–S4 for statistical scores, and Fig. 6 for a graphical summary.

	Highest spp. richness (top 25 %)	Lowest spp. richness (bottom 25 %)
Area of conservation sites within 500 m (%)	>33	<3
Area of freshwater systems within 500 m (%)	>26	<3
Surface area (m ²)	69 to 1047	>69,717
Mean annual temperature, 1988–2019 (°C)	>12.4 and < 17.1	<6.7 and > 26.3
Catchment area (m ²)	<9 × 10 ⁴	>7.8 × 10 ⁶
Mean annual rainfall, 1988–2019 (mm)	>957	<296
Year of establishment	<1993	>2005

et al., 2016). Also, farm dam age is likely to covary with other features not included in this study, such as the depth of the dam and the type of edges. As dams accumulate sediments over time, they develop shallower borders with emergent vegetation, with important benefits for frog species including oviposition sites and protection from predators and desiccation (Hazell et al., 2001; Hazell, 2003). Hence, the effects of farm dam age on frog biodiversity may strengthen after accounting for dam depth, density of emergent vegetation, and periodic dredging.

Local weather conditions were important explanatory factors of frog species richness at farm dams, with the 25 % highest values associated with intermediate annual temperatures (>12.4 and < 17.1 °C) and high rainfall levels (>931 mm; Table 1). These weather conditions correspond to the wet, tropical climate of Australia's east coast, which is a hotspot for frog biodiversity (Slatyer et al., 2007; Cutajar et al., 2022). However, prioritising conservation efforts should avoid undervaluing farm dams in arid or semi-arid habitats because of the relatively small subset of local frog species. For example, freshwater systems in less suitable habitats can support high population densities of local frog species and play an important ecological role in the environment (Pre-davec and Dickman, 1993). Encouragingly, our conclusions remained unchanged when analysing relative species richness at farm dams (i.e., the number of frog species near farm dams relative to the total frog species in the area) instead of observed frog species richness. This finding indicates that our results on the effects of farm dam area, catchment size, or nearby landscape features on frog species richness apply across Australia regardless of climate or local biodiversity levels.

Farm dams with large rainfall catchment areas had fewer frog species than those with small and medium catchments (<10⁵ m² or 10 ha). This may result from larger catchments being associated with larger dams (Pearson $r = 0.4$, $t_{8799} = 40.999$, $p < 0.001$). However, farm dams with larger catchments tend to occur in the arid and semi-arid climates of inland Australia, where regional frog species richness is lower than in coastal zones with smaller catchments (Fig. S3). Consistently, the catchment area stops being statistically significant when analysing the relative frog species richness (Fig. S2). With catchment size showing strong geographic patterns and being positively correlated with farm dam area, further studies should confirm our results on the effects of farm dam catchment area on frog biodiversity.

We found that the density of roads near farm dams showed a slight positive association with frog species richness. This finding is surprising, as it contradicts the large body of literature showing negative impacts of traffic near agricultural areas, including in Europe (Vos and Chardon, 1998; Vos et al., 2001; Lesbarrères et al., 2006), the USA (Crosby et al., 2009; Gabrielsen et al., 2013; Youngquist et al., 2017), and Japan (Kobayashi et al., 2013). Typically, the negative effects of roads and

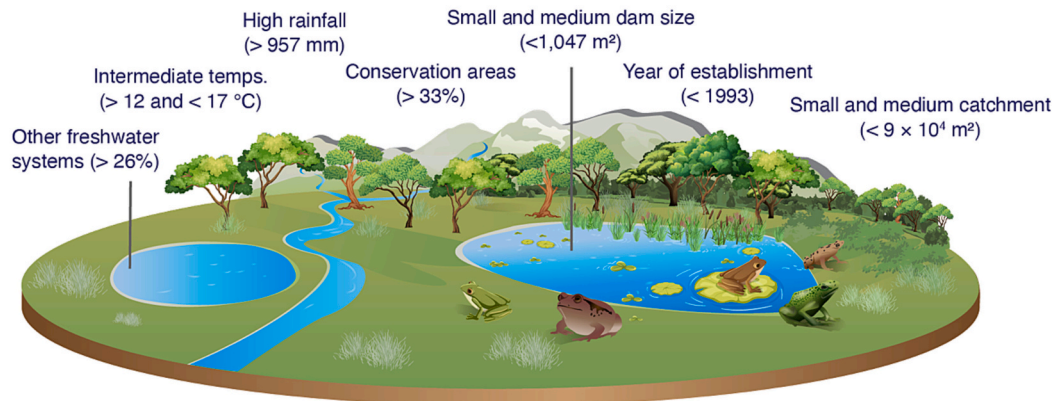
railways on amphibian populations are due to increased mortality from traffic, as well as the ecological barriers created by traffic noise, with demographic and genetic repercussions for frog biodiversity (Cova-rubias et al., 2020; Dixon et al., 2022). One explanation for our result is that survey effort in our dataset was positively correlated with the density of roads and railways – due to easier access for citizen scientists (Fig. S4). For example, there are no dams in our data with >10 surveys free of nearby roads and railways. Hence, the model may confuse the positive effects of sampling efforts on frog species richness with the concurrent increase in roads and railways near dams with multiple surveys. Indeed, the positive effect of roads and railways on frog species richness disappears when only considering farm dams with a single survey ($F_{1,4022} = 0.39$, $p = 0.53$), whereas the effects of all other covariates remain. Moreover, the parameter for roads and railways in the best-fitting model had the lowest explanatory power among all fitted variables (2.6 %). We suggest that the weak positive effect of nearby roads and railways is unreliable because our citizen-science data are inadequate to separate the effects of road and railway density from the effects of survey effort.

Besides the effects of roads and railways, our findings on the importance of local and landscape features of farm dams are consistent with previous research. Nevertheless, care must be taken when using the number of species as a biodiversity metric to analyse habitat characteristics. Previous research has shown that invasive species can balance or exceed the extinction rates of endemic species, leading to local species richness remaining constant or increasing while global species richness decreases (Thomas, 2013; Vellend, 2017; Hillebrand et al., 2018). However, the only invasive frog in our dataset was the cane toad (*Rhinella marina*), which was rarely recorded ($N = 490$, 0.47 % of all observations). Its exclusion from the analysis did not affect the interpretation of our results, suggesting that invasive species are unlikely to drive any of our conclusions. Future studies should supplement this analysis and compare the effects of farm dams against natural water-bodies using other biodiversity metrics to account for multiple aspects of species richness (e.g., identity, dominance, and rarity), such as abundance-based or richness-based species exchange ratios (Hillebrand et al., 2018).

Despite the potential benefits of offering suitable habitats to amphibian species, it is important to consider the broader implications of increasing numbers of farm dams in rural landscapes. For example, dams can reduce downstream flow to natural freshwater systems (Foote et al., 1996; Lowe et al., 2005; Nielsen et al., 2020), thus reducing the suitable habitat of species that rely on ephemeral ponds or streams to breed (Gould et al., 2022). Nevertheless, our records show that farm dams offer habitat for many frog species vulnerable to human impacts. In particular, of the Australian frog species with low tolerance to anthropogenic habitat modifications described in Liu et al. (2021), 82 % (49 out of 60) were detected at or near farm dams – including some of the most sensitive species (e.g., *Crinia pseudinsignifera*, *Geocrinia leai*, *Paracrinia haswelli*, *Pseudophryne guentheri*). Also, nearly 5 % of our records were of threatened frog species (following the classification by EPBC), indicating that farm dams can have substantial conservation value against frog extinction.

The attributes identified here that promote species richness in dams could inform “biodiversity credit” policies to reward farmers who invest in improving the condition of their land (Hein et al., 2013; Birrer et al., 2014). Based on our results, biodiversity credits could reward the restoration of dams with favourable characteristics for local biodiversity, such as older farm dams of intermediate size within small rainfall catchments, in areas with high rainfall and intermediate temperatures, and nearby freshwater systems and conservation sites. These initiatives aim to increase funding for conservation by creating a financial market that recognises the value of biodiversity services. In 2020, the global annual market size for biodiversity finance was USD 78–91 billion annually from public and private expenditures of NGOs, foundations, banks, and governments (OECD, 2020). While no initiative focuses on

A Highest frog species richness (top 25%)



B Lowest frog species richness (bottom 25%)

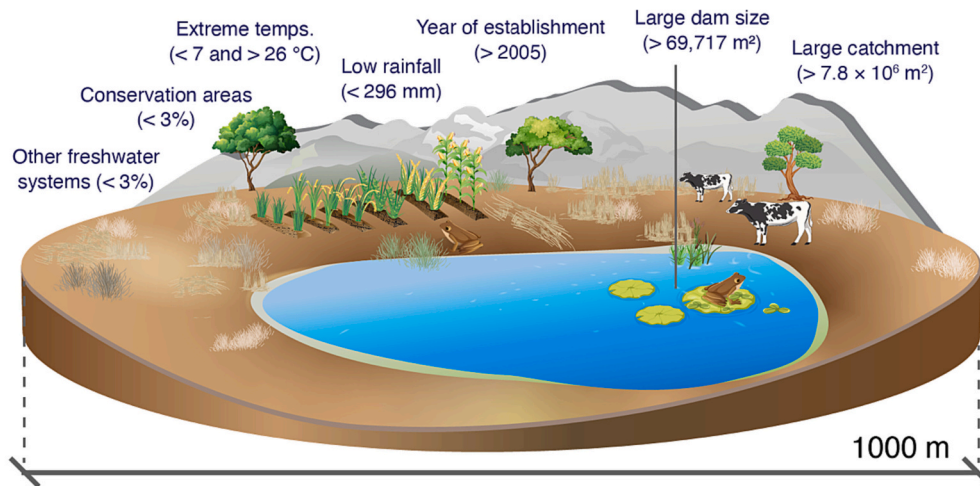


Fig. 6. Summary of features inducing the highest (A; top 25 %) and lowest (B; bottom 25 %) frog species richness in farm dams. The highest values of frog species richness were at old (> 20 years) farm dams with intermediate surface areas (10^3 m²) and small rainfall catchments ($< 10^4$ m²), and located in areas with high annual rainfall, intermediate annual temperatures, and near other freshwater systems and conservation sites. Each panel represents a landscape within a 500 m radius of the farm dam, and the labels indicate the range of conditions for the main characteristics found to promote or reduce frog species richness according to the best-fitting model. See Table 1 for ranges, Figs. 2, 3, and 5 for data and model fits, Fig. 4 for importance scores, and Tables S2–S4 for statistical scores.

farm dams, establishing incentives to improve their management may be a cost-effective strategy for a large-scale conservation program. For example, increasing vegetation around farm dams improves farm productivity and benefits livestock health (Dobes et al., 2021), while also increasing water quality (Westgate et al., 2022), reducing greenhouse gas emissions (Malerba et al., 2022a), and offering breeding habitats for crustaceans (Westgate et al., 2022), birds (Hamilton et al., 2017), and amphibians (Boissinot et al., 2019). With the potential for win-win outcomes for agricultural productivity and conservation, incentive schemes that promote the improvement of farm dams could be widely taken up with broad-scale benefits to farms and biodiversity.

5. Conclusions

This work offers the first study at large temporal (five years) and spatial (across Australia) scales on farm dam characteristics that promote frog species richness, offering management guidance to maximise

their biodiversity value (Table 1, Fig. 6). Given the continental scale of our dataset, these findings may be generally applicable as a guide to the restoration of frog communities in farm dams around the world. Moreover, patterns in frog biodiversity have the highest correlations with biodiversity patterns of other freshwater taxa (Tisseuil et al., 2013), which suggests that trends in frog species richness presented here could also be a guide for other taxa associated with farm dams. Overall, our results suggest that older farm dams, of intermediate size, and near other freshwater systems or conservation areas, should be prioritised for conservation and restoration. They also highlight that conservation areas and freshwater systems – both natural and artificial – are important for maintaining biodiversity in the surrounding landscape. Finally, we have demonstrated the value of large-scale citizen science datasets for identifying broadly generalisable relationships between habitat conditions and biodiversity. These datasets will become increasingly valuable for informing policy and management as they improve representativeness across disturbance gradients.

CRediT authorship contribution statement

M.E.M and D.A.D. designed the research, M.E.M., D.A.D., J. J.L.R., and J.F. collected the data, M.E.M. analysed the data, M.E.M. wrote the first draft, and all authors contributed to the final draft.

Declaration of competing interest

The authors declare no conflict of interest.

Data availability

Data, statistics, plots and R codes are publicly available from the corresponding author and at Mendeley Data (doi: [10.17632/cvfw5ygcsw3.1](https://doi.org/10.17632/cvfw5ygcsw3.1)).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2023.110270>.

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