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OPEN

Commonly collected thermal performance data can inform species distributions in a data-limited invader

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Predicting potential distributions of species in new areas is challenging. Physiological data can improve interpretation of predicted distributions and can be used in directed distribution models. Nonnative species provide useful case studies. Panther chameleons (*Furcifer pardalis*) are native to Madagascar and have established populations in Florida, USA, but standard correlative distribution modeling predicts no suitable habitat for *F. pardalis* there. We evaluated commonly collected thermal traits—thermal performance, tolerance, and preference—of *F. pardalis* and the acclimatization potential of these traits during exposure to naturally-occurring environmental conditions in North Central Florida. Though we observed temperature-dependent thermal performance, chameleons maintained similar thermal limits, performance, and preferences across seasons, despite long-term exposure to cool temperatures. Using the physiological data collected, we developed distribution models that varied in restriction: time-dependent exposure near and below critical thermal minima, predicted activity windows, and predicted performance thresholds. Our application of commonly collected physiological data improved interpretations on potential distributions of *F. pardalis*, compared with correlative distribution modeling approaches that predicted no suitable area in Florida. These straightforward approaches can be applied to other species with existing physiological data or after brief experiments on a limited number of individuals, as demonstrated here.

A key aim throughout many subfields of ecology is predicting where organisms occur. A common approach is to extract landscape and climate data from known occurrences for use in correlative distribution modeling^{1,2} but these require appropriate sampling of environmental preferences and have other limitations^{3–5}. For example, correlative distribution modeling relies on extensive sampling of species presences and an assumption that these presences reflect the existing fundamental niche for the species^{6,7}. Physiological data provide a basis for more mechanistic models and better inform prediction and forecasting of future distribution changes, especially for cryptic, rare, or introduced species^{8–11}. While collecting physiological data is resource-intensive, doing so can provide information about flexibility of traits, revealing more about the overall fundamental niche (rather than the existing fundamental niche, a best-case outcome for correlative models^{6,7}) and potential distribution. It is not uncommon for species with restricted distributions to have far broader physiological tolerances, allowing them to establish beyond their known current distribution^{5,12,13}.

A popular approach to integrating physiological data in predictive frameworks are mechanistic niche models, which utilize biophysics to derive physiological constraints and thresholds that can then be projected to the landscape-scale^{14,15}. The demands of many mechanistic modeling frameworks require strong knowledge of species ecophysiology¹⁶ and thus are most useful for testing hypotheses in well-studied, model systems⁷ or in well-funded species where reduced time to accrue the data may not be a priority. While predictions would admittedly be more accurate with comprehensive knowledge of a species, in practice, answers are often required under short timelines with limited prior data and funding. To try and address these demands, we aimed to investigate

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the utility of models based on easy-to-collect, well known physiological thresholds derived from commonly collected data on physiological tolerances.

We used a species that is cryptic, rare, and introduced to explore the potential seasonal plasticity of physiological tolerance and performance and the utility of different physiologically derived metrics in predicting potential distributions. Of the many potential physiological constraints, we focused on thermal tolerance as it is especially important for determining distributions of ectotherms, which comprise the majority of species on earth¹⁷. We assessed thermal traits in the panther chameleon, *Furcifer pardalis*, which occurs in several introduced populations in Florida, USA with the earliest report from 2008¹⁸. Introduced populations of chameleons tend to go unreported and some have been “seeded” in areas for later collection due to their high value in the pet trade¹⁹. Lack of reporting obscures the knowledge of the current extent of introduced populations, presenting challenges for directing management and regulatory actions. Predicting the distribution of this species in particular is difficult for two main reasons. First, there is relatively little known on thermal limits of this taxon, owing to limited studies of their thermal biology and limited information from related species in the native range in Madagascar^{20,21}. Second, the occurrence of populations in Florida at higher latitudes than the native range suggests a greater thermal tolerance than predicted based on its native range in Madagascar or invasive range of Réunion²². Panther chameleons have a fast life-history strategy, typically maturing within 14 months²³, allowing for the possibility of rapid adaptation of introduced populations to local thermal regimes. Thus, we opted to test the thermal traits of chameleons from a population from the highest known latitude²⁴, to account for potential extremes in thermal tolerance.

We assessed thermal tolerance, thermal performance, and thermal preference of *F. pardalis* exposed to seasonal fluctuations in climate. We hypothesized that chameleons would show a shift in thermal traits associated with seasonal exposure; in particular, we predicted that thermal preference may decrease and cold tolerance and performance at low temperatures would improve following exposure to winter conditions. We then used these trait data and fine-grain, daily temperature data to predict suitable winter habitats across Florida. We also constructed correlative niche models using native range occurrence data, which is often the only option for predicting suitable habitats in data-limited non-native species when physiological data are not available. We then evaluated which models and which thermal traits may be most useful for such predictions. We predicted that the correlative niche model would under-perform compared to models derived from physiological trait data, because of the apparent niche-shift in *F. pardalis* in Florida. Of the models integrating physiological trait data, we predicted that models integrating critical thermal minima would be most restrictive, followed by those integrating preference and performance.

Results

Thermal limits

Body size of chameleons was 13.6 ± 2.5 cm snout to vent length (SVL) and 70.7 ± 33.5 g. CT_{min} averaged 9.9 °C ± 2.0 (SD), with an average rate of chameleon temperature change of -0.6 °C ± 0.3 (SD) per minute. There was an effect of season on critical thermal minimum (CT_{min} ; $F_{2,9} = 4.31, p = 0.05$), though Tukey post-hoc tests did not reveal significant differences among seasons (all $p > 0.1$; Fig. 1). CT_{min} did not appear to be affected by which trial was experienced first ($F_{1,9} = 3.85, p = 0.08$). We did not find an interaction between chameleon temperature rate change and mass ($F_{1,9} = 0.80, p = 0.39$), and neither mass nor temperature rate change alone influenced CT_{min} ($F_{1,9} = 3.06, p = 0.11$; $F_{1,9} = 0.52, p = 0.49$, respectively).

CT_{gape} averaged 39.2 °C ± 1.4 (SD), with an average rate of chameleon temperature change of 0.6 °C ± 0.2 (SD) per minute. We did not find an effect of season on the high temperature at which gaping occurred (CT_{gape} ; $F_{2,9} = 2.18, p = 0.17$; Fig. 1). CT_{gape} was not affected by which trial was experienced first ($F_{1,9} = 0.08, p = 0.79$). We did not observe an interaction between chameleon temperature rate change and mass ($F_{1,9} = 0.56, p = 0.48$), nor did we observe an effect of mass ($F_{1,9} = 0.35, p = 0.57$). Rate of chameleon temperature change was negatively correlated to CT_{gape} , such that an increase of heating rate by 1 °C per minute led to lower CT_{gape} by 6.6 °C ($F_{1,9} = 6.18, p = 0.04$).

Average $T_{breadth}$ was 29.3 °C ± 2.7 (SD). There was an effect of season on thermal breadth ($T_{breadth}$; $F_{2,11} = 5.69, p = 0.02$), although Tukey post-hoc tests did not distinguish significant differences in $T_{breadth}$ among the seasons (all $p > 0.1$; Fig. 1). $T_{breadth}$ was not affected by which trial was experienced first ($F_{1,11} = 2.84, p = 0.12$), nor was it influenced by mass ($F_{1,11} = 1.81, p = 0.21$).

Thermal preference

The maximum body temperature reached during a preference trial was 40.6 °C and the minimum was 21.9 °C. Average preferred body temperature was 32.8 °C ± 2.9 and did not differ by season ($F_{2,12} = 1.23, p = 0.33$; Fig. 1), and was not affected by mass ($F_{1,12} = 0.011, p = 0.919$). The body temperature exhibited most often by each chameleon (mode) was 34.2 °C ± 4.7, and also did not differ by season ($F_{2,12} = 2.78, p = 0.10$) and was not affected by mass ($F_{1,12} = 0.32, p = 0.59$). The standard deviation of each chameleon's body temperature during a trial was 2.9 °C and also did not differ by season ($F_{2,12} = 2.78, p = 0.10$) and was not affected by mass ($F_{1,12} = 0.32, p = 0.59$).

Thermal performance

Thermal sensitivity of sprint performance (Q_{10}) differed significantly among temperature intervals ($F_{3,80} = 4.71, p = 0.005$). Tukey post hoc tests revealed that Q_{10} values for the 15–20 °C interval ($\bar{x} = 5.08$) differed significantly from the 25–30 °C interval ($\bar{x} = 1.86, p = 0.01$) and from the 30–35 °C interval ($\bar{x} = 4.50, p = 0.008$), but not the 20–25 °C interval ($\bar{x} = 2.78, p = 0.43$). Q_{10} values were not affected by SVL ($F_{1,80} = 0.008, p = 0.93$). Additionally, season had no impact on thermal sensitivity of sprint performance ($F_{2,80} = 0.052, p = 0.95$; Fig. 2).

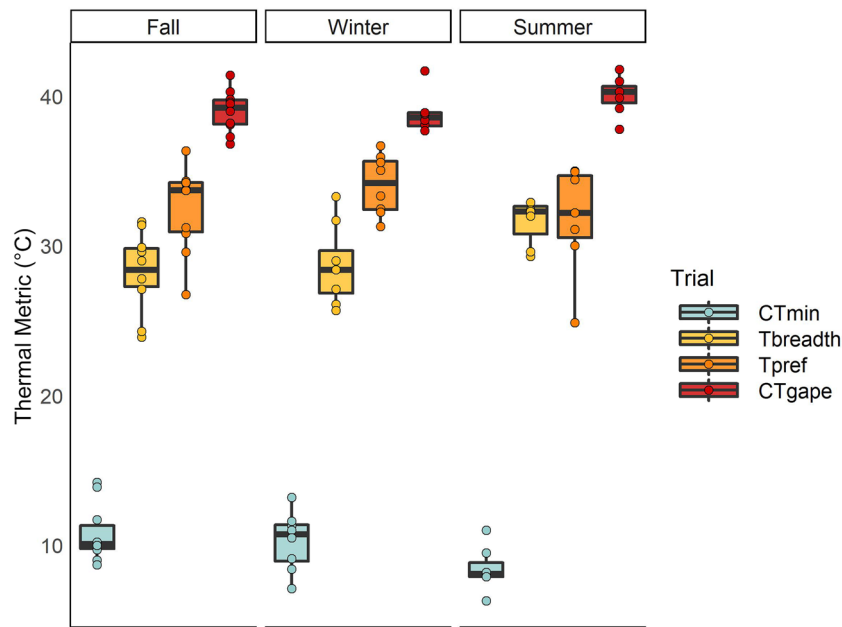


Figure 1. Thermal metrics and associated standard errors from chameleons collected from the northernmost established population of *Furcifer pardalis* in Florida, USA after exposure to seasonal fluctuations in temperature at USDA Wildlife Services National Wildlife Research Center in Gainesville, Florida, from October 2020 to August 2021. CT_{min} refers to the critical thermal minimum, the temperature at loss of righting response; CT_{gape} refers to the gaping threshold, the temperature at which chameleons gape to thermoregulate; $T_{breadth}$ refers to the difference between the CT_{gape} and CT_{min} ; T_{pref} refers the preferred body temperature, as the average body temperature selected in a thermal gradient.

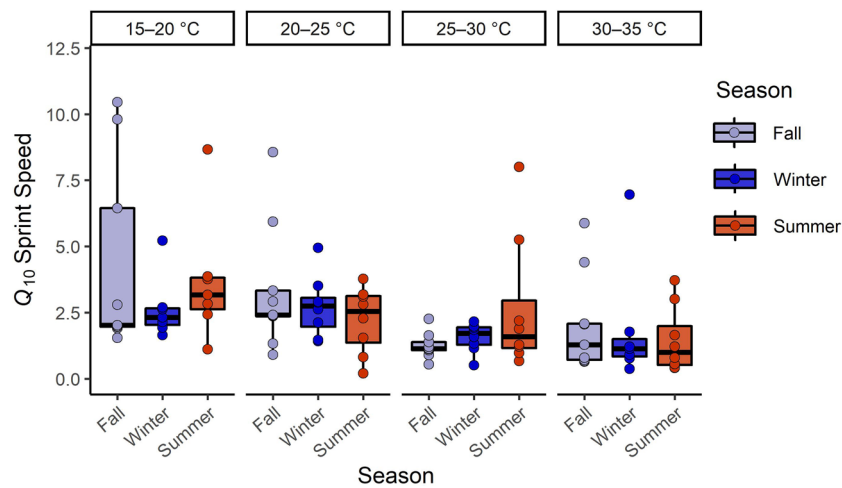


Figure 2. Q_{10} values calculated from maximal sprint speed for four temperature intervals tested in individuals from the northernmost established population of *Furcifer pardalis* in Florida, USA after exposure to seasonal fluctuations in temperature at USDA Wildlife Services National Wildlife Research Center in Gainesville, Florida, from October 2020 to August 2021. These values represent the magnitude of increase in a rate with a 10 °C increase in temperature, such that a value of two represents a doubling the rate per 10 °C increase, values of one represent thermal independence, and values of 0.5 represent a halving of the rate per 10 °C increase.

Correlative distribution model

The top model (Supplementary Fig. S4) predicted no suitable habitat for *F. pardalis* in Florida, despite established populations existing there. The top model had a regularization multiplier of 2 and used feature classes of linear, quadratic, hinge, product, and threshold, with $AIC_c = 3288.793$ and AUC of 0.916 (see data repository for details). The final set of layers and their percent contribution consisted of: temperature annual range (bio7,

82.32%), precipitation of wettest month (bio13, 12.53%), maximum temperature of the warmest month (bio5, 2.04%), precipitation of the warmest quarter (bio18, 2.01%), and isothermality (bio3, 1.10%).

Integrative distribution models

Summary data extracted from model projections at *F. pardalis* presences ($N=9$ distinct presences within the 1 km resolution of PRISM data) are presented in Table 1. *F. pardalis* populations have established in areas where the winter temperatures fell below the lowest critical thermal minimum for 6 consecutive hours an average of fewer than 10 days per season (Fig. 3, Table 1). At the other two thresholds, populations have established in areas experiencing the temperature threshold for under one month each winter (9°C , near average CT_{\min}) and 5 days per season (3°C , below CT_{\min} and exposed temperatures; Table 1; see Supplementary Fig. S5 online). The average activity window estimated for areas *F. pardalis* have established falls between 2.97 and 6.28 h of 11 h of available daylight per day (Table 1), and this window decreases with increasing latitude (Fig. 4). At the highest latitude populations, there is an average of 3–4 h per day through the winter period where ambient air temperatures are within the preferred temperatures of *F. pardalis* (Fig. 4). The entire state of Florida falls within 80% of the average predicted performance for *F. pardalis* during the winter period (Fig. 5), and the predicted performance at areas *F. pardalis* have established exists in a relatively narrow range of 44.5–63.2% (Table 1). The normalized activity window and predicted performance were relatively similar in their predictions; however, the activity window was slightly more conservative in its output, placing established populations in a threshold 10% more restrictive than the performance model (see Supplementary Fig. S6 online).

Metric	Days per winter below 3°C	Days per winter below 6°C	Days per winter below 9°C	Active hours	Percent of daylight active	Performance
Min	0.15	1.7	5.45	2.97	26.97%	44.54%
Max	4.8	12.9	28	6.28	57.13%	63.18%
Average	3.06	9.03	20.77	4.55	41.36%	53.61%

Table 1. Summary of values associated with presence localities ($N=9$) of *Furcifer pardalis* derived from experimental data on *F. pardalis* and climate data from winter 2001 to 2021. Days below a temperature threshold represent the average number of days per winter season that fell below the associated temperature threshold for a consecutive 6 h or more. Active Hours represents the average number of estimated active daylight hours per day across all winters. Percent of Daylight Active represents the percentage of hours during daylight that fall within the activity window for *F. pardalis*. Performance represents the average predicted performance represented as a % of maximum across all winters.

Days below 6°C for 6 consecutive hours per winter

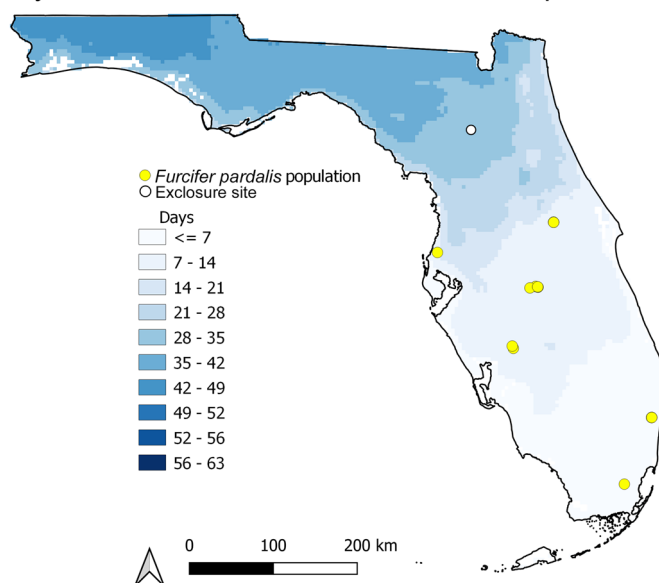


Figure 3. Average number of days during each winter (Dec 15–Feb 15) in Florida, USA, where temperature fell below the lowest critical thermal minimum of *Furcifer pardalis* for 6 or more hours, from 2001 to 2021. Yellow points indicate locations where *F. pardalis* populations have established. White point indicates the location of the experimental enclosure at USDA Wildlife Services National Wildlife Research Center in Gainesville, Florida.

Activity Window

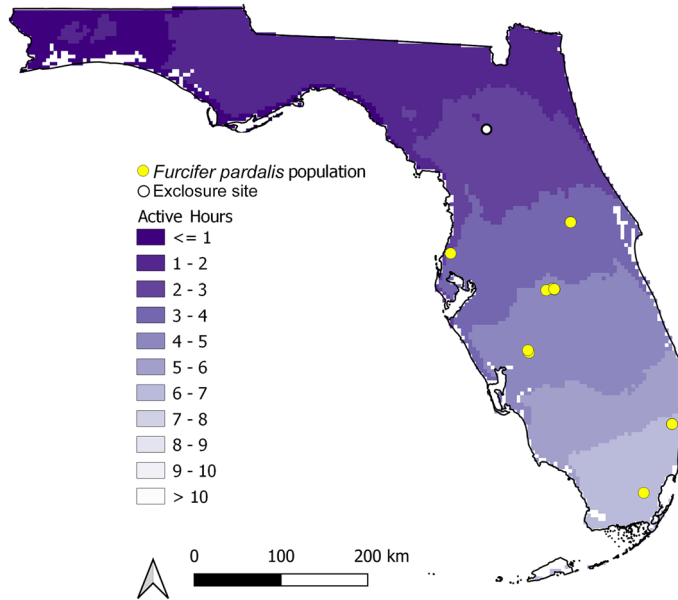


Figure 4. The average number of potential daylight hours *Furcifer pardalis* may be active in Florida, USA during the winter (Dec 15–Feb 15) from 2001 to 2021, based on thermal preference data for the northernmost population of this species in Florida. There are 11 possible total hours of daylight during this winter period. Yellow points indicate locations where *F. pardalis* populations have established. White point indicates the location of the experimental enclosure at USDA Wildlife Services National Wildlife Research Center in Gainesville, Florida.

Percent of Maximum Predicted Performance

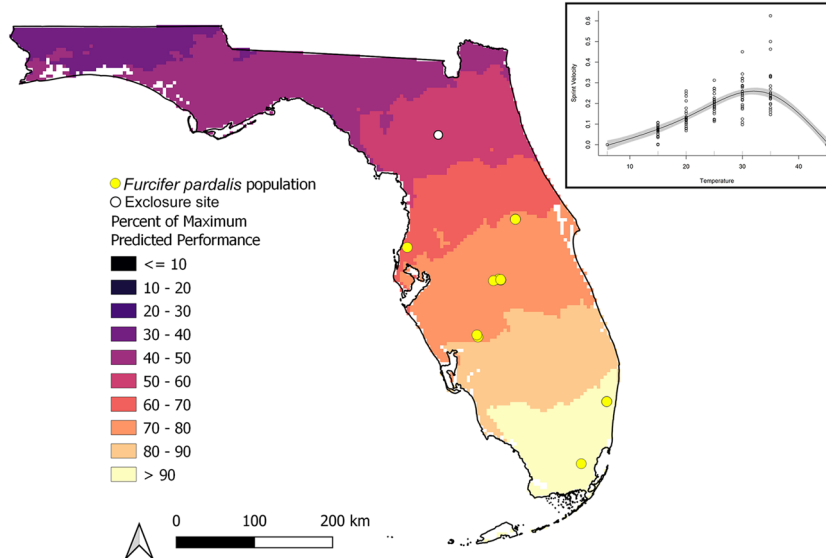


Figure 5. The predicted performance of *Furcifer pardalis* in Florida, USA, expressed as a percentage of the maximum predicted performance value from a generalized additive model of thermal performance data from the northernmost population of this species in Florida (inset). Yellow points indicate locations where *F. pardalis* populations have established. White point indicates the location of the experimental enclosure at USDA Wildlife Services National Wildlife Research Center in Gainesville, Florida.

Discussion

We conducted the first tests of seasonal acclimation of thermal traits in *Furcifer pardalis*, and found that CT_{min} , CT_{max} , T_{pref} and performance were not influenced by season. We anticipated seasonal acclimatization in thermal traits after exposure to low temperatures. For example, increased cold tolerance is reported after acclimation to cool temperatures in other arboreal lizards^{12,25}; increases in thermal preference follow increases in ambient temperatures in newts²⁶; and introduced geckos prefer lower temperatures in winter²⁷. Our general lack of observed seasonal acclimation may be partly influenced by experimental choice; namely exposure of chameleons to natural temperature fluctuations rather than constant temperature treatments in each season, combined with natural variation in acclimation ability among individuals²⁸, but see²⁹. In other tropical species, extended constant exposure to low temperatures may be necessary to observe acclimation of thermal traits e.g.³⁰. The influence of seasonal acclimatization on thermal traits varies widely³¹. Some species display acclimation of certain thermal traits, but not others. For example, introduced curly-tailed lizards show seasonal acclimation in CT_{max} but not CT_{min} ³², and in the frog *Pleurodema thaul* thermal performance and preference were not influenced by acclimation temperature, but thermal tolerance was³³. Other species may show inter-population variation in acclimation. In *A. cristatellus*, one population demonstrates ability to acclimate to cold temperatures, but another population of the same species does not¹², while in the armadillo girdled lizard (*Ouroborus cataphractus*), two populations maintain similar thermal preference despite seasonal change³⁴. Discrepancies and patterns in acclimation of thermal traits are well documented elsewhere e.g.³¹, and the underlying mechanisms for these deserve further study.

In the case of *F. pardalis*, a potential explanation for lack of observed acclimatization is that the study population may have adapted to local thermal conditions to express conserved thermal traits year-round. The fact that the individuals we tested are from the highest latitude documented for the species¹⁸, that *F. pardalis* have relatively fast generation times²³, and that this species does not typically burrow or seek shelter to buffer from cold temperatures (Claunch *pers obsv*) lends credence to the possibility of local adaptation. Adaptation without acclimation is not unprecedented. Another tree-dwelling lizard, *A. cristatellus*, demonstrates differences in CT_{min} among introduced and native populations, without associated acclimation ability in one of the introduced populations²⁵. Local adaptation of CT_{max} ³⁵; CT_{min} ^{36,37} and thermal preference²⁷ are documented among various lizard populations. It is important to note that our study is not equipped to test whether adaptation or acclimatization had occurred in the *F. pardalis* population prior to our testing. Unfortunately, our attempts to include chameleons from lower-latitude populations in a common-garden style comparison were thwarted due to collection-depletion and lack of public access at documented sites. The native-range origin of our study animals is also not known with certainty—coloration suggests they may be hybrids from multiple geographic origins¹⁸. Our preferred body temperature result is slightly higher than a previous study on *F. pardalis*—where Ferguson et al.²⁰ report preferred temperatures from three individuals as 31 °C, we report slightly higher preferred temperatures approaching 33 °C. While gaping thresholds are not reported, Ferguson et al.²⁰ report panting observed above 36 °C; this may represent the lowest observed panting threshold, as gaping typically precedes panting and we report gaping at temperatures averaging around 40 °C. Expanded sampling of multiple populations will be necessary to determine whether this population is representative of inherent thermal plasticity in *F. pardalis* or represents improved cold tolerance at the extremes of thermal plasticity in the species.

As anticipated, the correlative niche modeling approach, which did not integrate physiological data, under-predicted suitable habitat in the non-native range in Florida. This can largely be attributed to using native occurrences to model the invaded range. We chose this approach because it is the best practice approach in species distribution modeling of invasive species. Modeling invaded ranges using occurrences from within that range is problematic because of the lack of presumed equilibrium with the environment and often sparse occurrence data⁴. These issues especially limit the ability to effectively forecast distributions of nonnative species under climate changes^{7,38}. While it is possible to combine native and nonnative populations into a joint model of *F. pardalis* distribution, the data density remains weighted strongly towards the native range and the end result is a model tuning exercise to determine how to balance omission and commission errors, without a clear external means to assess optimal model quality. Here, our native-range model is not useful for informing about potential distributions of *F. pardalis* in Florida, but may instead provide important baseline niche information, which can be used to compare the magnitude of potential niche shift.

Models directly integrating physiological information may be the most effective way to improve predictions of potential distribution of invaders^{8,39,40}. Of the physiological traits we tested, cold tolerance is likely the most limiting factor for *F. pardalis* range expansion in Florida, given what we know about its native abiotic niche. Our lack of observed seasonal differences among thermal traits justify the use of average trait values, which simplifies modeling approaches and interpretation. Namely, our model predictions would remain largely unchanged if we had only used thermal trait data derived from a single sampling effort. Additionally, because we tested individuals from a population that is of higher latitude than its native range, data from this population may give a decent approximation of the limits of thermal flexibility of the species. At the very least, we demonstrate that physiological tolerance information even on a limited number of individuals can provide a better estimate of occurrence than comparatively abundant occurrence data from the native range. By integrating physiological data from populations at the edge of their niche into niche modeling frameworks, we can gain a more accurate picture of the niche limits of this species than is possible with occurrence data alone.

Our use of consecutive hours at each minimum temperature threshold is a conservative method to apply physiological data to understanding chameleon occurrence. Ectotherms can often survive brief exposure to temperatures below their CT_{min} , while longer exposure can lead to death, e.g.⁴¹. By considering length of exposure to cold thresholds, we may gain a more ecologically relevant insight into distribution limits and elucidate where population-limiting temperature thresholds occur. As expected, as temperature thresholds decrease, the average number of Florida-wide occurrences of each threshold also decreases. In areas where chameleons have

established, there are fewer instances of potential exposure to cool temperatures. Chameleons are potentially exposed to 4 total weeks where temperatures are 1 °C below their average CT_{\min} for at least 6 consecutive hours; whereas they potentially experience 2 weeks of temperatures at the lowest measured CT_{\min} , and less than one week at the 3 °C threshold (Fig. 3; see Supplementary Fig S5 online). Existing populations showed less variation in 6-h exposures to the lowest two temperature thresholds than near the average CT_{\min} . That the near-average CT_{\min} threshold was not as useful as the lowest and below- CT_{\min} thresholds suggests that the more extreme cold tolerance values more closely represent population-limiting temperature exposures, especially when considering the temperature values used in thresholds were derived from brief exposures to determine CT_{\min} .

The use of average critical thermal limit thresholds in distribution models has been criticized when applied as a filter of single-value temperature occurrences in a landscape (i.e., when not accounting for exposure time;⁴²), but also because CT_{\min} is often several degrees above the lethal minimum temperature¹⁶. In some cases species may be immobilized by cold but are able to survive long bouts of cold exposure⁴³. Lower lethal temperatures are unknown in *F. pardalis*. Ethical concerns aside, lethal temperature values may be too restrictive an approach to predicting suitable habitat. For example, a chameleon experiencing a chill coma (a temperature at or below CT_{\min}) may not die directly from low temperatures but the restricted foraging efforts, increased vulnerability to predators, and dampened immune function at low temperatures may manifest as population-level effects that prevent sustained survival of populations at higher-than-lethal temperature thresholds. The range in intra-species thermal tolerance can serve as a starting point for developing informative temperature thresholds on activity restriction in a species. A more holistic approach integrates chill coma temperatures or CT_{\min} as well as higher temperatures where activity and performance are reduced but may still limit population survival.

Activity window and thermal performance thresholds provide perspective on potential behavioral limitations using ambient temperature data. Calculation of activity windows from thermal trait data is not new; there are many frameworks used to estimate activity windows and activity budgets, ranging from models requiring many data inputs, (e.g.^{44–46}), to simpler threshold-based inputs (e.g.⁴⁷). Our approach differs slightly from others in the calculation of hourly trait values, and in our choice of thermal preference or selected body temperature data as the basis for an activity window. The range of body temperatures we recorded (22–40 °C) in the thermal preference trial encompasses the range of field body temperatures reported from *F. pardalis* in Madagascar exhibiting normal activity (24–36 °C²⁰). This demonstrates that our thermal preference data accurately reflect an activity window for the species. Our normalized data comparisons confirm that our activity window data derived from thermal preference are more restrictive than performance data. This is expected, as our activity window is constrained to temperature values chameleons chose, while the performance data clearly demonstrate that chameleons are capable of activity at higher and lower temperatures when induced to move.

The activity window and thermal performance thresholds represent different constraints and should be interpreted in different ways. The activity window, derived from thermal preference data, more likely demonstrates propensity to forage or explore, whereas temperatures outside this window are more likely directed towards seeking thermal refugia such as spending time basking to raise temperatures to levels where foraging can occur. The performance threshold more likely represents the ability to respond when extremely motivated to move, such as during pursuit by a predator. However, performance data may not be as useful a threshold in *F. pardalis* as it is for some other ectotherms. First, no area in Florida fell below 20% of the maximum predicted performance for this species, and predicted performance was around 50% at established populations, so variation in this trait was not particularly informative when applied to Florida winters. Second, sprint data may not correlate to success of escape from predators, as chameleons are fairly slow reptiles even at their best performance. Thermal preference data thus may be more biologically relevant, because if chameleons choose not to forage outside of their preferred temperatures they may not meet energy requirements to survive the winter. It is important to note these models do not account for potential radiative heating of basking chameleons to combat low ambient temperatures⁴⁸, and conversely do not account for convective or conductive cooling during wind or rainfall. Indeed, the combination of fine-scale behavior data with radiation, windspeed, and precipitation data may improve the resolution of predictions and has been proposed in more complex frameworks that also estimate activity budgets (e.g.^{44,45}). We chose to use only ambient temperature data as this is most commonly available⁴⁹ and may be the only climate data consistently available in regions of the world where ectotherm biodiversity is highest^{50–53}. We argue the value of our simple framework is that it can be applied in data-limited contexts, especially as global, fine-scale daily temperature data are now available worldwide⁴⁹.

Conclusions

We have shown that easy-to-collect physiological thermal trait and ambient temperature data can be used to accurately predict distributions of ectothermic organisms, in absence of native-range occurrence data. The thresholding approaches applied herein are relatively simple to execute, and limitations lie with computing power (which is typically not prohibitive), depending on the resolution and extent of predicted areas. While our case study focused on a non-native animal in an introduced range, the techniques herein are applicable beyond predicting distributions of invasive species. While mechanistic modeling approaches can have great utility for conservation with adequate inputs⁵⁴, the majority of terrestrial ectothermic diversity and in turn the majority of data-deficient and at-risk ectotherms with limited occurrence data are unlikely to be candidates for more sophisticated mechanistic modeling approaches⁷. However, daily global temperature data are becoming available⁴⁹, which creates opportunities for modeling approaches such as ours, which apply commonly available thermal trait data. These methods can thus be applied to improve understanding of distributions in data-deficient, rare, or threatened species using physiological data derived from a limited number of individuals. The methods could also be applied to simulate future distributions using predicted daily climate data. Finally, we provide predictions of potential

occurrences of *F. pardalis* in Florida that may help focus management surveillance efforts. The limitations and accuracy of our approaches for this particular species will become clearer as additional populations are located.

Methods

Animal collection and housing

Ten chameleons were captured from an established non-native population in Central Florida from October 2019–February 2020 ($N=7$ males, 2 females) and October 2020 ($N=1$ male). Adult panther chameleons were housed individually in an experimental mesh enclosure at the US Department of Agriculture (USDA), Wildlife Services, National Wildlife Research Center, Florida Field Station, located approximately 115 km north of the collection site in Gainesville, Florida from September 30, 2020, to July 28, 2021. Conflicts with residents at the site of the established population prevented collection of more individuals²⁴. Nine of the chameleons were housed by the authors prior to accessioning at USDA; the tenth was accessioned directly from the wild population to the enclosure in October 2020 (detailed in⁵⁵). Animals were housed individually in screen enclosures with natural vegetation and exposure to natural sunlight and weather patterns in the greater enclosure (see Supplementary Fig. S1 online). An automated misting system provided dripping water for drinking four times daily. Chameleons were fed every other day with crickets dusted with calcium without D3 (Rep-Cal, Rep-Cal Research Labs, Los Gatos, California, USA) at every feeding, except when replaced with a multivitamin (Reptivite, Zoo Med, San Luis Obispo, California, USA) dusting once every other week. Chameleons received visual wellness checks once daily. Chameleons were exposed to natural thermal regimes, including low nighttime temperatures (12 °C) in winter (Fig. 1). On nights forecast below 12 °C, 250 W heat emitters were turned on over the cages and tarps placed to cover the sides and roof (see Supplementary Fig. S1 online). On nights forecast below 7 °C, chameleons were brought indoors (65–70 °C) and held in individual cloth bags. Thermal data loggers (iButton DS1922L, resolution 0.06 °C, accuracy 0.5 °C, Maxim Integrated, San Jose, California, USA) were placed within screen enclosures to collect data on variation in ambient temperatures (see Supplementary Fig. S2 online). All protocols were approved by USDA QA-3214 (Study Director, Bryan Kluever) and University of Florida IACUC 201,910,938.

Assessing thermal traits

Thermal limit thresholds, preferences, and performance of chameleons were evaluated in three seasons: November 2020 (Fall), February 2021 (Winter), and July 2021 (Summer; see Supplementary Fig. S2 online). At each season, we collected mass using spring scales (Pesola Präzisionswaagen AG Schindellegi, Switzerland 0100 and 40,300 1 g and 2 g resolution, respectively) and SVL using a measuring tape (1 mm resolution). Animals were not evaluated in Spring due to outbreak of fungal infection (see⁵⁵). All animals were de-accessioned from the study as of 1 August 2021. Chameleons were assessed for critical thermal limit thresholds before preference or performance trials were conducted. We conducted linear mixed models using the lme function in package nlme⁵⁶ in R⁵⁷. The alpha level for all statistical tests was set at 0.05.

Critical thermal limit thresholds

Due to the proximity of critical thermal maximum to lethal maximum in some animals^{58,59} and the limited number of animals available for testing, we opted to measure the body temperature at which gaping occurred as a heat stress response (CT_{gape}) as our upper thermal threshold. We used the body temperature at loss of righting response (CT_{min}) as our lower temperature threshold.

At each season, individuals were randomly assigned to be tested first for either CT_{gape} or CT_{min} . After full recovery from each threshold, chameleons were returned to their cages and were tested the following day for the remaining threshold. Animals were acclimated to room temperature (26 °C) for at least one hour prior to conducting thermal limit threshold measurements. A thermal probe was inserted into the cloaca and secured with medical tape to allow continuous recording of animal body temperature every 10 s throughout the trial. For CT_{min} , animals were placed into a cooling incubator with windows (Benchmark Scientific, Sayreville, New Jersey, USA) set to 6 °C. When body temperatures were below 15 °C, we placed chameleons on their side with a gloved hand to test for righting response every 1.5 min and every 1 °C decrease in body temperature, whichever occurred first. When an animal was unable to right itself for 10 s after being flipped onto its side, we considered this CT_{min} , recorded the time, and removed the animal from the incubator to recover. For CT_{gape} , animals were placed into a heated incubator with windows (Labnet International Inc, Woodbridge, New Jersey, USA) set at 45 °C. We considered the gaping threshold reached when an animal held its mouth open for at least 5 s. We then recorded the time and removed the animal from the incubator to recover. All animals recovered from thermal limit threshold testing without incident. We extracted body temperatures for each threshold at the time each threshold was reached from the thermal logger data. We calculated the thermal breadth (T_{breadth}) for each season for each individual by subtracting the CT_{min} from the CT_{gape} value.

We conducted linear mixed models with gaussian error distribution with fixed response variables CT_{min} , CT_{gape} and T_{breadth} . Because rates of temperature change can influence thermal limit thresholds^{12,42} we calculated the average rate of body temperature change per minute during the trial and included this as a covariate in CT_{min} and CT_{gape} analyses. In the thermal threshold models we included the following variables: season, which trial was experienced first (i.e. CT_{min} or CT_{gape} trial), and the interaction between rate of body temperature change and mass. In the T_{breadth} model we included season, which trial was experienced first, and mass as covariates. To account for repeated measures, animal ID was included as a random intercept effect in all models. Animals that were moribund or in poor body condition were excluded from analyses ($N=1$ female in winter, $N=1$ male in summer; see Supplementary Fig. S2 online). Where a factor variable (e.g., season) indicated significance at a threshold of $\alpha=0.05$, we conducted a Tukey post-hoc test using package emmeans⁶⁰ in an attempt to discriminate differences among factor levels.

Thermal preference

To assess thermal preference, a thermal gradient was created in a 1.25 m by 2 m arena divided in half to create two lanes. To facilitate use by chameleons, two wooden dowels were inserted into the center of each lane. At one end, two 250 W and two 150 W ceramic heat emitters were arranged to provide a hot environment to 51 °C ambient temperature. The other end was surrounded by ice packs and a bucket of salted ice with two small electronic fans (Shenzhen Glovion Technology Co., Shenzhen, China) to maintain cool air flow to 18 °C ambient temperature (see Supplementary Fig. S3 online). A curtain was drawn to prevent chameleons from reacting to researcher presence. Chameleons were monitored occasionally from behind the curtain to ensure they remained on the dowels. Chameleons had a thermocouple (0.076 mm diameter, Item 5SRTC-TT-K-40-72, Omega Engineering) inserted into the cloaca and secured with medical tape, attached by a 1.8 m lead to a datalogger (Item# OM-HL-EH-TC, Omega Engineering, resolution 0.1 °C, accuracy 0.8 °C) set to collect temperatures every 10 s for 65 min. The length of thermocouple leads and their small size and weight allowed for unrestrained movement throughout the area. Chameleons were initially placed in the middle of gradient. The first 5 min of data after animals were introduced to the arena were discarded to account for an acclimation period to the arena and after thermocouple insertion.

We extracted the average, mode, and standard deviation in body temperature from each chameleon's thermal preference trial thermal logger data for analysis. Two chameleons' thermocouples fell out within 15 min of the end of the trial (Fall season), and two chameleons exited the gradient mid-trial at which point they were replaced into the gradient and the portion of data where the chameleon was outside the gradient plus one minute after being replaced was discarded (Fall season). We used the remaining within-gradient trial data for analysis for these cases.

After confirming normality of data, we conducted a linear mixed model on the response variables of average, mode, and standard deviation of body temperature during the thermal preference trials. To account for repeated measures, we included chameleon ID as a random effect. We included mass and season as covariates. All chameleons walked to the hot end of the gradient after initial placement, thus starting choice was not included in analysis.

Thermal performance

To assess thermal performance we tested chameleon sprint speed at five different body temperatures. Chameleons were randomly assigned to be tested at either "warm" (30 and 35 °C) or "cool" (15, 20, and 25 °C) temperatures per day. To achieve the assigned body temperature, chameleons were placed into either a cooling or heating incubator (described above in Critical Thermal Limit Thresholds) and continually monitored until the target temperature was reached, indicated by thermocouple in the cloaca. After reaching the target temperature, thermocouples were removed, and we placed chameleons at one end of a rubber mat divided into six, 0.25 m segments, and encouraged them to sprint across the mat by simultaneously tapping their tail gently with a gloved hand and luring with a bamboo branch ahead of the chameleon as it moved to the other side. During this, an observer used a stopwatch to record the time for the tip of the chameleon's snout to pass each 0.25 m segment (segment time). Upon completing the entire length of the mat (1.5 m), we immediately repeated the process at the starting point of the mat; thus every trial consisted of two "laps". Chameleons were allowed a minimum of 30 min rest between trials and chameleons completed two trials at each temperature. If the chameleon refused to move or was uncooperative (i.e., clearly performed submaximally), we denoted trials as being unsuccessful and excluded these trials from further analyses. We calculated the velocity of each segment by dividing the distance by segment time. For each acclimation temperature and chameleon, we retained only the maximal sprint speed over a 0.25-m segment for further analysis.

To compare the thermal sensitivity of sprint performance among seasons, we calculated Q_{10} values for each temperature interval. These values represent the magnitude of increase in a rate with a 10 °C increase in temperature, such that a value of two represents a doubling the rate per 10 °C increase, values of one represent thermal independence, and values of 0.5 represent a halving of the rate per 10 °C increase. Q_{10} values were calculated using the following equation⁶¹:

$$Q_{10} = \left(\frac{v_2}{v_1} \right)^{\left(\frac{10}{T_2 - T_1} \right)}, \quad (1)$$

where v_i represents velocity and T_i the corresponding acclimation temperature. We calculated four Q_{10} values corresponding to intervals of 15–20, 20–25, 25–30, and 30–35 °C. Trials were discarded if they spanned larger intervals (i.e., if an individual was only tested at 15 and 25 °C). To determine if season affected thermal sensitivity, we performed a linear mixed model with Gaussian distribution on the Q_{10} values. We used temperature interval and SVL as covariates; SVL was log-transformed to account for allometric effects. To account for repeated measures, we included individual ID as a random factor. All Q_{10} values were natural-log-transformed to meet model assumptions of homoskedasticity.

Distribution modeling

Correlative niche model

We used Maxent to construct correlative niche models using native range occurrence and climate data to project onto Florida. Occurrence data for *F. pardalis* spanning from 1876 to 2022 were downloaded from various databases^{62–64} and were sorted to remove duplicate records, records without georeferences, and improbable georeferences based on locality descriptions. Only points from the native range (Madagascar) were considered; we did not include data from nearby introduced populations of *F. pardalis* on Réunion. We thinned the points at a 4 km threshold to a total of 149 remaining points.

We calibrated models using ENMeval⁶⁵, using the ENMevaluate function with extrapolation and without clamping using default parameters and input of 19 bioclimatic layers at 1 km² resolution (WorldClim2⁶⁶) in the native range region. This method evaluates models constructed with varying combinations of regularization multipliers (0.5, 1, 2, 3, 4) and feature classes (linear, linear—quadratic, linear-quadratic-hinge, linear-quadratic-hinge-product, and linear-quadratic-hinge-product-threshold). Before running models in ENMevaluate, and to avoid potentially problematic multicollinearity in our models, we calculated the variance inflation factors (VIF) of our initial model with all 19 bioclimatic variables. If any predictor variable had a VIF > 5, we removed the variable with the lowest permutation contribution to the model. ENMevaluate was used to select the top model based on the AICc value within 2 to the lowest AIC model. We then used the top model to project onto Florida using the Maxent graphical user interface⁶⁷ with extrapolation and no clamping and 10,000 background points.

Thresholded winter temperatures: cold tolerance, activity window, predicted performance

Because cold tolerance is often the most limiting factor for ectotherms at higher latitudes⁶⁸, and because *F. pardalis* CT_{gape} exceeds typical annual maximum ambient temperatures in Florida, we chose to subset our distribution modeling to winter environmental data. To examine physiological data in the context of environmental temperatures in Florida, we created thresholds based on our thermal trait data. First, we assembled PRISM climate data for the extent of Florida for December 15 to February 15 from 2001 to 2021^{69,70} at 800 m resolution and extracted daily minimum (T_{min}) and maximum (T_{max}) temperatures. These dates encompass the 7 years prior to the first reported population, to account for potential lag times in reporting or discovery of this and other populations⁷¹. While ambient air temperature data has been criticized for use in predictive modeling frameworks (reviewed in¹⁶), such data may provide a decent approximation of available temperatures in this arboreal species⁷².

We used package ChillR to calculate hourly temperatures for each 800 m pixel in Florida for each day over December 15th to February 15th time period for all years. ChillR takes as input T_{min} and T_{max} as well as sunrise and sunset times, and latitude⁷³. It then applies an algorithm from⁷⁴ which models hourly temperatures by fitting a sine curve for daytime temperatures, and a logarithmic decay function for nighttime temperatures. To assess how cold tolerance (CT_{min}) may influence *F. pardalis* distribution in Florida, we flagged the hourly temperature data where the temperature was below three different thresholds (see below) for six or more consecutive hours. The six-hour exposure time threshold accounts for time to overcome thermal inertia associated with differences in cooling rates of ambient temperature and body temperature¹⁶, as well as removes potential noise in the data associated with rapid but unsustainable changes in temperature (e.g., a passing storm front). We counted the number of days that met this condition for each threshold for each yearly period, and then averaged the number of occurrences across those winter periods for reporting. The thresholds were: 9 °C, representing ~ 1 °C below the average measured CT_{min} in this study; 6 °C, representing the lowest individual CT_{min} recorded in this study and the lowest temperature experienced in the enclosure; and 3 °C, below temperatures experienced by chameleons in this study and below recorded CT_{min} for the species.

To examine the remaining thermal traits, we subset the hourly temperature data to daylight hours, as *F. pardalis* is diurnal and reliably falls asleep upon darkness (Claunch and Goodman *pers obs*). We calculated an activity window for *F. pardalis* by categorizing all temperatures during daylight hours that fell within the recorded body temperatures in the thermal preference gradient as active hours. We examined the activity window in two ways: first by averaging the number of active hours across all winters for each pixel in Florida, then by calculating the percent of active hours falling within available daylight hours across all winters for each pixel. We also calculated predicted performance during winter to serve as a proxy for the relative ability for *F. pardalis* to forage or engage in escape behaviors. To do this, we generated a performance curve using a generalized additive model of the maximum individual velocities per 25 cm segment at each test temperature bookended by velocities equaling 0 at CT_{min} and CT_{max} test temperatures, with $k=5$ and smoothing parameter = 0.1 (Fig. 5). From this curve, we calculated the predicted performance for each daylight hour's temperature at each pixel. We assessed performance in two ways: (1) by averaging the predicted performance across all winters per pixel; (2) by thresholding performance values that fell within 80% of maximum performance in the GAM across all winters per pixel.

Assessing model predictions

We assessed model predictions in two ways. First, we overlaid known established or formerly established presences in Florida on the Florida projections from all models described above, then extracted the associated data at these localities for comparison and evaluation. Because verified established presences are limited in number for *F. pardalis*, we also compared state-wide model projections produced by each metric. Second, to compare the utility of activity *versus* performance models, we normalized model outputs by setting the lowest value to 0 and the maximum value to 1; this was achieved by subtracting the lowest output value from all records, then dividing all output records by the resultant maximum value for each model. Thus, the scale reflects relative predicted activity and performance such that a value closer to 0 reflects the minimum predicted activity or performance, while a value closer to 1 reflects the maximum predicted activity or performance.

Ethical approval

All applicable institutional and/or national guidelines for the care and use of animals were followed. All protocols were approved by USDA QA-3214 (Study Director, Bryan Kluever) and University of Florida IACUC 201,910,938. The reporting in the manuscript follows the recommendations in the ARRIVE guidelines.

Data availability

Data for experimental determination of thermal traits are archived with USDA⁷⁵. The data and code generated during the current study are available at GitHub [https://github.com/nmclaunch/F_pardalis_thermal].

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Author contributions

All authors conceived the ideas and designed methodology; N.C. and C.G. collected the data; N.C., C.G., N.B. and R.G. analyzed the data; N.C. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Competing interests

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How fire interacts with habitat loss and fragmentation

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ABSTRACT

Biodiversity faces many threats and these can interact to produce outcomes that may not be predicted by considering their effects in isolation. Habitat loss and fragmentation (hereafter ‘fragmentation’) and altered fire regimes are important threats to biodiversity, but their interactions have not been systematically evaluated across the globe. In this comprehensive synthesis, including 162 papers which provided 274 cases, we offer a framework for understanding how fire interacts with fragmentation. Fire and fragmentation interact in three main ways: (i) fire influences fragmentation (59% of 274 cases), where fire either destroys and fragments habitat or creates and connects habitat; (ii) fragmentation influences fire (25% of cases) where, after habitat is reduced in area and fragmented, fire in the landscape is subsequently altered because people suppress or ignite fires, or there is increased edge flammability or increased obstruction to fire spread; and (iii) where the two do not influence each other, but fire interacts with fragmentation to affect responses like species richness, abundance and extinction risk (16% of cases). Where fire and fragmentation do influence each other, feedback loops are possible that can lead to ecosystem conversion (e.g. forest to grassland). This is a well-documented threat in the tropics but with potential also to be important elsewhere. Fire interacts with fragmentation through scale-specific mechanisms: fire creates edges and drives edge effects; fire alters patch quality; and fire alters landscape-scale connectivity. We found only 12 cases in which studies reported the four essential strata for testing a full interaction, which were fragmented and unfragmented landscapes that both span contrasting fire histories, such as recently burnt and long unburnt vegetation. Simulation and empirical studies show that fire and fragmentation can interact synergistically, multiplicatively, antagonistically or additively. These cases highlight a key reason why understanding interactions is so important: when fire and fragmentation act together they can cause

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local extinctions, even when their separate effects are neutral. Whether fire–fragmentation interactions benefit or disadvantage species is often determined by the species' preferred successional stage. Adding fire to landscapes generally benefits early-successional plant and animal species, whereas it is detrimental to late-successional species. However, when fire interacts with fragmentation, the direction of effect of fire on a species could be reversed from the effect expected by successional preferences. Adding fire to fragmented landscapes can be detrimental for species that would normally co-exist with fire, because species may no longer be able to disperse to their preferred successional stage. Further, animals may be attracted to particular successional stages leading to unexpected responses to fragmentation, such as higher abundance in more isolated unburnt patches. Growing human populations and increasing resource consumption suggest that fragmentation trends will worsen over coming years. Combined with increasing alteration of fire regimes due to climate change and human-caused ignitions, interactions of fire with fragmentation are likely to become more common. Our new framework paves the way for developing a better understanding of how fire interacts with fragmentation, and for conserving biodiversity in the face of these emerging challenges.

Key words: habitat fragmentation, habitat loss, fire, planned burn, wildfire, prescribed burning, interactions, succession, landscape, edge effect

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I. INTRODUCTION

Biodiversity is in crisis (IPBES, 2019) and faces many direct threats instigated by the actions of people (Driscoll *et al.*, 2018). The current framework for classifying these threats uses a hierarchical classification of individual threats (IUCN, 2020). However, recent literature has placed growing emphasis on interactions between threats (Segan, Murray & Watson, 2016; Geary *et al.*, 2019). Threats to

biodiversity can interact synergistically, leading to worse conservation outcomes than the sum of individual effects (Brook, Sodhi & Bradshaw, 2008). For example, biodiversity loss can be accelerated by interactions of climate change with habitat loss (Mantyka-Pringle, Martin & Rhodes, 2012), pesticides with parasites (Coors & De Meester, 2008), and invasive predators with land-clearing, grazing and fire (Doherty *et al.*, 2015). However, other interactions are also possible,

including potential beneficial outcomes (Regan *et al.*, 2011), additive outcomes that are the sum of separate effects, or antagonistic outcomes that are smaller than the largest independent effect (Cote, Darling & Brown, 2016). Understanding how and where multiple threats interact is important for identifying conservation risks and determining appropriate management actions (Segan *et al.*, 2016; Geary *et al.*, 2019).

Habitat loss and fragmentation (hereafter ‘fragmentation’) and altered fire regimes are major drivers of biodiversity decline (WWF, 2018). Fragmentation threatens more than 14000 species on the International Union for Conservation of Nature’s threatened species *Red List* (~80% of threatened species) (IUCN, 2020). Changes in fire regimes, such as too much fire, not enough fire, and inappropriate season or severity, are also major ecological and evolutionary disruptions (He, Lamont & Pausas, 2019; Kelly & Brotons, 2017; Bowman *et al.*, 2020) that threaten 14.6% of vulnerable, endangered and critically endangered species (4,407 species worldwide; IUCN, 2020). These two processes can interact to affect outcomes for species (Templeton, Brazeal & Neuwald, 2011; Tulloch *et al.*, 2016; Cochrane, 2003). For example, single habitat fragments may not offer a suitable post-fire environment for a population, such as an early- or late-successional plant species. If local extinctions occur in habitat patches that are too far apart for individuals or propagules to move between them, landscape-wide declines can result (Leach & Givnish, 1996; Nimmo *et al.*, 2019). This kind of synergy can occur, even if the site-level fire regime is not altered (Fenner & Bull, 2007). Furthermore, with many species adapted to particular successional stages after fire, fire can also cause (Latta, Sondreal & Brown, 2000) or negate (Allen, Parrott & Kyle, 2016) fragmentation by creating habitat edges (Parkins, York & Di Stefano, 2018; Menezes, Cazetta & Dodonov, 2019) and altering the spatial arrangement of suitable habitat.

Despite the potential importance of interactions between fire and fragmentation, there is no framework for evaluating their joint effects. Past reviews on this topic have been confined to specific ecosystems such as tropical rainforest or eucalypt forest (Gill & Williams, 1996; Cochrane *et al.*, 1999; Cochrane, 2003), limiting the range of mechanisms that have been documented and synthesised. We address this knowledge gap by asking: how does fragmentation interact with fire and how does the interaction influence biodiversity?

II. EMERGENT FRAMEWORK

We structure our review around three main pathways by which fire and fragmentation can interact (Fig. 1). First, fire can influence fragmentation, such as when fire destroys or creates habitat. For example, wildfires in the Sierra Nevada, USA, destroyed the long-unburnt habitat of the fisher (*Martes pennanti*), increasing habitat fragmentation for this species (Scheller *et al.*, 2011). Second, fragmentation can influence fire, such as when habitat loss increases human access, which increases ignitions (e.g. Armenteras, Gonzalez &

Retana, 2013). This is common in tropical forests, where people clearing land and moving into areas with new roads ignite many fires (Cochrane, 2001) that potentially spark a positive feedback of increasingly flammable vegetation (Cochrane *et al.*, 1999). Third, fire and fragmentation can also have interactive effects on a biotic response, such as abundance or species richness, even when fire and fragmentation do not directly influence each other (Hossack *et al.*, 2013; Alstad & Damschen, 2016). That is, fragmentation is primarily a result of clearing for agriculture or urbanisation, not fire, and this clearing has not changed the fire regime. However, when fire occurs in fragmented landscapes, the effect of fire on species can differ from when either process acts alone, because succession within patches can drive local extinctions and patch isolation can prevent recolonisation (Nimmo *et al.*, 2019). We use these three broad ways that fire and fragmentation can interact as a framework for classifying interactions, and to synthesise empirical and modelling evidence of how they affect biodiversity.

III. APPROACH

We searched *Web of Science* for papers with titles, abstracts or key words (‘topic’ field) that included the terms (fire OR burn) AND (fragment* OR connectivity OR ‘habitat patch’ OR ‘remnant patch’ OR ‘remnant vegetation’ OR ‘habitat amount’), and sourced additional papers from *Google Scholar*. We then searched for these key words and the words ‘edge’, ‘isolation’, ‘dispersal’ or ‘movement’, in the titles or abstracts. Papers with both a fire and a fragmentation term were retained (1359 papers). We then followed eight rules for excluding papers related to relevance of the topic (e.g. excluding papers on ‘bullet fragments’ after ‘firing weapons’), whether fire and fragmentation were considered together, and whether any interactions reported were supported by data or simulations (see online Supporting information, Appendix S1, Table S1). After this screening, 162 papers remained from which we collected data that guided our synthesis. All authors contributed to screening papers.

Throughout, we use ‘cases’ to refer to individual responses. Where papers reported results for many species, we recorded only cases that represented different responses, rather than every case. For example, different species of the same taxon category (amphibian, reptile, etc.) that showed the same response to fire and fragmentation were recorded as a single case. On the other hand, a species showing a different response to others (regardless of taxon category), or responding to a different fire trait or fragmentation trait, was recorded as a separate case. Contrasting responses identified for the same species were also recorded as separate cases. We did this to limit the extent to which individual papers could dominate our summary tables and to maintain the data-extraction process at a manageable level. Using this rule, we never recorded more than six cases per paper. An

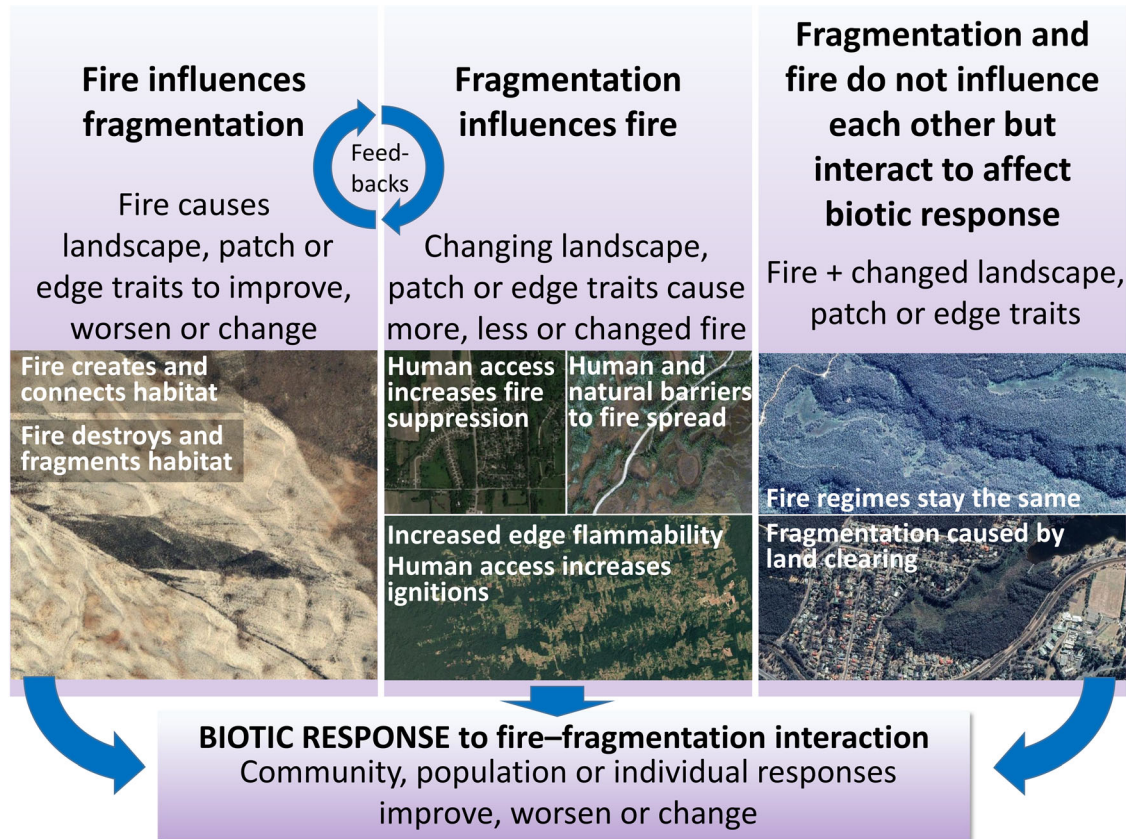


Fig 1. There are three main ways that fire and fragmentation interact: (1) fire can influence fragmentation (left) by causing fragmentation traits at a landscape, patch or edge scale to improve (e.g. reduced fragmentation), worsen (e.g. reduced patch size), or change (e.g. non-linear responses or changes to an edge effect that are not directional); (2) fragmentation can influence fire (centre), such as when edge drying causes more frequent fire, fire suppression or anthropogenic ignitions with increased access to forests; and (3) neither may influence the other, but together have an interactive effect on a biotic response (right), such as when habitat fragmentation and loss increase due to land clearing (e.g. isolating populations), and subsequent fire or lack of fire causes local extinctions. These three types of interaction can cause community, population- or individual-level traits to improve, worsen or change. The circular arrow indicates that feedbacks can occur where fragmentation and fire influence each other (Fig. 2A). There is the potential for a transition between ‘fire influences fragmentation’ and ‘fire and fragmentation do not influence each other’ as fire size approaches patch size (Fig. 2B). Illustrative background images from *Google Earth* (Landsat/Copernicus/CNES/Airbus/Maxar Technologies) including fragmented mallee woodland in Australia where fire destroys habitat for old-growth-specialist birds, but creates habitat for open-country species (Berry *et al.*, 2015) (left), prairie remnants fragmented by agriculture and urbanisation where people suppress fires (Leach & Givnish, 1996) (centre top left), expansion of wetlands and infrastructure fragments flammable Scotts Pine in Siberia (Wirth *et al.*, 1999) (centre top right); herringbone-patterned land clearing in Brazil where edges become more flammable and graziers deliberately set fire to the landscape (Cumming *et al.*, 2012) (centre bottom), perched swamps in Blue Mountains Australia where fire regimes are not substantially changed by fragmentation, and the primary cause of fragmentation is clearing for urbanisation, not fire (Gorissen *et al.*, 2015) (right).

alternative approach would have been to extract every response and then use a resampling approach for analysis, but we deemed our approach the most efficient.

Cases described in the papers were classified into three categories of interaction: (i) fire influences fragmentation; (ii) fragmentation influences fire; and (iii) neither influences the other but they act together to influence a biotic response (‘fire and fragmentation do not influence each other’). For some papers in the third category, fire did influence patch quality and so could potentially be reported in the first category. However, these studies had a focus on fragmentation traits

that were unaffected by fire so were better classified in the third category [e.g. distribution of restored habitat or patches in urban landscapes (Conlisk *et al.*, 2014; Ramalho *et al.*, 2018)]. Data collected from each paper included fragmentation traits (e.g. edge condition, patch size, landscape connectivity), fire traits (e.g. frequency, extent, time since fire), biotic responses (e.g. abundance, richness, extinction rate, edge effect) and direction of effects (e.g. unchanged, decrease, increase; see Appendices S2 and S3). For each paper, we also recorded the experimental design, the ecosystem and region. After classification, we qualitatively

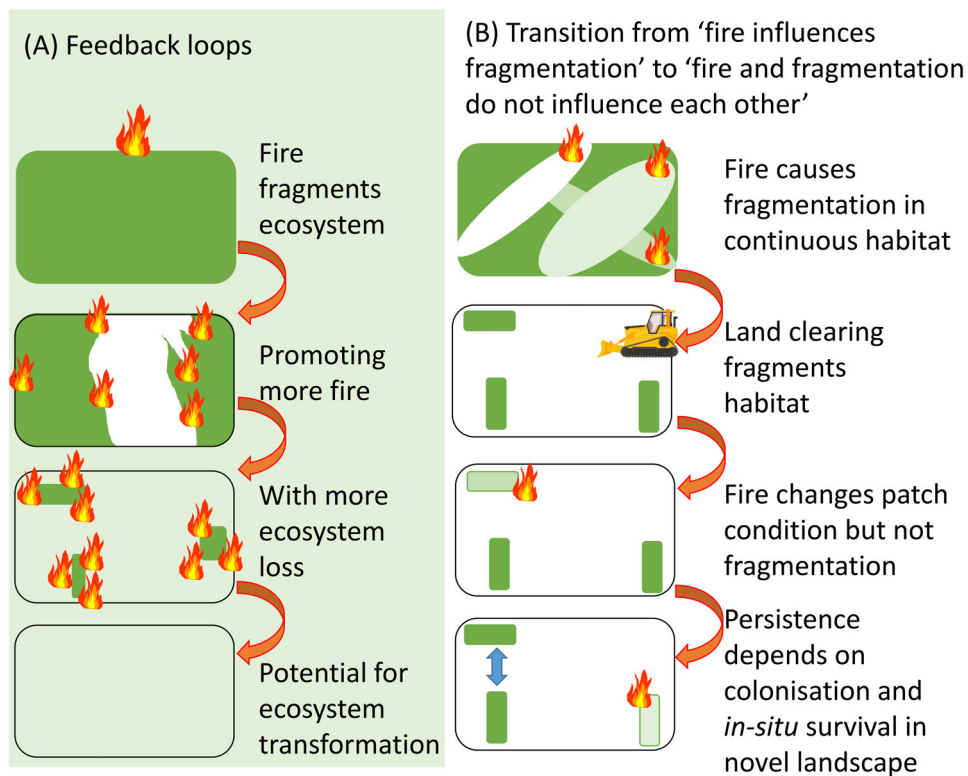


Fig 2. (A) Feedback loops. Fire can influence fragmentation by, for example, destroying habitat, and increased fragmentation can increase fire risk, such as by creating more flammable edges or increased anthropogenic ignitions, with potential for this feedback to transform ecosystems. (B) Transitions between categories. Where patch size is large enough to contain multiple fires, fire may cause (or reduce) fragmentation within the patch, representing ‘fire influences fragmentation’ cases. If such intact landscapes are subsequently converted to agriculture or urbanised, remnant patch sizes may be too small to include a fire mosaic. Consequently, the effects of fire are on patch quality rather than the main cause of landscape fragmentation. Thus, cases of ‘fire influences fragmentation’, when patch size is large relative to fire size, can transition to ‘fire and fragmentation do not influence each other’, where fire is no longer the main cause of fragmentation. To persist in highly fragmented landscapes subjected to fire, species must either disperse through the novel matrix between patches of suitable habitat (blue arrow in bottom panel) or survive *in situ*, alongside other pressures from the altered matrix (Driscoll *et al.*, 2013).

synthesised the literature, using the classification as the framework to organise our ideas.

To standardise the way in which relationships between fire and fragmentation were recorded, we specified a direction of change for fire or fragmentation, depending on the type of interaction. For example, where increasing fire severity caused increased fragmentation, we could also have recorded that decreasing fire reduced fragmentation. Therefore, we always standardise to record how fragmentation and biotic responses changed in response to increasing fire, such as increasing severity, extent or frequency. This allows a logical next step to report how the fragmentation trait was influenced by an increase in the amount of fire, and subsequently how those two together affected a biotic response. Similarly, when fragmentation led to reduced fire, we recorded the effect of increasing fragmentation, then noted the fire trait affected, such as fire frequency, and the direction of change, in this example, a decrease.

Considering the number of different fire traits, fragmentation traits and the 20 possible biotic response variables, there

was an unmanageable number (>200000) of potential joint categories. Thus, we further simplified the responses and only report summaries at higher levels. Simplified categories are defined below and detailed in Appendix S3, including classifying biotic responses to their level of biological organisation (individual, population, community) and fragmentation traits by scale (landscape, patch, edge). Although we collected data on when habitat loss *per se* and habitat fragmentation *per se* were reported (Fahrig, 2017), there were only four such cases from two simulation papers (Turner *et al.*, 1994; Pausas, 2006). For simplicity, we therefore refer to habitat loss acting together with the breaking apart of habitat as ‘fragmentation’, and use ‘fragmentation *per se*’ or ‘habitat loss *per se*’ when effects were reported separately.

There were 28 combinations of fragmentation traits and direction of change among the fire influences fragmentation cases. We further simplified these into five categories (Appendix S4): worsen (e.g. fragmentation increases, patch condition decreases, edge length increases), improve (e.g. fragmentation decreases, patch size increases), non-

linear (U or hump shaped), changed (direction cannot logically be applied), or unchanged. Increasing edge length does not always lead to worse biotic responses, and we note these exceptions in the results. There were 13 combinations of fire traits and direction among the cases of fragmentation influences fire, which we reduced to three categories (Appendix S5): more fire (e.g. increase in extent, severity, frequency, intensity, occurrence), less fire and non-linear change in fire.

There were 56 combinations of biotic response and direction of effect for the fire influences fragmentation interactions. We reclassified these to nine levels (Appendix S6): worsens, improves, non-linear, changed, unchanged, edge worsens (e.g. amount of edge increases), edge improves, edge unchanged, or no biotic response. For example, when biotic responses like abundance, richness and habitat use increased, the response was scored as 'improve'. When the response increased at an edge or into the burnt habitat, we scored the response as 'edge improves'. Similar simplifications were made for cases where fragmentation influences fire (Appendix S7) and fragmentation and fire do not influence each other (Appendix S8). Scoring was completed by K.B., and all scores reviewed by D.A.D., following Appendices S1–S8.

With cases showing that almost any response to any combination of fire and fragmentation interaction is possible, further insights might be obtained by defining responses that were contingent on other variables. For fire influences fragmentation cases, we used Fisher's exact tests to determine whether the number of cases that 'improve' or 'worsen' fragmentation and biotic responses depended on ecosystem, region, taxon, experimental design, or organisation level of the biotic response. Some papers reported multiple cases, but this test would be valid only with one case per paper providing independent data points. Using a permutation approach, we randomly removed cases for papers with multiple cases so that only one case was included per paper, and then performed Fisher's exact test. We repeated this procedure 100 times, interpreting differences among classes (ecosystem, region, etc.) using the distribution of the *P* values from these tests. For fragmentation influences fire cases, there were few biotic responses, precluding analogous tests to those applied in the fire influences fragmentation cases. We instead used the same permutation of Fisher's exact tests, but tested whether worsening

landscape-scale fragmentation led to less or more fire, depending on ecosystem, region, and experimental design.

IV. OVERVIEW OF CASES REPORTED

We identified 274 cases from the 162 papers we reviewed. How fire influenced fragmentation was assessed in 162 cases (59% of all cases) from 96 papers, how fragmentation influenced fire was assessed in 69 cases (25% of all cases) from 41 papers, and how fire and fragmentation did not influence each other but acted together to influence a biotic response was assessed in 43 cases (16% of all cases) from 28 papers. In relation to fire traits, 133 of the 274 cases (49%) referred to fire occurrence (the impact of a single fire), with other attributes of the fire regime examined less often, such as frequency (21%), extent (12%) and time since fire (11%) (Table 1). Habitat fragmentation and loss were referred to together in 108 of 274 cases (39%), with other fragmentation traits examined less often, such as edges caused by fire (11%), patch condition (11%), edge condition (10%), landscape connectivity (9%) and patch size (9%) (Table 2).

V. FIRE INFLUENCES FRAGMENTATION

(1) How does increasing fire alter fragmentation and biotic responses?

There were similar numbers of cases where increased fire improved (36 cases) or worsened (40 cases) fragmentation traits and biotic responses (Table 3). Evidence that these outcomes depended on ecosystem or other covariates was weak (Table 4). For example, increasing fire was most often reported to reduce the severity of fragmentation traits and improve the biotic response in woodlands and savannah; whereas the reverse was more commonly reported for forests. However, when considering only one case from each paper in a permutation test, these differences had mean *P* values >0.1 (Table 4).

Table 1. Number of cases examining each fire trait across the three types of interactions. Correlation among fires describes when fires are spatially and/or temporally correlated

Fire trait	Fire influences fragmentation	Fragmentation influences fire	Neither influences the other	Total
Occurrence	113	12	8	133
Frequency	14	29	14	57
Extent	11	10	12	33
Time since fire	22	1	7	30
Intensity	0	13	0	13
Severity	1	2	2	5
Correlation among fires	0	2	0	2
Patchiness	1	0	0	1
Total	162	69	43	274

Table 2. Number of cases that examined each fragmentation trait across the three types of interaction

Fragmentation trait	Fire influences fragmentation	Fragmentation influences fire	Neither influences the other	Total
Fragmentation	56	34	18	108
Patch condition	29	0	0	29
Edge	29	0	0	29
Edge condition	9	17	2	28
Landscape connectivity	15	2	8	25
Patch size	10	7	8	25
Patch connectivity	1	3	5	9
Patch edge length	2	6	0	8
Inferred fragmentation & loss	5	0	0	5
Fragmentation <i>per se</i>	1	0	2	3
Matrix condition	3	0	0	3
Habitat amount <i>per se</i>	2	0	0	2
Total	162	69	43	274

Table 3. Number of cases reporting changes to biotic responses caused by increasing fire which influences fragmentation traits. Fragmentation traits are classified in relation to landscape, patch or edge scale (see Appendices S3–S6, for details of classification scheme)

Scale	Biotic response	Change in fragmentation traits by increasing fire				
		Improve	Worsen	Changed	Unchanged	Non-linear
Landscape	Improves	22	5	1	0	0
Landscape	Worsens	1	26	0	1	0
Landscape	Changed	0	4	1	0	0
Landscape	Unchanged	1	4	1	1	0
Landscape	Non-linear	2	1	0	0	0
Landscape	None	2	8	0	0	1
Patch	Improves	14	3	3	0	0
Patch	Worsens	0	13	1	0	1
Patch	Unchanged	0	0	3	0	0
Patch	None	1	2	0	1	0
Edge	Edge improves	0	0	0	10	0
Edge	Edge worsens	0	1	3	15	0
Edge	Edge unchanged	0	0	0	1	0
Edge	Unchanged	0	0	0	5	0
Edge	Changed	0	0	0	1	0
Edge	None	0	0	2	0	0

(a) Landscape scale

Most cases where fire reduced the impacts of fragmentation occurred in landscapes in which there had been a history of sustained suppression or exclusion of fire by humans over past decades, particularly savannah woodlands (Table 4). These characteristically open plant communities, and the fauna dependent upon them, were often threatened by tree encroachment when fire was excluded [e.g. lesser prairie-chicken (*Tympanuchus pallidicinctus*) in North America (Boggie *et al.*, 2017)]. Several studies covering a range of taxa [e.g. birds, reptiles, amphibians and mammals from Australia and North America (Brown *et al.*, 2013; Smith *et al.*, 2016; Murphy, Evans & Storfer, 2010; Allen *et al.*, 2016)] indicated that more frequent fire in such landscapes improved connectivity between populations of the focal species. The species that benefitted from increased fire tended to be those that prefer early-successional

vegetation [e.g. pyrophilous beetles in Canada (Saint-Germain, Drapeau & Hibbert, 2013), open-country birds in Spain (Zozaya, Brotons & Saura, 2012a)]. Exploitation of such short-lived patches of suitable habitat requires regimes of frequent, highly connected disturbance to create new patches, or species that are highly mobile and can readily disperse to and colonise physically isolated, recently burnt patches [e.g. the beetle *Stephanopachys linearis* in Sweden (Ranius *et al.*, 2014)].

Studies showing that fire increased habitat fragmentation tended to be of species that had known preferences for mid- to late-successional stages, such as the Hispaniolan white-winged crossbill (*Loxia leucoptera megaplaga*), from the Dominican Republic (Latta *et al.*, 2000); or species that had weak dispersal capabilities, including the tree *Allosyncarpia temata* in Australia (Bowman & Dingle, 2006) and the arboreal red tree vole (*Arborimus longicaudus*) in the USA (Linnell *et al.*, 2017). Increased isolation caused by fire can result in increased inbreeding, as

Table 4. Number of cases in which increased fire improved or worsened fragmentation and the biotic response, depending on ecosystem, region, taxon, experimental design, or organisation level of the biotic response

Variable	Category	Improve	Worsen
<u>Ecosystem</u>	Forest	10	19
$P = 0.028$	Grassland/prairie	3	5
Mean P (SD) = 0.253 (0.11)	Shrub/heathland	4	9
Range = 0.124–0.426	Woodland/savannah	15	5
	Other/multiple	4	2
<u>Region</u>	North America	24	20
$P = 0.113$	South America	0	3
Mean P (SD) = 0.234 (0.073)	Oceania	8	15
Range = 0.107–0.354	Rest of world	4	2
<u>Taxa</u>	Amphibian	1	2
$P = 0.435$	Bird	11	12
Mean P (SD) = 0.675 (0.089)	Ecosystem	0	2
Range = 0.542–0.815	Insect	4	2
	Mammal	6	10
	Plant	3	6
	Reptile	11	6
<u>Experimental design</u>	Before–after	4	3
$P = 0.426$	BACI	4	7
Mean P (SD) = 0.294 (0.075)	Control–impact	4	9
Range = 0.141–0.414	Longitudinal	3	5
	Space for time	20	15
<u>Organisation level</u>	Individual	9	10
$P = 0.188$	Population	26	24
Mean P (SD) = 0.151 (0.134)	Community	1	6
Range = 0.008–0.551			

BACI, before–after–control–impact design; Mean P , average P value of 100 tests after randomly sampling only one case from each paper; P , P value of Fisher's exact test using all data; SD, standard deviation of the mean.

documented in the brown tree frog (*Litoria ewingii*), Victorian frog (*L. paraewingii*) (Potvin *et al.*, 2017), and Utah juniper tree (*Juniperus osteosperma*) (Allphin, Hunt & Anderson, 2007).

A small passerine bird, the mallee emu-wren (*Stipiturus mallee*) (Brown *et al.*, 2013), illustrates the potential for transition from an interaction where fire influences fragmentation to a situation where fire no longer influences fragmentation but they interact to affect a biotic response (Fig. 2B). Before habitat loss due to agricultural land-clearing, mallee emu-wren habitats were large enough to include a fire mosaic, with fire destroying sub-sets of habitat, which recovered subsequently. This spatial turnover led to low genetic structuring due to frequent population turnover (Brown *et al.*, 2013). However, when fragmentation was caused by land-clearing, land-clearing became the dominant spatial process and the effect of fire was reduced to one of habitat degradation where all or most of a habitat patch could be burnt at once; a situation that aligns with fire and fragmentation having independent effects that combine to drive the species towards extinction. Translocations are needed to counter these declining trends (Brown *et al.*, 2013).

(b) Patch scale

When fire affected patches, a similar number of cases reported improved (14 cases) and worsened outcomes (13 cases) for the biotic response (Table 3). For example, fire

enhanced patch condition by increasing seed availability, leading to increased abundance of the early-successional Henslow's sparrow (*Ammodramus henslowii*), in the USA (Bechtoldt & Stouffer, 2005). Introducing fire to woodlands in the USA improved the size and quality of open glades by reducing woody cover, leading to increased population size of the eastern collared lizard (*Crotaphytus collaris collaris*) (Templeton *et al.*, 2011), and higher occupancy of savannah patches by the perennial herb *Penstemon grandiflorus* and the plains pocket gopher (*Geomys bursarius*) (Davis *et al.*, 1997).

Habitat condition was typically (11 of 13 cases) reduced when fire had a negative effect at the patch scale. Fire occurrence degraded patch quality for a reptile in Australian grasslands (Fenner & Bull, 2007), a bird in USA grasslands (Curnutt *et al.*, 1998), birds in Australian woodlands (Berry, Lindenmayer & Driscoll, 2015), birds in Mediterranean (Herrando & Brotons, 2002) and Australian forests (Catterall, Kingston & Park, 1997), and mammals in Amazonian forests (Mendes-Oliveira *et al.*, 2012). Effects of fire on patch quality can also influence the risk of local extinction. For example, under a regime of fire suppression, patch quality can decline for mid-successional forest species as the ecosystem transitions to rainforest, as found for the arboreal marsupial, the mahogany glider (*Petaurus gracilis*), in Australia (Jackson *et al.*, 2011). When threatened species already have reduced abundance in fragmented landscapes, the impacts of fire on

patch quality can be detrimental, even when fire regimes are unchanged. The pygmy blue-tongue lizard (*Tiliqua adelaidensis*) was less able to forage in remnant, recently burnt, grasslands in Australia, reducing reproduction and body condition, potentially increasing the risk of local extinction and with no prospect of natural recolonisation (Fenner & Bull, 2007). In the case of prairie remnants in the USA, loss of biodiversity under fire suppression meant that reinstating fire was not enough to restore bird and plant species richness to habitat patches, and translocations were also needed (Van Dyke *et al.*, 2004).

(c) Edge scale

Fire-maintained edges ('unchanged' edge response, Table 3) could improve (10 cases) or worsen (15 cases) the biotic response, generally reflecting different species' preferences for unburnt or recently burnt habitat (also see Parkins *et al.*, 2018). For example, in Canadian spruce forests, species richness and abundance of spiders with a forest affiliation was higher on the unburnt side of the edge, while open-country species were most abundant in the fire-maintained ecosystem (Larrivee, Drapeau & Fahrig, 2008). A similar response was reported across fire-maintained edges for plants in New Caledonia (Ibanez *et al.*, 2013). Edge studies involving fire-maintained edges often show an overall negative effect on biodiversity, with generalist species doing well in the fire-maintained ecosystem, and forest specialists declining [e.g. plants in the Mojave Desert, USA (Lybbert *et al.*, 2017); oribatid mites in Swedish pine forests (Zaitsev *et al.*, 2014); plants in Atlantic forests, Brazil (Menezes *et al.*, 2019)]. Fire-maintained edges also affect ecosystem processes, such as by limiting seed dispersal and reducing seed predation into early-successional habitat compared with unburnt rainforest in Colombia (Aide & Cavellier, 1994).

The edge patterns reported by most studies correspond to a 'spillover' edge effect (Villaseñor *et al.*, 2014), whereby there is a gradual transition from one side of the edge to the other. Edges caused by fire led to very few positive edge effects, where there are higher values at the edge and lower values on either side. Examples included log abundance, broadleaf regeneration and bryophyte species richness which were higher at boreal forest edges (Barbe, Fenton & Bergeron, 2017b; Harper *et al.*, 2015).

(d) Unexpected responses

In a few cases, when fire led to improved landscape or patch metrics, biotic responses worsened. For example, the beetle *Stephanopachys linearis* only breeds in burnt trees, but surprisingly, its extinction probability increased when fire increased connectivity in Sweden (Ranius *et al.*, 2014). This may have occurred due to higher predation at more connected sites, or faster depletion of resources at more connected sites due to higher immigration.

There were several cases where fire worsened a landscape or patch metric, but the biotic response was positive: typically, this was due to increases in species that prefer disturbed habitat such as invasive species (e.g. Litton & Santelices, 2002;

Peeler & Smithwick, 2018), or 'open-country' specialists (Barbe, Fenton & Bergeron, 2017a). In an unexpected result, the abundance of eight bird species increased as isolation of unburnt patches increased within large burnt areas in Australian mallee woodlands (Berry *et al.*, 2015). Only one of the eight species was typical of open country, but all species were also common in the surrounding five-year-old burnt habitat. It appeared that unburnt habitat was providing important resources to which birds were willing to travel, with more birds accumulating in unburnt patches when these were more isolated and, therefore, rare in the landscape (Berry *et al.*, 2015). A similar response has been suggested for salamanders concentrating in recently burnt patches (Hossack *et al.*, 2013). A case illustrating another mechanism comes from fire-mediated mosaics on the Iberian Peninsula, where patches with a higher edge-to-area ratio nevertheless had higher bird species richness because birds were attracted to edges (Herrando & Brotons, 2002).

(2) Effects of fire traits

All fire traits with more than one case, including extent, frequency, occurrence and time since fire, had examples in which increasing incidence of fire in the landscape improved fragmentation traits, as well as the opposite, in which increasing fire worsened fragmentation traits (Table 5). The directions of these effects depended on whether the study had a focus on early-successional habitats, where more fire improved outcomes, or late-successional habitats, where fire was detrimental. Thus, increasing fire extent improved connectivity of open habitat used by open-country birds (Zozaya *et al.*, 2012a), increasing fire frequency increased connectivity for early-successional reptiles (Smith *et al.*, 2016), and decreasing time since fire increased occurrence and colonisation of a beetle that breeds in burnt trees (Ranius *et al.*, 2014). On the other hand, increasing fire extent worsened fragmentation and loss of tropical rainforest (Cumming *et al.*, 2012), increasing fire frequency threatened rainforest refuges of the Carpentarian rock rat (*Zyromys palatalis*) (Brook, Griffiths & Puckey, 2002), and decreasing time since fire increased habitat fragmentation for bark beetles that depend on mature trees (Seidl *et al.*, 2016).

There were more cases of fire extent, frequency and occurrence influencing landscape-scale metrics than patch metrics (extent: 10 landscape, one patch; frequency: 9, 5; occurrence: 52, 24; Table 5). By contrast, for time since fire there were nine cases at a landscape scale and 12 at a patch scale. This likely reflects the utility of time since fire in measuring habitat quality within patches. For example, time since fire was used as a patch-level predictor of black pine snake (*Pituophis melanoleucus lodingi*) habitat in the USA (Baxley, Lipps & Qualls, 2011), with patch quality and occupancy higher at shorter times since fire. Similarly, short times since fire increased patch size and condition, increasing eastern collared lizard abundance in the USA (Templeton *et al.*, 2011). In both cases, short times since fire also had landscape-scale effects, reducing fragmentation and increasing connectivity (Baxley *et al.*, 2011; Templeton

Table 5. Number of cases reporting how different aspects of the fire regime influenced fragmentation traits at the landscape, patch and edge scale (see Appendices S3–S6 for details of classification scheme)

Scale	Fire trait and direction	Improve	Worsen	Unchanged	Changed	Non-linear
Landscape	Extent increase	4	6	0	0	0
Landscape	Frequency increase	1	7	0	0	1
Landscape	Occurrence	17	32	2	1	0
Landscape	Patchiness decrease	0	0	0	1	0
Landscape	Severity increase	0	0	0	1	0
Landscape	Time since fire decrease	6	3	0	0	0
Patch	Extent increase	0	1	0	0	0
Patch	Frequency increase	3	1	1	0	0
Patch	Occurrence	4	13	0	7	0
Patch	Time since fire decrease	8	3	0	0	1
Edge	Occurrence	0	0	32	5	0
Edge	Time since fire decrease	0	1	0	0	0

Fire responses represent increasing fire.

Table 6. Number of papers reporting worsening fragmentation traits which influence the amount of fire and, in a small number of cases, subsequently influence a biotic response (None: no biotic response reported). Fragmentation traits are classified as landscape, patch or edge scale (see Appendices S3–S5 and S7 for details of classification scheme)

Scale	Biotic response	Less fire	More fire	Non-linear
Landscape	Improves	3	1	0
Landscape	Worsens	5	0	0
Landscape	Non-linear	2	0	0
Landscape	None	6	17	2
Patch	Worsens	2	0	0
Patch	None	4	8	1
Edge	Edge improves	2	0	0
Edge	Edge worsens	0	2	0
Edge	None	0	12	0

et al., 2011), emphasising the general point that the effects of fire traits can be measured across scales. Further, in the few papers where the biotic effects of fire were measured at multiple scales, the direction of the effect was the same. We found only three papers, from Canada and the USA, which reported how a particular biotic response was affected by fire occurrence or time since fire at multiple scales. All found that more fire led to improved outcomes at both patch and landscape scales (Barbe *et al.*, 2017a; Baxley *et al.*, 2011; Davis *et al.*, 1997).

VI. FRAGMENTATION INFLUENCES FIRE

(1) How does worsening fragmentation affect fire and biotic responses?

When fragmentation traits worsened, such as increased habitat fragmentation, reduced patch size, or increased edge, fire

increased in 40 cases but decreased in 24 cases (Table 6). Examples spanned an increase in fire occurrence, frequency, extent, intensity and correlation among fires (Costafreda-Aumedes, Comas & Vega-Garcia, 2016; Benchimol & Peres, 2015a; Alencar *et al.*, 2015; Silva *et al.*, 2018; Cochrane & Laurance, 2002). There were two main ways that worsening fragmentation traits caused fire to increase, reported from Europe and the Americas: by increasing anthropogenic ignitions (Armenteras *et al.*, 2013; Salvati & Ferrara, 2014; da Silva *et al.*, 2018) and increasing edge flammability (Benchimol & Peres, 2015a; Brudvig, Wagner & Damschen, 2012; Roman-Cuesta, Gracia & Retana, 2009). Among the 24 cases reporting reduced fire as a consequence of worsening fragmentation traits, cases from Europe and North America reported that fire was reduced when fragmentation impeded fire spread. Fire spread was limited by expansion of non-flammable vegetation types or physical obstruction by infrastructure (Wirth *et al.*, 1999; Azevedo *et al.*, 2013; Breining *et al.*, 2006). Worsening fragmentation was also associated with anthropogenic fire suppression in cases in Australia and North America (Leach & Givnish, 1996; Yates & Broadhurst, 2002).

Whether worsening fragmentation led to more or less fire was significantly related to ecosystem type and geographic region (Table 7). In Central and South America, worsening fragmentation always led to more fire. In these tropical forest and savannah ecosystems, fragmentation caused edges to become more susceptible to fire (Benchimol & Peres, 2015a; Armenteras *et al.*, 2013; Durigan, De Siqueira & Franco, 2007) and typically there was more fire in the landscape because cattle ranchers use fire to clear forest and improve forage (Armenteras *et al.*, 2013). Consequently, forest fires always increased in response to fragmentation in cases from Central and South America (e.g. Roman-Cuesta, Gracia & Retana, 2003). Although we did not sample studies that reported less fire with fragmentation in South America, reduced fire occurrence has recently been reported from Chilean agricultural land (McWethy *et al.*, 2018). The geographic bias also likely explains the

Table 7. Number of cases where worsening landscape-scale fragmentation led to less or more fire, depending on ecosystem, region, and experimental design

Variable	Category	Less fire	More fire
<u>Ecosystem</u>	Forest	9	37
$P < 0.001$	Woodland/ savanna	5	2
Mean P (SD) = 0.013 (0.017)	Shrub/ heathland	7	1
Range = 0.000–0.058	Grassland/ prairie	2	0
	Other/multiple	1	2
<u>Region</u>	North America	9	4
$P < 0.001$	South America	0	31
Mean P (SD) = 0.000 (0.000)	Oceania	6	1
Range = NA	Rest of world	9	6
<u>Experimental design</u>	BACI	0	1
$P = 0.030$	Control-Impact	1	7
Mean P (SD) = 0.080 (0.066)	Edge influences fire	3	16
Range = 0.011–0.209	Longitudinal	4	5
	Space-for-time	15	13

Mean P , average P value of 100 tests after randomly sampling only one case from papers that presented more than one case; P , \bar{P} value of Fisher's exact test using all data; SD, standard deviation.

significant effect of ecosystem type on whether fragmentation led to more or less fire (Table 7). Fragmentation of forest ecosystems was most commonly reported to lead to more fire, and 30 of 37 forest cases with more fire were from Central and South America.

Fifty of 67 cases (75%) that reported how fragmentation influences fire did not report a biotic response (Table 6). That is, three quarters of research into ecosystems where fragmentation influences fire had a narrow focus on the fragmentation and fire aspects, rather than also considering the consequences for the biota. This contrasts with the fire influences fragmentation cases, where only 10.5% (17 of 162) did not report a biotic response (Table 3).

(a) Landscape scale

Worsening fragmentation at a landscape scale was reported by 18 cases to increase fire and by 16 cases to reduce fire (Table 6). When worsening landscape fragmentation altered fire, four cases reported an improvement and five a worsening of the biotic response (Table 6). For example, more fire associated with tropical forest edges increased the mortality of Amazonian trees with thin bark and low wood density (Brando *et al.*, 2012, 2014). Conversely, less fire resulting from expanding wetlands and roads that impeded fire spread increased the growth of Siberian Scots pine (*Pinus sylvestris*) (Wirth *et al.*, 1999). However, for fire-affiliated species, fragmentation that led to less fire was detrimental, including for North American

prairie species such as the herb *Ceanothus americana* (Leach & Givnish, 1996) or the tree *Pinus palustris* (Loudermilk & Cropper, 2007). Similarly, in the Florida Scrub, USA, fire suppression in fragmented farming landscapes reduced habitat quality and consequently reduced survival of the Florida scrub jay (*Aphelocoma coerulescens*) (Breininger *et al.*, 2006).

(b) Patch scale

Two cases showed that worsening conditions at the patch level led to less fire, and reported biotic responses (Table 6). Using structural equation modelling, Ramalho *et al.* (2014) showed that smaller patches of Australian *Banksia* woodlands had reduced fire frequency, which was significantly associated with a decline in richness of woody plant species. Similarly, in northern Sweden, small islands had longer times since the most recent fire than large islands, and this decreased the genetic variation of Norway spruce (*Picea abies*) because clonal growth was more common on small islands (Wang *et al.*, 2003). In the Australian example, fire was reduced due to anthropogenic fire suppression, whereas in the Swedish example, small islands were less likely to be struck by lightning.

(c) Edge scale

Altered edge conditions typically led to more fire (Table 6) due to fuel accumulation (Benchimol & Peres, 2015a), drying (Brando *et al.*, 2014), and more ignitions by people (Armenteras *et al.*, 2013). In two cases where a biotic response was reported, this led to increased Amazonian tree mortality (Brando *et al.*, 2014). By contrast, in holm oak (*Quercus ilex*) woodlands in Portugal, edges reduced fire because fires burnt through shrublands and typically stopped at the damp woodland edges (Azevedo *et al.*, 2013). In these cases, plant abundance and species richness increased on the burnt side of the edge, the only cases of improved biotic responses at edges (Azevedo *et al.*, 2013).

(2) Which fragmentation traits influence fire?

Considering the effect of specific fragmentation traits on fire, rather than just considering the scale, changes in edge condition and increases in edge length were most often reported to lead to more fire (Table 8). Thirteen of 17 cases reporting an association between edge condition and fire were from Central or South America, particularly tropical forests (e.g. Silva *et al.*, 2018; Cochrane, 2001; Armenteras *et al.*, 2013). They reported higher occurrence of fire close to edges (Cochrane, 2001), and greater fire frequency and intensity (Silva *et al.*, 2018). For other fragmentation traits there were no strong trends; worsening fragmentation can lead to both less or more fire, and occasionally non-linear fire responses.

Table 8. Number of cases where changes in particular fragmentation traits led to less fire, more fire, or non-linear changes in fire

Scale	Fragmentation change	Less fire	More fire	Non-linear
Landscape	Fragmentation increase	13	14	2
Landscape	Fragmentation occurred	2	3	0
Landscape	Landscape connectivity decreases	1	1	0
Patch	Patch connectivity decreases	2	1	0
Patch	Patch edge length increases	0	5	1
Patch	Patch size decreases	4	3	0
Edge	Edge condition changes	2	15	0

Table 9. The number of cases where fire and fragmentation traits do not influence each other but act together to influence the biotic response, classified by (A) scale; (B) fire trait and direction; and (C) fragmentation trait and direction. (A) The number of cases reporting how increasing fire and deteriorating landscape, patch and edge metrics combine to influence a biotic response. (B) Number of cases reporting the effect on a biotic response of worsening fragmentation traits and particular changes in the fire regime. (C) Number of cases reporting the effect on a biotic response of increased fire alongside particular changes in the fragmentation trait (see Appendices S3–S5 and S8 for details of classification scheme)

	Effect on biotic response				
	Improves	Worsens	Unchanged	Non-linear	Edge worsens
(A) Scale					
Landscape	5	14	5	3	1
Patch	1	7	5	0	0
Edge	0	0	1	0	1
(B) Fire trait and direction					
Extent increase	1	11	0	0	0
Frequency increase	4	4	3	3	0
Occurrence	1	3	3	0	1
Severity increase	0	2	0	0	0
Time since fire decrease	0	1	5	0	1
(C) Fragmentation trait and direction					
Edge condition changes	0	0	1	0	1
Fragmentation increase	1	8	4	2	1
Fragmentation <i>per se</i> increases	1	1	0	0	0
Fragmentation occurred	2	0	0	0	0
Landscape connectivity decreases	1	5	1	1	0
Patch connectivity decreases	1	3	1	0	0
Patch size decreases	0	4	4	0	0

VII. FIRE AND FRAGMENTATION DO NOT INFLUENCE EACH OTHER, BUT THERE IS A BIOTIC RESPONSE

There were 43 cases (25 simulation models with data, 18 empirical) in which fire and fragmentation did not influence each other but acted together to influence a biotic response (Table 9). For most cases, this scenario transpired in landscapes where fragmentation arose due to clearing for agriculture, urbanisation or infrastructure development, and fire occurred in that already fragmented landscape. There was a high proportion of simulation studies in this category (58%), compared with 18% in the fire influences fragmentation category and 12% in the fragmentation influences fire category. In simulations, fire and fragmentation could be implemented independently, even though in the real-life landscapes that were being modelled fragmentation often

served to increase (Tierney, 2018) or decrease (Regan *et al.*, 2010) fire. The high number of simulation cases in this category reflects, in part, that simulations typically implement fire and fragmentation independently, and not that simulations more often focus on systems in which fire is actually independent of fragmentation.

(1) Landscape scale

Most cases (28 of 43, 65%, including 10 empirical cases) examined fragmentation traits at a landscape scale. Half of these (14, including 11 simulations) reported that the interaction with fire worsened the biotic response (Table 9). More fire in increasingly fragmented landscapes led to decreased population abundance across taxa, including simulation studies on mammals (Ramalho *et al.*, 2018), plants (Conlisk *et al.*, 2012), and fish (Falke *et al.*, 2015), and empirical studies

on amphibians (Hossack *et al.*, 2013) and insects (Marschalek *et al.*, 2016). It also decreased the simulated occurrence of birds in remaining habitat patches [e.g. San Diego cactus wren (*Campylorhynchus brunneicapillus sandiegensis*) in coastal sage scrub, USA (Conlisk *et al.*, 2014)], and increased simulated extinction risk for mammals in peri-urban landscapes [southern brown bandicoot (*Isodon obesulus*) in Australia (Ramalho *et al.*, 2018)]. In most cases, fire reduced population size in habitat patches, and fragmentation reduced colonisation (except Hossack *et al.*, 2013), which together led to worse outcomes for biodiversity.

Improvements in biotic responses were infrequently documented (1 empirical and 4 simulation cases at the landscape scale) and all were for plants (Table 9). For the threatened Australian shrub tranquillity mintbush (*Prostanthera askania*) in fragmented agricultural landscapes, simulations suggested an increase in fire frequency was associated with decreased extinction risk and increased abundance (Tierney, 2018). In longleaf pine (*Pinus palustris*) woodlands, USA, higher fire frequency also increased plant species richness in sites that were species poor due to historical land clearing (Brudvig & Damschen, 2011). The three cases reporting non-linear biotic responses were from simulation studies of plants and indicated that intermediate fire frequency was beneficial, but the magnitude of the effect depended on the amount of fragmentation. For example, the simulated abundance of the obligate-seeding shrub *Ceanothus greggii* from the USA was highest at 40 year fire-return intervals and intermediate to high fragmentation levels, provided that fire was spatially uncorrelated (Regan *et al.*, 2010). However, if fires were correlated and burnt across the whole landscape, then fragmentation reduced the benefits of intermediate fire-return intervals, decreasing abundance (Regan *et al.*, 2010).

There were a further five empirical cases at the landscape scale where fire and fragmentation did not influence each other, and their combined effect did not influence the biotic response (unchanged response; Table 9). For example, using occurrence data for 44 plant species from rosemary scrub, USA, Miller *et al.* (2012) found weak effects of fire on extinction rates and no effects of patch size, connectivity or their interaction with fire on extinction rates. Persistent seed banks may have contributed to these muted responses (Miller *et al.*, 2012). That these null responses were all empirical studies suggests that in some cases, ecological processes intervene to prevent fire–fragmentation interactions, and such effects are typically not incorporated in simulations.

(2) Patch scale

At the patch scale, effects of patch connectivity and patch size were reported (Table 9). Reducing patch connectivity in combination with increasing fire had similar effects to landscape-scale fragmentation and loss (4 simulation, 1 data case). For example, Tulloch *et al.* (2016) simulated *Banksia* tree dynamics in Australia and found that most species had positive population growth rates at mid-level fire intervals

(40–80 years, *cf.* <20 or > 80 years), with greater sensitivity to fire interval when connectivity was low.

When decreasing patch size interacted with more fire it led to worse outcomes for biodiversity in four of eight cases, two of which were simulations. For example, Brooker & Brooker (1994) simulated the effects of patch size, fire extent and frequency on extinction risk of the splendid fairy-wren (*Malurus splendens*), in fragmented Australian farmlands. When patch size was large (2000 ha), only annual burning over the entire patch led to a 100% extinction rate. However, as patch size declined, the range of fire frequency and extent that led to 100% extinction rate expanded, so that in 40-ha patches, fire every 1.6 years and with ~60% of the patch area burnt led to a 100% extinction rate.

In two empirical examples, patch size influenced the effect of fire within the patch, but in opposite directions. On large islands in a hydro-electric dam in Brazil, vertebrate species richness was unaffected by fire, but on small islands, severe fire caused richness to decline by approximately four species more than the effect of small patch size alone (Benchimol & Peres, 2015*b*). By contrast, fire in small patches of prairie in the USA did not cause species to decline, because disturbance-sensitive birds typically did not occur on small patches (Herkert, 1994). However, species that prefer longer times since fire could be found in large patches, so would be at risk if large patches were entirely burnt (Herkert, 1994).

(3) Edge scale

We found only two cases examining edge effects, where fire and fragmentation did not influence each other (Table 9). Fire had an important influence on forest regeneration in Panamanian pastures (Hooper, Legendre & Condit, 2004). Wind-dispersed, light-dependent species were most abundant near the forest edge in recently burnt grassland, but there was no edge effect when experimental plots remained unburnt (Hooper *et al.*, 2004). In a second empirical case, examining an invasive grass (*Avena barbata*) in Australia, Gosper *et al.* (2011) found that fire did not significantly increase its biomass or density at remnant woodland edges beyond the edge effect itself.

VIII. FEEDBACK LOOPS: FIRE AND FRAGMENTATION INFLUENCE EACH OTHER

Because fire can influence fragmentation and *vice versa*, there is the potential for feedbacks between these two processes (Fig. 2A). Some studies described feedbacks in a system but very few studies demonstrated closure of feedback loops. For example, large fires in less-fragmented Canadian forests resulted in more, small unburnt forest patches (Gralewicz, Nelson & Wulder, 2012). These small forest patches were subsequently burnt more often than large patches, but without fire, they could recover over a 20-year period. The study did not clarify whether burning within that 20-year time

period led to further fragmentation and subsequently greater fire susceptibility of remaining patches (i.e. a closed feedback loop) (Gralewicz *et al.*, 2012). A feedback loop was demonstrated in Amazonian forests, where forest fragmentation led to increased anthropogenic fire ignitions as a pasture-management tool. The increased fire ignitions increased the incidences of fire ‘escaping’ into remaining fragmented forest, which in turn promoted further forest loss through burning and post-fire logging (da Silva *et al.*, 2018; Cumming *et al.*, 2012). A similar situation has been described for Australian forests (Lindenmayer *et al.*, 2011).

It is possible that more examples of feedback loops exist, given the number of studies that identified possible feedback scenarios [e.g. where fire influenced fragmentation (98 cases), or where fragmentation influenced fire (41 cases had possible feedbacks)]. Moreover, there is a substantial literature showing that conversion of wooded ecosystems to grassy or similarly open ecosystems involves a positive feedback with fire (Staver, Archibald & Levin, 2011). These feedbacks favour expansion of open, more flammable ecosystems under topographic and climatic conditions that permit fires to occur (Hoffmann *et al.*, 2012; Tepley *et al.*, 2018). Limited evidence

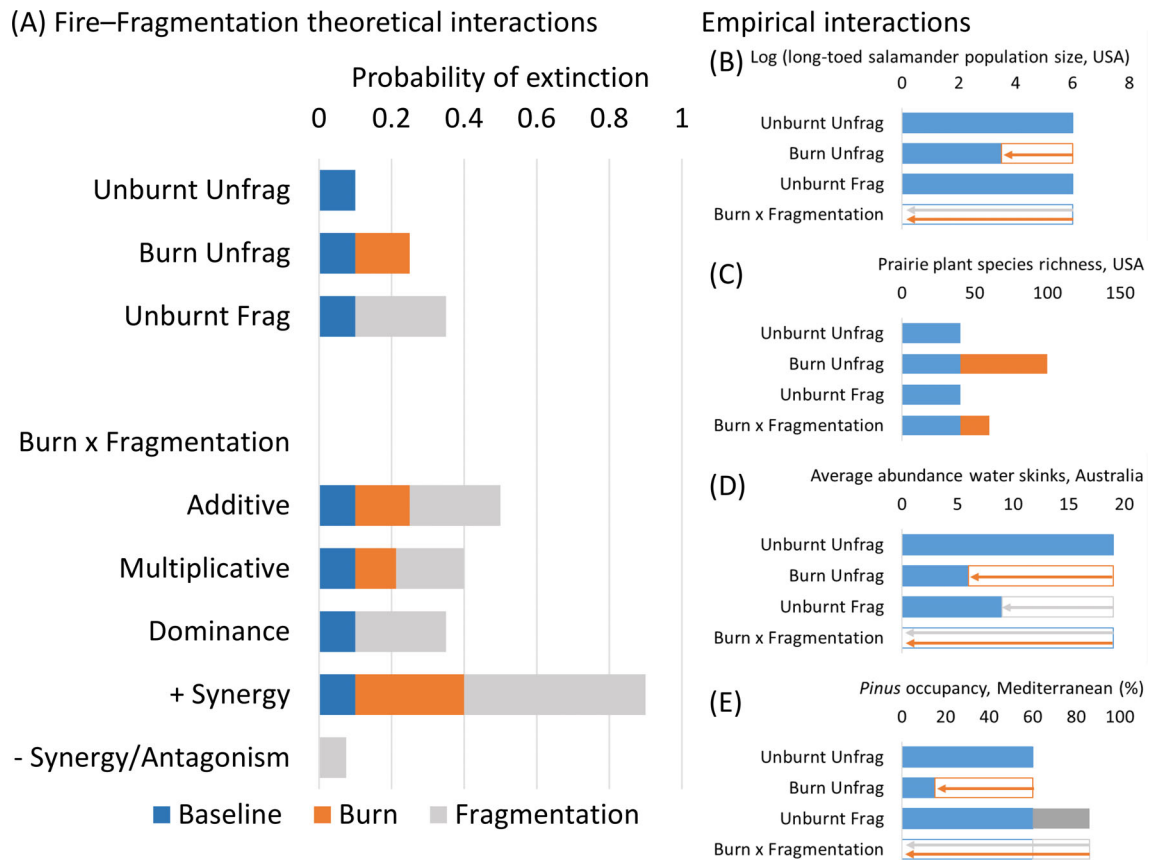


Fig 3. (A) Defining different types of interactions where the independent and joint effects of fire and fragmentation have been evaluated (after Cote *et al.*, 2016), for a hypothetical species that is disadvantaged by both fire and fragmentation. Unburnt Unfrag: effect in areas that represent a long unburnt unfragmented area (blue bar). Burn Unfrag: areas burnt but not fragmented (difference from baseline as orange bar). Unburnt Frag: areas not burnt but subject to fragmentation (difference from baseline as grey bar). Burn × Fragmentation has five alternative responses: Additive – overall effect is equal to the sum of the effects of burn and fragmentation; Multiplicative – effect is smaller than the summed effects but larger than the largest individual effect; Dominance – an effect equal to the largest independent effect of fragmentation or fire; +Synergy – the effect is larger than the sum of independent effects; –Synergy – the effect is smaller than the smallest individual effect. Values for the interaction that are less than additive have also been called antagonisms (Cote *et al.*, 2016). (B) Long-toed salamander (*Ambystoma macrodactylum*) population size in wetlands, USA (Hossack *et al.*, 2013). (C) Plant community richness in prairie remnants in the USA (Alstad & Damschen, 2016). (D) Average abundance of water skinks (*Eulamprus leuraensis*) in bogs embedded in forest from Australia (Gorissen *et al.*, 2015). (E) Simulated *Pinus* occupancy in the Mediterranean (Pausas, 2006). In B, D and E, effects driving values below the ‘baseline’ are indicated by unfilled rectangles and left-pointing arrows (for example, in B, fire had a negative effect in unfragmented landscapes, reducing log(population size) from 6 to ~3.5). In the theoretical example (A), interaction effects such as +synergy are illustrated as consisting of increases in both the effects of fire and fragmentation. However, in the empirical and simulation examples (B–E), interactions (Burn × Fragmentation) cannot be attributed to individual changes in effects of fire and fragmentation. Interactions are therefore indicated by the parallel left-pointing arrows.

for feedback loops to date is probably because few studies run long enough to detect a mutually reinforcing loop or because feedback loops are not explicitly studied in a fragmentation context.

IX. TYPES OF INTERACTIONS

At its simplest, four classes of results, which we refer to as strata, are needed to evaluate a fire–fragmentation interaction fully: (i) a baseline effect in unfragmented, unburnt habitat; (ii) the effect of fire in unfragmented habitat; (iii) the effect of fragmentation in unburnt habitat; and (iv) the effects of fire and fragmentation together (Fig. 3A). There were only 12 cases from 10 papers for which we were able to extract the independent and interactive effects of fire and fragmentation traits.

Of the 12 cases reporting independent and interactive effects of fire and fragmentation, six were empirical, and four of those reported synergies, where the combined effect was greater than their summed independent effects. For example, wetlands in fragmented landscapes in the USA had similar-sized populations of the long-toed salamander (*Ambystoma macrodactylum*) as wetlands in protected landscapes (Fig. 3B) (Hossack *et al.*, 2013). Population size was reduced as the area of high-severity fire within 2 km of wetlands increased, but the reduction was higher in fragmented landscapes reflecting a positive synergy (Fig. 3B). Fires in protected landscapes reduced population size by a factor of seven, but in fragmented landscapes, fire eliminated populations. While fire creates a matrix that is hostile to the desiccation-prone salamander, the authors did not offer an explanation for this synergy.

In a contrasting example, plant species richness in prairie remnants in the USA was positively associated with connectivity in sites that had been recently burnt, but was unrelated to connectivity in unburnt sites (Fig. 3C). Fire promoted germination and establishment, while connectivity allowed propagules to arrive, with both needed to increase species richness (Alstad & Damschen, 2016). The reduced benefit of fire in fragmented landscapes suggests a multiplicative interaction (smaller than summed effects but larger than largest individual effect; Fig. 3C). Gorissen *et al.* (2015) provide an example where both fire and fragmentation had negative effects on abundance of the Blue Mountains water skink (*Eulamprus leuraensis*) in perched swamps in Australia, but when acting together resulted in population extinction (Fig. 3D). The large independent effects of fragmentation and fire make it difficult to identify if the effect was additive (summed effects), multiplicative or synergistic in this case.

In one of two papers that examine fragmentation *per se*, Pausas (2006) simulated the proportion of the landscape occupied by the tree genus *Pinus* in the Mediterranean, for five levels of forest configuration and six levels of fire frequency. Fire interacted with fragmentation to more than offset the benefits of fragmentation, in a strong synergy (Fig. 3E). One other study based on simulations also reported

synergistic interactions (Rodriguez-Buritica & Suding, 2013), although other simulation studies reported additive (Lindenmayer & Possingham, 1996) or multiplicative interactions (Tulloch *et al.*, 2016; Conlisk *et al.*, 2012).

X. DISCUSSION

A significant challenge in understanding, and responding to, global threats to biodiversity is that threats can interact in complex ways (Segan *et al.*, 2016; Geary *et al.*, 2019). Understanding interactions between threatening processes can be critical; some threats acting alone can have limited or no negative effects, but acting together can drive populations to extinction (Fig. 3D, E). This also suggests a need to recognise interactions in IUCN threat classifications (IUCN, 2020) because, acting alone, some processes might not be threatening but in situations where they act together, may need recognition and action. Here, we reviewed the global literature to assess potential interactions between two major threats to biodiversity, altered fire regimes and habitat fragmentation. We synthesised 162 studies using a framework that highlights three broad categories of interactions: fire influences fragmentation; fragmentation influences fire; and neither influences each other directly but they act together to influence biotic responses.

Conceptually, the same ecological processes take place in all three categories of our framework (Fig. 1), such as changes in edge effects and the effects of condition, amount and spatial arrangement of habitat. However, the papers reporting that fragmentation influences fire, or that neither influences the other, include landscapes that have incurred habitat conversion for agricultural or other human uses. In these situations, the level of fragmentation is primarily determined by land-use change and fragmentation dynamics are linked to the rate of land clearing and land abandonment. If land is abandoned, the landscape may recover through revegetation (Jonson, 2010), transition through succession (Hooper *et al.*, 2004), or remain locked in a cleared stable state (Standish *et al.*, 2007). By contrast, when fire influences fragmentation, fragmentation dynamics are typically associated with mosaics of fire in extensive natural systems, with dynamics dominated by succession. From a conservation and management perspective, instances of fire influencing fragmentation can be addressed primarily by changes to fire management, and reintroductions if poorly dispersing species are lost (Rickards, 2016). However, for the other fire–fragmentation interactions, the underlying causes and consequences of land clearing, abandonment, and changes to the fire regime must be addressed.

A common theme emerging across our three categories of interaction was that the direction of the effect of the fire–fragmentation interaction was frequently determined by the successional preferences of species. Adding fire to landscapes where fire has been suppressed benefitted early-successional species, whereas increasing the amount of fire was detrimental to late-successional species. This was generally true

regardless of scale, the aspect of the fire regime examined, or the fragmentation traits considered. It was also true across a wide range of ecosystems. For example, fire has caused patch-quality decline in grasslands (Fenner & Bull, 2007; Curnutt *et al.*, 1998), woodlands (Berry *et al.*, 2015), Mediterranean forests (Herrando & Brotons, 2002), subtropical forests (Catterall *et al.*, 1997) and rainforests (Mendes-Oliveira *et al.*, 2012). In fire-sensitive rainforest, most plant species are disadvantaged, while a few pioneer plant species benefit from fire (Tabarelli, Peres & Melo, 2012). Frequent fire also disadvantages species that prefer long-unburnt habitat in what might be regarded as fire-adapted ecosystems such as grasslands (Herkert, 1994; Fenner & Bull, 2007; Curnutt *et al.*, 1998), woodlands and forests (Berry *et al.*, 2015; Herrando & Brotons, 2002; Catterall *et al.*, 1997). That species respond according to their successional preferences is consistent with long-standing expectations from disturbance theory (Pulsford, Lindenmayer & Driscoll, 2016) and explains why, generally, the same processes can be observed across ecosystems; the species in all ecosystems represent a spectrum of successional preferences.

Our review also shows that the typical effects of fire based on succession can be modified in interaction with fragmentation. Habitat fragmentation by land clearing can change the effects of fire, from a benign or beneficial effect, to a process that threatens the persistence of species. Cases from our review included when specialists in grassland, an ecosystem that is commonly burnt, are disadvantaged by fire (Fenner & Bull, 2007), and when fire fails to have the expected benefits because colonists cannot reach isolated remnants to access their favoured successional stage (Van Dyke *et al.*, 2004; Brown *et al.*, 2013; Alstad & Damschen, 2016). Small patch size can also magnify the short-term impacts of fire on species because populations are small, making them more vulnerable to extinction when patches are burnt, even though in large areas of habitat fire would rarely cause extinction (Brooker & Brooker, 1994; Benchimol & Peres, 2015b).

Further unexpected responses arose when fire improved or worsened the landscape or patch metrics, but the biotic response was in the opposite direction. These cases show that complex behaviours or interactions can arise to alter expected relationships. Examples included higher predation or faster depletion of resources when fire improves connectivity (Ranius *et al.*, 2014), higher abundance in more isolated unburnt patches due to local attraction (Berry *et al.*, 2015), and edge attraction which increases species richness in patches that would generally be regarded as more degraded by having higher edge to area ratios (Herrando & Brotons, 2002).

Substantial variation in how fragmentation affected fire was introduced by differences in human use of fire. In a longitudinal study from Canada, Weir, Johnson & Miyanishi (2000) reported that fires during the land-clearing phase in the 1890s occurred more frequently than the background rate because fire was used to help clear land. However, by the mid-1940s when land clearing was complete, fire declined, which is typical of many agricultural landscapes that suffer from too little fire due to fire suppression (Leach &

Givnish, 1996; Yates & Broadhurst, 2002). On the other hand, some grazing landscapes experience higher rates of fire, most notoriously in South American landscapes with remnant tropical rainforest (Le Page *et al.*, 2017; Cochrane, 2001). Managing the fire–fragmentation interaction is therefore intimately entwined with how people suppress or exploit fire, and now much research attention is being given to social aspects of improving fire management (Eloy *et al.*, 2019; Mistry *et al.*, 2019; Moura *et al.*, 2019).

Very few studies have examined the effects of fire and fragmentation on a particular biotic response across multiple scales, including landscape, patch and edge scales. In the four papers we found that did so, the effects were in the same direction, suggesting that so far there is no evidence that scale interacts with fire and fragmentation to change the direction of effect, for example on abundance or species richness (Barbe *et al.*, 2017a; Baxley *et al.*, 2011; Davis *et al.*, 1997; Miller *et al.*, 2012). Fire, nevertheless, does have characteristic effects at different scales, by definition: causing or reducing fragmentation and loss, improving or worsening patch quality, and improving or worsening edge effects.

Our review demonstrates that research at each of these scales has provided insight into different mechanisms influencing the fire–fragmentation interaction. This includes the widely reported pattern that flammability typically increases at forest edges due to being drier and having more vegetation and dead plants. With expectations that climate change will bring increased drying and warming to many parts of the world, edge flammability will likely become a more important factor driving landscape fires (Le Page *et al.*, 2017; Cochrane, 2003; Malhi *et al.*, 2009).

(1) Knowledge gaps

Among 274 cases of fire and fragmentation interacting, we found only 12 cases reporting full interactions that included the four essential strata, which were fragmented and unfragmented landscapes that both span contrasting fire histories (Fig. 3), highlighting a substantial knowledge gap. There are some papers where the data seemed to be available, but the authors did not test for an interaction, either because it was not their key focus (Yates & Ladd, 2005), or possibly because statistical power was limiting, making it hard to fit interaction models (McLean *et al.*, 2018; Van Dyke *et al.*, 2007). Some progress may therefore be possible if researchers explicitly test for interactions whenever their data allow.

The small number of cases showing the four strata of the full fire–fragmentation interaction (Fig. 3) is partially because fire and fragmentation are not independent in studies in which fire influences fragmentation or fragmentation influences fire. In cases where fire creates habitat and reduces fragmentation, or when fire destroys habitat and increases fragmentation, there are no conditions for evaluating the effect of fire alone. Similarly, when fragmentation influences fire, these processes are always correlated, with more fragmentation leading to more or less fire. However, if fire can

be decoupled from fragmentation then independent effects of fire and fragmentation could be examined more often. Decoupling is readily achieved using simulations (Tierney, 2018; Regan *et al.*, 2010). However, in reality, decoupling could be achieved by using fire suppression at more flammable edges or natural variation in fire occurrence (e.g. Benchimol & Peres, 2015*b*), by introducing fire to fire-suppressed landscapes, or by changing burning practices of local land users to reduce burning.

Unfortunately, many ecosystems are entirely fragmented so opportunities to define the interaction fully have already been lost. Nevertheless, important inferences for conservation management can be made by using subsets of the four strata, particularly fragmented strata if there are also contrasting fire histories (e.g. the timing, type and severity of fires) (Fig. 3). These highlight the effects of fire in a fragmented landscape and, regardless of independent effects of fragmentation and fire, the conservation benefits of increased (Fig. 3C) or decreased fire (Fig. 3B, D and E) can still be recognised (e.g. Marschalek *et al.*, 2016; Wirth *et al.*, 1999).

When fragmentation affected fire, two-thirds of papers (28 papers) reported the change in fire only, not its consequences for biodiversity. Of those papers, 21 used remotely sensed data or other mapping, suggesting this bias may have arisen because desk-top studies are more feasible than costly fieldwork. Understanding how fire is affected by fragmentation is the essential first step. However, taking the next step to understand the consequences for species will enhance our knowledge of fire–fragmentation interactions. Given the rapidly changing, and in many cases novel conditions now emerging in many ecosystems driven by fire (Nolan *et al.*, 2020), the value of empirical information on biotic responses for making cost-effective management decisions (Bolam *et al.*, 2019) may justify more research attention.

While feedback mechanisms were partially identified, full feedback loops between fire and fragmentation resulting in habitat conversion (Fig. 2A) have been characterised only in the destruction of the Amazon (da Silva *et al.*, 2018; Cumming *et al.*, 2012). Feedback loops are possible in ecosystems where fire can degrade habitat and where either more fire is introduced by people or there are strong edge effects increasing fire risk. This potential for feedbacks has also been identified in Canada (Gralewicz *et al.*, 2012), and so feedbacks may be a more widespread threat to ecosystems than currently recognised. Research to define these mechanisms and support management to break the feedback is a priority.

Almost half of the cases examined fire occurrence, with valuable implications drawn across taxa, scales and geographic regions. But given that recent fires in Australia achieved ‘unprecedented’ status based on their massive extent (Nolan *et al.*, 2020), better understanding of the effects of fire extent is imperative. For species that must disperse to colonise patches with suitable habitat, the limited consideration of the extent of fires relative to the species’ dispersal capability and pattern of fragmentation is a major knowledge gap. A second important gap is our knowledge of fragmentation interactions with fire severity. Fire severity had

conspicuously few cases in our review (Table 1) (Benchimol & Peres, 2015*b*; Brown *et al.*, 2018; Hossack *et al.*, 2013), but severity is expected to increase in many places with climate change (Flannigan *et al.*, 2013). Measuring severity can be challenging, particularly separating ground fires from unburnt areas beneath intact tree canopies (Gibson *et al.*, 2020). However, new remote-sensing analyses are improving our capacity to map severity across large areas (Gibson *et al.*, 2020; Quintano, Fernández-Manso & Roberts, 2020).

There was almost no research on the independent effects of habitat fragmentation *per se* and habitat loss *per se* in interaction with fire. Fragmentation and loss are typically correlated, making it hard to separate their effects (Fletcher *et al.*, 2018). Habitat loss must by definition, be detrimental, but fragmentation *per se* has both positive and negative outcomes, and there is debate over how often those outcomes should be expected (Fahrig, 2017; Fletcher *et al.*, 2018). Habitat configuration nevertheless has an important influence on species and communities, *via* mechanisms linked to dispersal (Fahrig, 2017). Because conservation management may be able to manipulate habitat configuration to improve conservation outcomes, understanding the effects of fragmentation *per se* in interaction with fire could prove informative. Although a substantial undertaking, future research could stratify sampling in landscapes by the interaction of remaining habitat and degree of fragmentation *per se* (Radford & Bennett, 2007), with an additional stratification of aspects of the fire regime.

Looking to the future, the most rapid progress in this field may come from natural experiments by studying ecosystems that span a range of fragmentation levels and have contrasting fire histories. Natural experiments take advantage of the natural variation in parameters of interest, and will play an important part in understanding interactions among threatening processes because other approaches can be infeasible (Turner *et al.*, 2020). Natural experiments can be used to explore realistic fire sizes and severities, overlaying actual fragmented habitat, with potential to use space-for-time substitutions to examine processes that can span thousands of years (Wang *et al.*, 2003). Data from this kind of study could be used to inform simulation models that further explore interactions. Manipulative experiments have a role, such as for understanding short-term effects of planned burning and disentangling fine-scale mechanisms (Fordyce *et al.*, 2016), but they are usually limited to low fire severities at small spatial and temporal scales (Driscoll *et al.*, 2010). Natural experiments offer opportunities to expand our knowledge of fire–fragmentation interactions rapidly, provided that other environmental variables do not confound results profoundly (Driscoll *et al.*, 2010).

The extraordinary series of fires that extended down the east coast of Australia in 2019–2020 burnt 12 million ha and were the product of extreme drought associated with human-caused climate change (Nolan *et al.*, 2020). Climate change is likely to alter fire regimes in most parts of the globe, with many increases and some decreases in fire occurrence (Flannigan *et al.*, 2013; Pechony & Shindell, 2010; Syphard *et al.*, 2019). At the same time, demands from a growing

human population motivate land clearing (IPBES, 2019), and in some parts of the world, such as the Amazon basin, deforestation fires ignited by people generate exceptionally large burnt areas during dry periods (Withey *et al.*, 2018). Consequently, we can expect increasing interactions between altered fire regimes and habitat fragmentation and loss. We hope the framework that we have developed in this review will help to guide clear thinking about the nature of these interactions and how best to approach framing and designing research into fire–fragmentation interactions.

XI. CONCLUSIONS

- (1) Fire–fragmentation interactions can be classified as either: (i) fire influences fragmentation, where fire in relatively intact landscapes either destroys and fragments habitat, or creates and connects habitat; (ii) fragmentation influences fire, where, after habitat is reduced in area and fragmented, fire progression is obstructed, or fire in the landscape is subsequently altered by suppression or ignition of fires by people or by increased edge flammability, and; (iii) fire and fragmentation do not influence each other but interact to affect a biotic response, whereby habitats are fragmented by causes other than fire, but fire still occurs in the landscape, and together they affect responses like species richness, abundance and extinction risk in a way that can differ from their independent effects.
- (2) Where fire and fragmentation influence each other, feedback loops are possible that can lead to ecosystem conversion; a key threatening process in the Amazon, but with potential to impact other biomes.
- (3) Fire interacts with fragmentation through scale-specific mechanisms, such as by creating edges and driving edge effects, by altering patch quality and by altering landscape-scale connectivity.
- (4) Examination of interactions requires four essential strata: unburnt–unfragmented, unburnt–fragmented, burnt–unfragmented and burnt–fragmented. We found only 12 cases that examined all four strata, highlighting a key knowledge gap. Nevertheless, these simulation and empirical studies show that fire and fragmentation can interact synergistically, multiplicatively, antagonistically or additively.
- (5) The direction of effect of fire–fragmentation interactions upon biota is often determined by the preferred successional stage of a species; adding fire to landscapes benefits early-successional species, whereas reducing fire benefits late-successional species.
- (6) When fire interacts with fragmentation, the direction of effect of fire on a biotic response could be substantially modified from the effect expected by a species' successional preferences. Adding fire to fragmented landscapes can be detrimental for species that would normally co-exist with fire.

- (7) Human land use and behaviour has an important influence on how fragmentation affects fire, by humans igniting or suppressing fires.
- (8) Climate change will increasingly alter fire regimes throughout the world, and a growing human population ensures that habitat loss and fragmentation will be a permanent feature of our landscapes. Developing improved understanding of how fire interacts with fragmentation is needed for conserving biodiversity faced with these challenges.

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XIV. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Appendix S1. Methods for selecting papers used in the review.

Table S1. Rules used to exclude papers and the number of papers excluded at each step.

Appendix S2. Data collected from each case within the three categories of fire–fragmentation interaction and other data collected for all papers.

Appendix S3. Categories within each of the areas of data collection.

Appendix S4. Converting fragmentation trait and direction of response to simplified categories.

Appendix S5. Converting fire trait and direction of response to simplified categories.

Appendix S6. Converting biotic responses and their direction of effect for fire influences fragmentation to simplified categories.

Appendix S7. Converting biotic responses and their direction of effect for fragmentation influences fire to simplified categories.

Appendix S8. Converting biotic responses and their direction of effect for fragmentation and fire do not influence each other to simplified categories.

Opinion

Macrobehaviour: behavioural variation across space, time, and taxa

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We explore how integrating behavioural ecology and macroecology can provide fundamental new insight into both fields, with particular relevance for understanding ecological responses to rapid environmental change. We outline the field of macrobehaviour, which aims to unite these disciplines explicitly, and highlight examples of research in this space. Macrobehaviour can be envisaged as a spectrum, where behavioural ecologists and macroecologists use new data and borrow tools and approaches from one another. At the heart of this spectrum, interdisciplinary research considers how selection in the context of large-scale factors can lead to systematic patterns in behavioural variation across space, time, and taxa, and in turn, influence macroecological patterns and processes. Macrobehaviour has the potential to enhance forecasts of future biodiversity change.

'Bigging up' behaviour

Behaviour can be a key component of responses to rapid environmental change [1–3] and can also structure patterns above the scale of populations, from context-dependent dynamics in ecological communities [4] to range boundaries for species geographical distributions [5]. Despite these clear links, explicit consideration of behaviour as a mediator of ecological processes across large scales is broadly missing [5,6]. Accurately predicting the effects of environmental change on ecological communities will likely require bringing behaviour into the fold. We believe that research at the interface of **macroecology** (see [Glossary](#)) and **behavioural ecology** would greatly enhance both fields.

Behavioural ecology aims to elucidate how animal behaviour influences, and is shaped by, ecological and evolutionary processes [4]. Yet, how behaviour varies across large extents in space, time, and taxa (i.e., dozens of populations, generations, or species [7]) is broadly unquantified. Existing behavioural ecological theory is based almost exclusively on selection. Explaining patterns of behavioural variation above the population level requires considering factors such as dispersal limitation and biogeographic history. In other words, selection happens against the backdrop of larger-scale processes (Figure 1). For instance, extra-pair paternity in birds exhibits a latitudinal pattern [8,9], with higher rates occurring at lower latitudes. However, this is not a simple case of selection varying along a latitudinal gradient; the pattern also results from variation in biogeographic and diversification histories of different regions. Scaling up comes with the sorts of challenges macroecologists have been grappling with for decades (e.g., **transmutation**, nonlinearity, and **emergent properties**).

Macroecology seeks to explain patterns such as diversity gradients, abundance distributions, and the nature of geographic ranges across large spatial, temporal, or taxonomic extents [7]. Four correspondingly large-scale processes are traditionally invoked to explain these patterns: speciation, movement, **maintenance**, and extinction. Given that all these processes can be influenced by variation in behaviour within and across lineages, and could iteratively influence

Highlights

Behaviour is often the first response of organisms to rapid environmental change and can be a key mediator of ecological responses at higher organisational levels.

Macroecology seeks to understand patterns and processes that emerge from the interaction of many smaller components, and behaviour is an important but understudied category of component.

We propose the new field of macrobehaviour, which aims to unify behavioural ecology and macroecology. Researchers from both disciplines can take advantage of new tools, approaches, concepts, and data, and ultimately ask new interdisciplinary questions.

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behaviour itself, we believe there is much to be gained by linking these two disciplines under the framework of **macrobehaviour** (Figure 1).

What is macrobehaviour?

Although rare, research that integrates behavioural ecology and macroecology exists (Figure 2; Boxes 1 and 2). Unfortunately, these works are currently scattered, hindering the potential to identify commonalities that could elucidate systematic links between behaviour and macroecology. Conceptually, we believe that there are also opportunities to push beyond existing efforts by considering explicitly how selection operates against the backdrop of macroecological processes, and by developing solutions to issues that arise when scaling up from dynamics at the individual or population level to macroscale patterns and processes. We believe that the most effective way forward is to establish a new field that coalesces current research threads and fosters a coherent research community that can recognise recurring themes, responses, and questions, and take aim at new challenges.

We define macrobehaviour as the ‘investigation of variation in behaviour over large geographic, taxonomic, and temporal scales, and the ecological and evolutionary consequences of this variation’, which draws on the definition of macrophysiology [10]. Macrobehaviour can be envisaged as a spectrum across which investigators from the established disciplines borrow data, methods, and concepts from one another. At one end, we can quantify variation in behaviour at large scales, and apply macroecological methods and concepts to test existing behavioural ecology theory in new ways. At the other end, we can use data and concepts from behavioural ecology to explore the influence of behaviour on macroecological patterns and processes (Figure 2; Boxes 1 and 2).

Macrobehaviour seeks to combine the mechanistic perspective of behavioural ecology with macroecology, which is classically focused on emergent properties of aggregated ecological entities (e.g., species in an assemblage; [11]). Here, we focus on the behaviour of animals, but we recognise that behaviour is observable in plants, fungi, bacteria, and protists, and the same concepts apply broadly across those groups. We arrange examples of existing work along a spectrum in Figure 2 from left to right, but the exact placement is somewhat arbitrary and simply aims to illustrate the range of possibilities under the macrobehaviour umbrella.

We note that the term macrobehaviour has been used in a handful of works in social science [12], materials science [13], and comparative psychology [14] in reference to other phenomena, but to our knowledge has not been used in biology.

Enhancing behavioural ecology by drawing on macroecology

Understanding how the behaviour of animals evolves in response to variation in the abiotic and biotic environment is the major focus of behavioural ecology. The first step towards this endeavour is often to quantify variation in the behaviour of interest across an environmental gradient that is hypothesised to drive selection. The more of the gradient that can be captured, the stronger the test will be. By encompassing a wide range of environmental conditions, such data also allow us to evaluate the extent to which a given theory is **generalisable** (e.g., across taxa or continent) versus context-dependent [15,16] (Box 1). If high context-dependency is evident, we can then use this substantial dataset to tease apart which aspects of the context are most important. These are the tools of macroecology (Figure 2, left of spectrum).

Examples of this approach include Oteyza *et al.* [17], who leveraged differences in body size and survival probability across latitude to test hypotheses about parental risk-taking. The large spatial

Glossary

Behavioural ecology: the study of behaviour in an ecological and evolutionary context.

Emergent property: property of an ecological unit that is unpredictable from observations of its components.

Generalisable: conclusions that can be applied to multiple contexts such as different locations, taxa, and times.

Macrobehaviour: the investigation of variation in behaviour over large geographic, taxonomic, and temporal scales and the ecological and evolutionary implications of this variation.

Macroecology: the study of emergent phenomena across large spatial, temporal, or taxonomic scales.

Maintenance: acquisition and allocation of energy.

Territoriality: a form of social dominance in which the resident individual or group has priority of access to resources or mates in a particular area.

Transmutation: mathematical process of scaling up changes the properties of functions and becomes increasingly problematic with increasing non-linearity and variance.

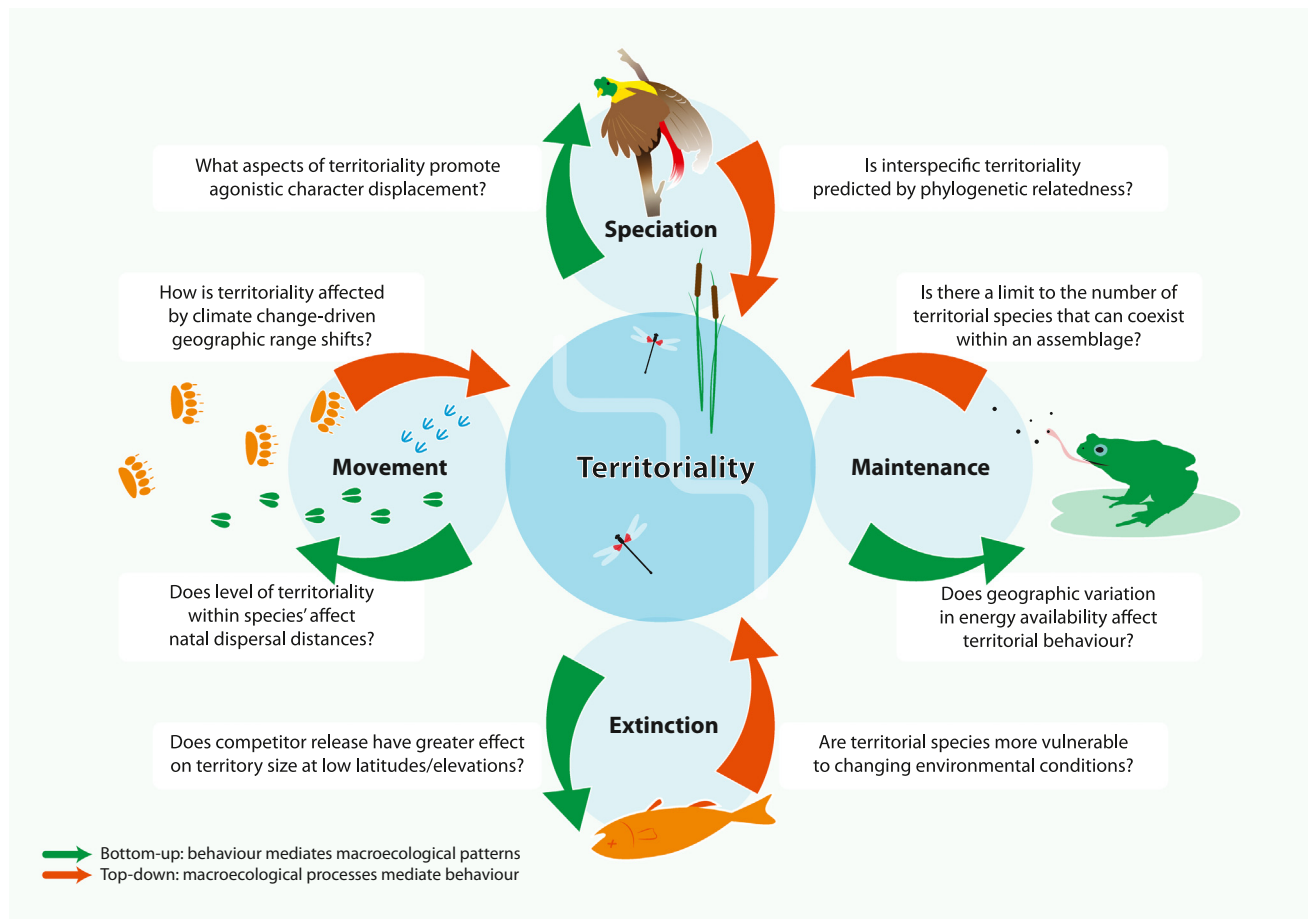
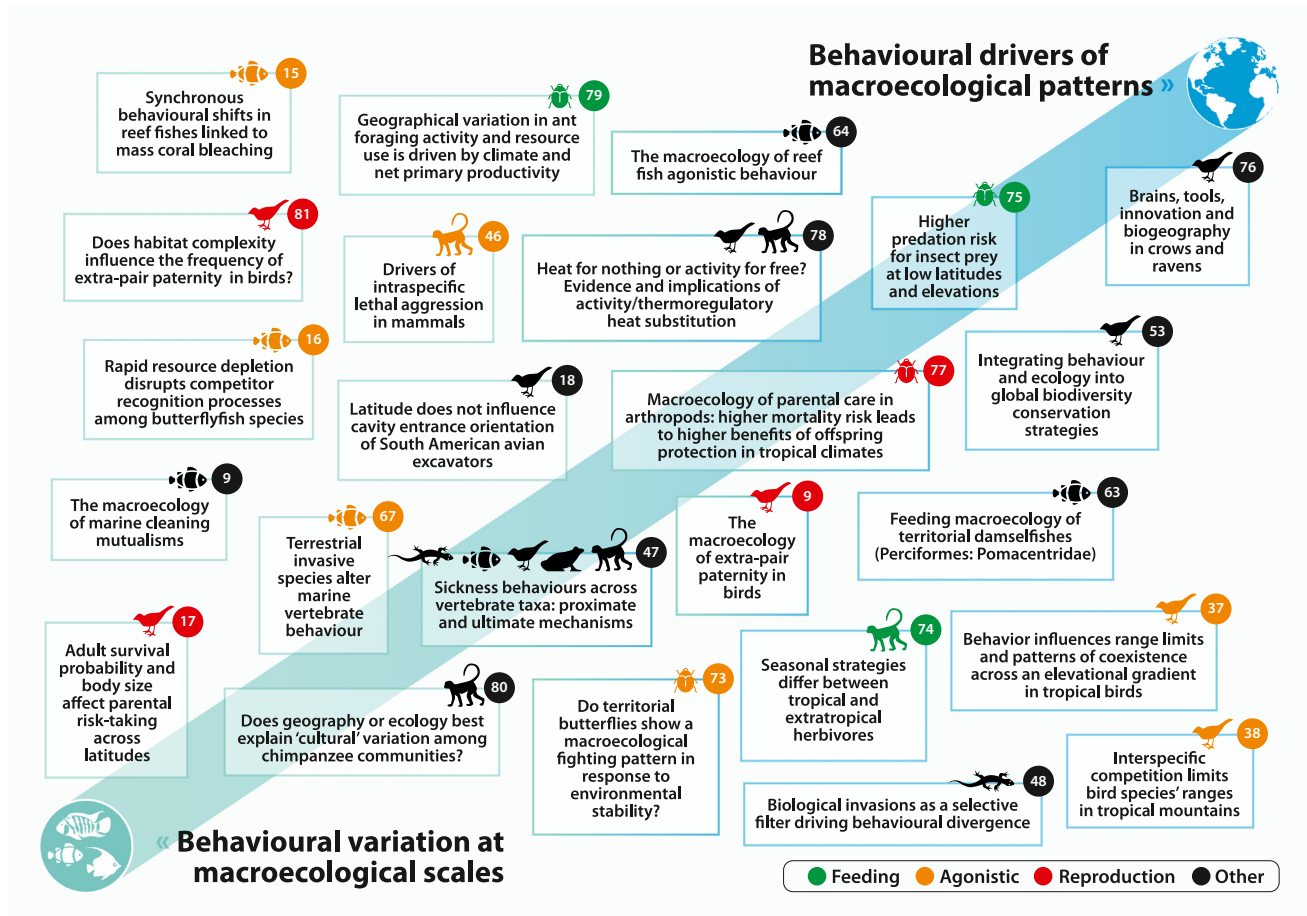
**Trends in Ecology & Evolution**

Figure 1. New questions that are possible under the macrobehaviour framework. Here, we use territoriality as an example of a type of behaviour that can influence (bottom-up) or be influenced by macroecological processes (top-down). In some cases, these are adaptations of existing hypotheses, while others are newly proposed here. For example, the Species Interactions–Abiotic Stress Hypothesis [72] predicts that release from an interference competitor due to their extinction should have a greater effect on range boundaries at low elevations or latitudes than at high elevations or latitudes. Many of these questions also include an element linked to rapid environmental change or disturbance. Note that these questions are not exhaustive for this topic but give a flavour for the types of questions that can emerge from the macrobehaviour framework.

and taxonomic scale also enabled the broad conclusion that smaller, longer-lived birds were more risk averse [17]. Using data collected along a latitudinal gradient, Ojeda *et al.* [18] showed that the non-random orientations of nests in 25 cavity-nesting bird species were not angled to optimise solar radiation, and instead appear to be driven by a complex interplay of multiscale factors. At a global scale, the influence of climatic conditions on breeding season was predictive of reproductive strategies for harvestman (Opiliones), suggestive of broad macroecological patterns in sexual selection [19].

Considerations of scaling up

Behavioural theory has largely been developed on, and tested using, scales below that used by macroecology. Whilst this is not an issue in itself – those theories may work perfectly well at the scales for which they were intended – when we try to apply these theories at larger scales, problems could arise. We touch on this briefly here and refer the reader to [7] for a more in-depth discussion.



Trends in Ecology & Evolution

Figure 2. The spectrum of macrobehaviour. Recent examples are represented by paper titles, animal class (bird, mammal, fish, reptile, amphibian, or insect silhouette), and type of behaviour (colour). This is not an exhaustive list of all papers that would fit under the umbrella of macrobehaviour but is intended to illustrate its broad reach across the spectrum. Papers were identified with a whole-text search for "macroecolog*" AND "behavio*" in Web of Science on 6 January 2023 and filtered for relevance. See [9,15–18,37,38,46–48,53,63,64,67,73–81].

One consideration is that the dominant processes may change with scale [20]. For example, if we think about how the abundance of a population changes in response to rising temperatures, behavioural responses such as behavioural thermoregulation [21] may dominate. However, if we scale up to thinking about how rising temperatures affect aggregate patterns, such as abundance distributions of species assemblages, larger-scale processes such as colonisation and extinction may dominate [22]. That is not to say that behavioural thermoregulation of different populations is not important but that it can only inform predictions about abundance distributions if it is embedded within the context of larger-scale processes.

Abundance distributions are emergent because their characteristics (e.g., evenness, and frequency of rare/common species) cannot be predicted solely by understanding an individual component (abundance of one species) of the system. Emergent properties do not directly scale or relate to the properties studied at smaller scales [7] but are often used in place of smaller-scale mechanistic properties to enable broad general patterns to be identified. For a more direct example that would fall under macrobehaviour, the distribution of foraging strategies across a species assemblage cannot be predicted from the foraging strategy of one species, and

Box 1. Reef fish across the spectrum

Coral reefs are globally important hyperdiverse ecosystems that offer an excellent opportunity to explore macrobehaviour. Distributed throughout the tropics, they show clear geographical patterns in species diversity [40] facilitating replication across locations, and species interactions abound leading to rich behavioural tapestries [61].

Meta-analyses that combine data from existing literature are one way to tackle macrobehavioural questions. Data from 231 species across eight sites in the Atlantic and Pacific Oceans, and the Mediterranean Sea revealed that relationships between cleaner fish and their clients were structured by neutrality, offering fundamental insights into species coexistence and community assembly mechanisms [62]. Analyses of bite rates for damselfishes from three ocean basins across a gradient of 8°C variation in mean annual sea surface temperature (SST) suggested that higher metabolic requirements in warmer water drove higher feeding rates in aggressive farming damselfishes [63].

Macrobehaviour of coral reef fish has also been explored with primary data. Fontoura *et al.* [64] quantified change in reef fish agonistic interactions across a 34 000 km longitudinal gradient of species richness. Agonistic networks were nested in structure with a core of highly aggressive territorial species, and similar frequencies of agonistic interactions regardless of regional richness. Therefore, emergent agonistic behaviour appears to be constrained locally, supporting the idea that common structuring mechanisms underlie species coexistence [64].

Coral reefs are experiencing increasingly frequent and severe disturbances [65]. A global coral bleaching event in 2016 led to mass mortality of corals across the Indo-Pacific, providing a natural experiment to explore effects of rapid resource depletion, replicated across multiple regions (Figure 1). Coral-feeding butterflyfishes became less aggressive, as predicted by economic defendability theory [15], and their ability to recognise, and respond appropriately to, competitors was compromised [16]. The replication of this response across multiple regions offers strong support for its generalisability. Longer-term disturbances also offer useful experimental set-ups. A subset of Chagos Archipelago islands were invaded by rats in the 1800s, disrupting nutrient flows that connect terrestrial and marine systems via bird guano [66]. This disruption depleted the nutritional quality of damselfish food around rat-infested islands, causing their territorial behaviour to lessen, with unknown consequences for the ecosystem [67]. By exploiting environmental disturbances, we can both test fundamental behavioural theory and reveal behavioural adjustments that could have important ramifications for vulnerability of coral reef communities due to disruption of species coexistence mechanisms and ecosystem function.

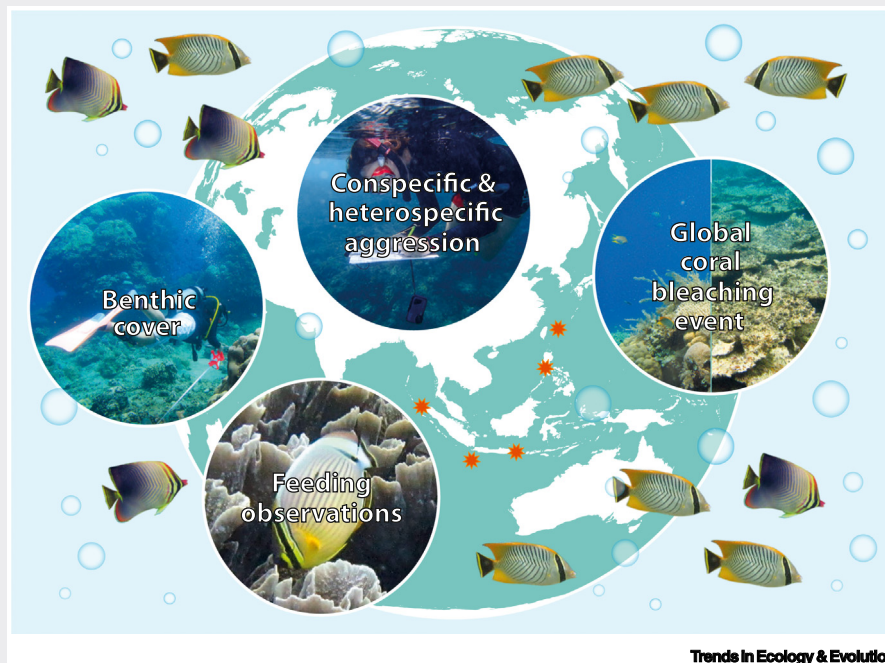


Figure 1. Example set-up for reef fish macrobehaviour research. Individuals from 38 species of butterflyfish were observed at 17 reefs across five regions (stars on map) in the central Indo-Pacific, spanning ~4000 km latitudinally and ~3000 km longitudinally. Data on aggression, feeding, and benthic (coral, algal, or substrate) cover were collected before and after a global coral bleaching event in 2016 that caused mass coral mortality, providing a natural experiment replicated across multiple localities. Photo credits: Erika Woolsey, Sally Keith.

we would need to consider other factors such as habitat structure and interactions between species (already the purview of behavioural ecology) against the backdrop of assemblage composition generated by speciation, dispersal, and extinction (macroecology).

Finding a way to predict emergent properties mathematically by linking equations of individual or population level behaviour, to equations at larger hierarchical scales, is further hampered by the transmutation problem [23], which states that scaling of equations across hierarchies can be exact only in systems with linear responses or no variability – a rarity in ecological systems. The use of probability distributions as dependent variables (e.g., Bayesian approaches) and process-based or mechanistic models can offer solutions [20,24]. However, a significant challenge remains, both for modelling and to target primary data collection, in identifying which small-scale mechanisms are essential for predicting macroscale patterns, while remaining tractable and interpretable [22].

Harnessing environmental change as natural experiments

Identification of the behavioural impacts of anthropogenic global change is one factor that motivates many papers outlined in Figure 2, and therefore global change is at the heart of the macrobehavioural endeavour. However, in addition to providing the impetus for examining geographical variation in behaviour, environmental changes can offer natural experiments (Box 1). Urbanisation is a prime example. Associated with sweeping changes in abiotic and biotic conditions, an entire subfield of behavioural ecology aims to understand the mechanisms driving urban shifts in behaviour [25]. For instance, the combination of increased noise with decreased predation and pathogen pressures in urban environments selected for increased call complexity in urban Túngara frogs (*Physalaemus pustulosus*) in comparison to their forest-dwelling counterparts [26], and asymmetries in bird dominance interactions were more likely to lead to aggressive exclusion in highly urbanised environments [27].

Invasion biology examines the impacts of non-native species after anthropogenic factors lead to their establishment in a new location [28]. A growing number of empirical case studies demonstrate that behavioural interference often plays a key role in determining the pace and outcome of invasions [29]. In both the USA and China, the introduction of the mosquito *Aedes albopictus* has driven a rapid decline in *Aedes aegypti* owing to an asymmetry in the fitness impacts of reproductive interference [30,31]. Similarly, agonistic interactions between a native gecko species (*Lepidodactylus lugubris*) and the invasive house gecko (*Hemidactylus frenatus*) have led to rapid declines in native species on islands throughout the Pacific [32].

Enhancing macroecology by drawing on behavioural ecology

Macroecology is an approach that brings together multiple disciplines to reveal and explain repeated patterns in the abundance, diversity, and distribution of life on Earth [7,11,33,34]. It aims to identify properties of ecological entities (e.g., communities) that emerge from the relative noise of many individual components (e.g., species), and understand the processes that generate and maintain those properties [7,11,34]. Macroecological questions are diverse and include those directed towards understanding the relationship between life history strategies and extinction risk; assembly rules for local communities from regional species pools (e.g., neutral models); allometric scaling relationships such as body size and speciation rates; and geographic patterns in species diversity and abundance [35]. One element that is largely missing from explanations of macroecological patterns and processes is the explicit consideration of behaviour, potentially leading to spurious results. For example, behavioural flexibility and species interactions were shown to be essential components to generate accurate species distribution models for Alpine chamois (*Rupicapra rupicapra*) [36]. Therefore, at this other end of the spectrum, we believe it is

Box 2. Eco–evo models and the Red Queen hypothesis

Classical behavioural ecology theory takes population persistence as a given, which limits its utility for explaining patterns above the population level and for predicting responses to environmental change. Relaxing this assumption can yield important insights about the relevance of behaviour for species coexistence, and by extension, larger scale patterns. Grether and Okamoto [68] used an individual-based model grounded on the life cycle of territorial birds to examine whether selection could rescue a superior interference competitor from extinction without driving a superior exploitative competitor extinct, and vice versa. Their eco–evo simulations showed that coexistence was possible over a wide range of ecologically plausible scenarios, and up to the highest levels of resource overlap, but only if the species continually coevolved (Figure 1). One implication is that reductions in population size and genetic variation could destabilise coexistence between territorial species.

We believe a generalised version of this model might help explain a large-scale pattern in the fossil record, namely that for most groups of organisms the probability of extinction is independent on the age of a taxon [69]. To explain the pattern, Van Valen [69] famously proposed that competing species can only increase in fitness by evolving at the expense of each other, resulting in a zero-sum (Red Queen) game in which none of the species increases in fitness over the long term. While Van Valen framed it in group selection terms, Grether and Okamoto [68] showed that a similar zero-sum game can emerge from individual-level selection.

Whether eco–evo models can be scaled up to test mechanistic explanations for emergent macroecological patterns is an open question (see Outstanding questions). It may be that fundamentally different processes operate at different spatial and temporal scales (e.g., demography and individual-level selection at local scales and species sorting and species-level selection at regional scales) [7]. However, purely ecological (Lotka–Volterra-based) models have been used with some success to reproduce well-documented macroecological patterns [70,71]. In principle at least, modelling approaches that explicitly account for behaviour and allow species to evolve in response to each other could prove useful for evaluating whether macroecological patterns are likely to arise from microscale processes.

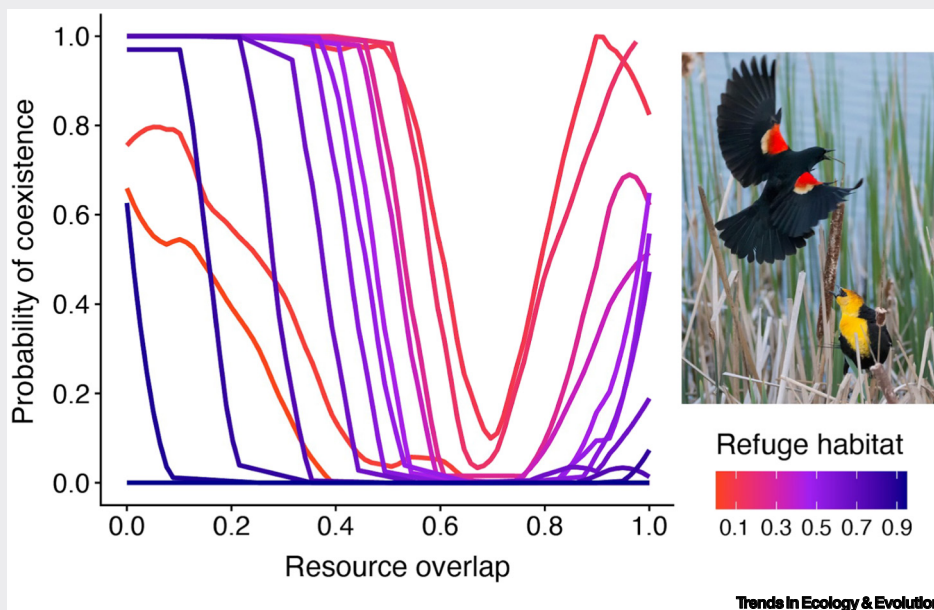


Figure 1. Probability of coexistence under territoriality. Coexistence depends on resource overlap and the fraction of the habitat where the superior resource competitor could breed without interference from the superior interference competitor. For further details, see Grether and Okamoto [68]. Inset photo: territorial fight between red-winged blackbird (*Agelaius phoeniceus*) and yellow-headed blackbird (*Xanthocephalus xanthocephalus*) on a marsh in British Columbia, Canada. Photo credit: Feng Yu / Alamy Stock Photo (with permission).

beneficial to incorporate behaviour explicitly as an underlying mechanism. For instance, territorial behaviour is a key predictor of tropical bird species' elevational range limits [37,38], highlighting the importance of incorporating behaviour when forecasting altitudinal range shifts under climate change [5].

Rapid behavioural change mediates top-down drivers

Hypotheses to explain macroecological patterns in abundance, diversity, and distributions abound, with >100 hypotheses aiming to explain the latitudinal diversity gradient alone [39]. Macroecological hypotheses tend to involve top-down processes that operate over long time scales, such as selective colonisation driven by plate tectonic movements [40,41], differences in speciation rates [42], and relationships between body size and metabolism [43]. By contrast, behavioural change can be rapid, on the scale of days, and is often the first response of individuals to both acute and chronic disturbance in a world of human-induced rapid environmental change [1,5]. For example, temperature tolerance as a predictor of species geographic range distributions is modified strongly in terrestrial ectotherms by fine-scale behavioural thermoregulation [21,44]. Understanding the role of behaviour in mediating these top-down processes is likely to be increasingly important.

Predicting the future of biodiversity requires context

To achieve its aim of generalisability, macroecology requires data across large geographical, taxonomic, or temporal extents, but it can be challenging to measure all potentially relevant variables. The omission of behavioural and physiological variables was acknowledged at the inception of macroecology to be ‘...more a matter of practicality than philosophy...’, and it was suggested that ‘...the morphology, physiology, and behaviour of individual organisms play major roles in causing, or at least constraining large-scale patterns of distribution and abundance, both within and among species.’ [33]. It is now increasingly recognised that ecological outcomes are context-dependent, and that in many cases, taking behaviour into account is necessary to understand context dependency [4]. Without this level of detail, we may be unable to predict species responses into the future, highlighting the need to take a more mechanistic approach [7,24]. For example, the addition of feeding behaviour to data on abundance and temperature predicted diminished trophic interactions for reef fish in response to global warming, highlighting the potential loss of critical ecosystem functions by 2050 [45].

Asking new questions

The true integration of these disciplines is where questions are posed with the explicit recognition of both disciplines from the outset (Figure 1 and Figure 2 middle of spectrum). We offer a schematic to think through how a given behaviour, here **territoriality**, might interlink with the four key macroecological processes (Figure 1 and Box 2). Some of these questions draw on established hypotheses or theories from one or both disciplines, while others are more exploratory and aimed, in the first instance, at quantifying patterns. While we talk about these questions as new, we note that Brown [33] used allometry to develop hypotheses that linked body size, geographic range size, population density, space use, and territoriality, predicting increased territoriality in modal-sized species. Therefore, rather than claiming all questions in this space are new, it is more accurate to say that some are resurrected, some will coalesce, and some are yet to be asked.

Although scarce, macrobehavioural studies have been carried out on each major axis of scale. At a large spatial scale, geographical gradients in intraspecific lethal aggression in mammals could be predicted by photoperiod seasonality, leading to the hypothesis that variation in lethality across mammalian assemblages is driven by hormonal control [46]. At a large taxonomic scale, the characteristics of sickness behaviours and their potential implications for disease spread were explored across the five vertebrate classes [47]. One finding was that fever is triggered by similar molecular pathways in both ectotherms and endotherms despite differences in how body temperature is regulated (i.e., behaviourally vs. physiologically), suggesting that fever is highly adaptive. Finally, at a large temporal scale, behaviour of skinks (*Lampropholis delicata*)

was shown to diverge from native counterparts after invasion of new localities in the Pacific Ocean, leading to greater individual plasticity and lower inter-individual variation on invaded islands [48]. All these examples deliver new fundamental insight into behavioural variation across space, taxa, and time, as well as generating results with ramifications for conservation.

While we largely focus here on leveraging spatial and relatively shallow (i.e., decadal) temporal variation in behaviour to test hypotheses, we can also examine variation over deeper timescales (i.e., millions of years). Macroevolutionary approaches have been used to illuminate the pathways through which behaviours arise (e.g., tail vibration pre-dated the evolution of rattles in rattlesnakes [49]) as well as the ways in which behaviours have themselves impacted rates of speciation (e.g., migratory behaviour leads to high speciation rates resulting from the evolution of sedentary daughter lineages [50]). These examples suggest that a merger of behaviour and macroevolution may yield similarly valuable insights as a merger of behaviour and macroecology (e.g., see speciation and extinction in Figure 1). The boundary between macroecology and macroevolution is often blurred and we encourage similar vision here.

Conservation relevance

The difficulty of linking large-scale patterns to underlying mechanisms has hampered the application of macroecology to conservation problems [51], while it is often difficult to extrapolate behavioural ecology beyond the system in which results were obtained. As behaviours respond plastically to buffer the effects of environmental change, or species fall into ecological traps, the way behaviour mediates ecological patterns and processes at large scales in space, time, and taxa will become increasingly visible and critically important as a consideration for conservation [5,52]. It is our hope that macrobehaviour can improve integration of both macroecology and behavioural ecology into conservation.

From a macroecology perspective, geographical and ecological traits can be used to infer species vulnerability. Estimates of bird extinction risk were improved with the addition of behavioural traits such as foraging strategy, suggesting that integrating behaviour into global conservation strategies is desirable [53]. Priority areas were identified as targets for light pollution mitigation to reduce potential disruption to migratory behaviour using global maps of 298 routes for nocturnally migrating bird species combined with light pollution maps from satellite data [54,55]. Integrating the presence of vocalisations via acoustic monitoring data into species distribution models can indicate suitability of a location for reproductive, territorial, and predation behaviour, bolstering information on the suitability of environmental conditions [56].

Behaviour can offer an early indicator of future changes to population dynamics [57] and could potentially be applied geographically to identify and triage at-risk populations. For instance, effects of fishing on shoaling and reproductive behaviour are anticipated to have repercussions through trophic food webs, with ramifications for local economies [58,59], potentially affecting human wellbeing if subsistence fisheries become less efficient.

Moving forward with macrobehaviour

Moving forward with this research agenda will require cross-disciplinary collaboration and data. Teams must bring together expertise in both disciplines, and perhaps most importantly, a willingness to listen and learn from one another. We hope that over time, macrobehaviour will move from multidisciplinary to true interdisciplinary research, asking new questions and tackling them with skills drawn from across the disciplines. In particular, we must begin to disentangle how selection interacts iteratively with macroecological processes of movement, maintenance, speciation, and extinction, and to tackle methodological and conceptual challenges inherent to scaling up.

The biggest challenge to conducting macrobehavioural research is generating the data required to test hypotheses at scale. Nevertheless, there are several ways forward, including open-access databases, globally distributed experiments, observational approaches (Box 1), and modelling techniques (e.g., individual-based simulations) (Box 2). It is also advantageous to recognise that one set of behavioural data collected across large scales can provide fundamental insight for both macroecology (e.g., how behaviour influences range distributions) and behavioural ecology (e.g., stronger tests of theory) simultaneously. For some questions, it could be that existing behavioural data can be compiled from online sources, whilst other questions will require collection of primary for-purpose data [60]. Brown [33] notes that experiments must be replicated in multiple localities, and preferably habitats, if we are to reach generalisable conclusions.

Concluding remarks

Macrobehaviour offers a new field to unite the disciplines of behavioural ecology and macroecology. It is particularly pertinent in an era of rapid environmental change where behavioural change is often the first response to altered conditions. Macrobehaviour offers a spectrum of involvement where researchers can draw on as little or as much as they wish from the less familiar field, ultimately reaching questions that would not be asked without the explicit consideration of both disciplines (see Outstanding questions). This can lead us towards new fundamental insights that have the potential to be relevant for conservation action, making it imperative that we coordinate efforts and share knowledge to push these frontiers forward as fast as possible. Fully linking behaviour to macroecological scales will require investigations of transmutation and emergent properties, and explicit recognition that selection operates against a backdrop of differential speciation, extinction, and movement. We hope that by uniting existing work and encouraging new research in this area, we can learn from one another more easily and new coherent lines of inquiry can be developed and tested.

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Declaration of interests

No interests are declared.

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Outstanding questions

Conceptual

Which behaviours are most likely to vary geographically and why?

How can variation in behaviour structure biogeographic patterns of species distributions, abundance, and diversity?

How do different behaviours scale allometrically, for example, with body size?

What is the importance of behaviour relative to other factors in structuring macroecological patterns?

Are there fundamental differences in behavioural variation in different biomes and/or ecosystems, and how can any such differences be explained?

Can ecoevolutionary models (e.g., of species interactions) be scaled up to test mechanistic explanations for macroecological patterns?

Can data on the behaviour of extant taxa be used to test explanations for patterns in the fossil record, such as the original Red Queen hypothesis?

Can sound inferences be drawn from macroecological patterns about the behaviour of the component taxa?

Methodological

Which macroecological approaches are most useful for testing theories and hypotheses from behavioural ecology?

What are the advantages and disadvantages of different methods (e.g., collating existing data from literature, primary data collection) for collecting behavioural data for macroecological questions?

How far can we make dual use of behavioural data for both behavioural ecology and macroecology in the same study?

How can we standardise collection of behavioural data for use in macrobehaviour? What details are we willing to trade-off to achieve generality?

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How do we best initiate and consolidate collaboration across disciplines?

How do we avoid statistical pitfalls when scaling up?

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