Thematic Review

Searching for synthetic mechanisms on how biological traits mediate species responses to climate change

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Abstract: Climate change will likely be the most significant challenge faced by species in this century, and species' ability to cope with climate change depends on their life history and ecological and evolutionary traits. Understanding how these traits mediate species' responses is beneficial for identifying more vulnerable species or prone to extinction risk. Here, we carried out a literature review describing how four traits commonly used in vulnerability assessments (i.e. clutch size, diet breadth, dispersal ability, and climatic tolerance) may determine species vulnerability. We also portray the possible mechanisms that explain how these traits govern species responses to climate change. The literature suggests different mechanisms operating for the evaluated traits. The mechanism of response to climate change differs between species inhabiting tropical and temperate regions: while species from the temperate areas may respond positively to temperature rise, tropical species may be severely affected. Since ectotherms depend on environment temperature, they are more sensitive and present different response mechanisms from endotherms.
Keywords: *Global warming; extinction risk; phenology; physiology; species traits.*

Em busca de mecanismos sintéticos sobre como os atributos biológicos mediam as respostas das espécies às mudanças climáticas

Resumo: A mudança climática provavelmente será o maior desafio enfrentado pelas espécies neste século e a capacidade das espécies em lidar com a mudança climática depende de seus próprios atributos de história de vida, ecológicos e evolutivos. Entender como esses atributos mediam as respostas das espécies é extremamente útil para identificar espécies que são mais vulneráveis ou sujeitas ao risco de extinção. Aqui, realizamos uma revisão da literatura com foco na descrição de como quatro atributos comumente usados em avaliações de vulnerabilidade (tamanho da ninhada, amplitude da dieta, capacidade de dispersão e tolerância climática) podem realmente determinar a vulnerabilidade das espécies. Também retratamos os possíveis mecanismos que explicam como esses atributos governam as respostas das espécies à mudança climática. A literatura sugere diferentes mecanismos operando para os atributos avaliados. O mecanismo de resposta à mudança climática difere entre as espécies que habitam as regiões tropicais e temperadas: enquanto as espécies das regiões temperadas podem responder positivamente ao aumento da temperatura, as espécies tropicais podem ser severamente afetadas. Como os ectotérmicos dependem da temperatura ambiente, eles são mais sensíveis e apresentam mecanismos de resposta diferentes dos endotérmicos.
Palavras-chave: *Aquecimento global; risco de extinção; fenologia; fisiologia; atributos das espécies.*

Introduction

Climate change will likely be the most significant challenge faced by species this century. The observed effects include changes in distribution areas, phenology, morphology, demography, and abundance (Parmesan and Yohe 2003; Parmesan 2006; Lane et al. 2012). Species ability to respond to climate change depends on their life-history traits (Végvári et al. 2010; Angert et al. 2011; Pacifici et al. 2017), which can help predict species that will be more vulnerable and direct conservation efforts (Foden et al. 2013).

In this sense, the use of trait-based Climate Change Vulnerability Assessments (CCVAs) has become popular in studies that assess climate change impact on species vulnerability (Foden et al. 2018). In the context of CCVAs, the term "trait" refers to a wide range of species characteristics (such as diet breadth and climatic tolerance) instead of referring to specific features of an individual (*sensu* Violle et al. 2007). Trait-based CCVAs combine scores based on exposure to climate change (extrinsic factors) with biological characteristics of species (intrinsic factors), which define their sensitivity and adaptive capacity to obtain a general measure of vulnerability (Pacifici et al. 2015).

Vulnerability is assessed based on these three components: exposure, sensitivity, and adaptive capacity, so that species with high exposure, high sensitivity, and low adaptive capacity will be the most vulnerable to climate change (Dawson et al. 2011; Foden et al. 2013). Exposure is determined by the rate and magnitude of climate change within the species' distribution area. Sensitivity is characterised by the ability to tolerate climate change and is generally associated with physiological tolerance and habitat specialisation. Adaptive capacity refers to the ability of a given species to deal with climate change, whether adapting to new local conditions or dispersing to more suitable areas (Dawson et al. 2011).

Despite the importance of biological traits in determining species vulnerability, there is no agreement on which traits should be used in assessments. Their selection depends on data availability and the opinion of experts (Foden et al. 2013, 2018). Biological traits may help identify species with higher extinction risk (Mckinney 1997; Purvis and Hector 2000). However, species responses depend on the type of threat they are exposed to (González-Suarez et al. 2013). Species that present larger body size is more threatened by hunting, while smaller and ecologically specialised species are more threatened by habitat loss and fragmentation (Owens and Bennett 2000; González-Suarez et al. 2013).

Under the threat of climate change, biological traits might play a fundamental role in species responses, influencing their vulnerability (Jiguet et al. 2007; Angert et al. 2011; Estrada et al. 2015). Clutch size is strongly influenced by climatic variables (Jetz et al. 2008), and species may present rapid physiological adjustments of this trait in response to climatic changes (Baker 1995; Coe and Rotenberry 2003). Species that reproduce frequently or prematurely, with high fecundity, should have greater opportunities to colonise new environments (Angert et al. 2011). Species with generalist diets can change their feeding habits to other resources when climate affects the availability of preferred items (Rubolini et al. 2003; Bojarska and Selva 2012) and, consequently, they might have a higher ability to change their distributions to follow suitable climatic conditions (Angert et al. 2011). Dispersal ability is a crucial trait that allows species to change their distribution areas to follow a suitable climate. Species with higher dispersal ability might respond more quickly to climate change, facing lower extinction

risk (Pöyry et al. 2009; Corlett and Westcott 2013). Species that can physiologically tolerate higher climatic variation and live in environments where temperatures are far from their upper thermal limit will be more likely to persist under climate change (Deutsch et al. 2008; Huey et al. 2012). There is a growing interest in using biological traits to assess species vulnerability in response to climate change (Gardali et al. 2012; Foden et al. 2013; Garcia et al. 2014; Böhm et al. 2016; Reside et al. 2016; Borges et al. 2019). However, potentially important traits from some taxa are still frequently unavailable, which leads to the use of morphological proxies, measurements from congeneric species or the knowledge of experts (Foden et al. 2013, 2018).

Identifying the most informative traits and responding to climate change is a priority if we want to assess the vulnerability of different species groups. However, a study showed that less than half of the studies that evaluated the relationship between traits and changes in species distributions have specified hypothesis for the ecological processes involved in the relationship (Estrada et al. 2016). To advise appropriate conservation measures, it is essential to explain the reasons for choosing traits and the specific mechanisms underlying climate change impacts on species of interest (Foden et al. 2018).

We did a literature review to understand how four traits (clutch size, diet breadth, dispersal ability and climatic tolerance) might determine species vulnerability. We also aimed to describe the possible mechanisms that explain how traits influence species responses to climatic changes. Specifically, our goals were: 1) to verify whether it is possible to use the four chosen traits to understand the mechanisms underlying the impacts caused by climate change based on the ecology literature produced so far, and 2) to present and explain the main mechanisms found. Including details regarding these mechanisms will help substantiate trait choice and broaden the discussion about future conservation strategies of assessed species.

Material and Methods

We searched the literature for studies that evaluated variation in the four traits mentioned earlier in response to recent climate change regarding organisms from any taxa within any level (population, community, and ecosystem). We chose these four traits because they are commonly used in CCVAs (Gardali et al. 2012; Reside et al. 2016; Borges et al. 2019) and are more widely available in the literature. As the study's objective was to present a broad discussion for each trait, more traits would excessively increase the number of pages in the study. The search was carried out in July 2019 in the Thomson Reuters ISI Web of Science online database. It included articles published between 1945 and 2019, using the following search terms: ("trait" OR "clutch size" OR "diet" OR "dispersion" OR "climatic tolerance" OR "thermic tolerance" OR "heat tolerance") AND ("climate change" OR "global warming" OR "temperature increase").

We excluded studies that: (1) belonged to Web of Science categories not related to ecology (*e.g.* agronomy, veterinary medicine, tropical medicine), (2) did not relate (directly or indirectly) possible trait changes to climate change, and (3) did not present any explanation (through empirical data) to the mechanisms involved in the observed responses (*e.g.* changes in distribution areas, phenology and abundance). Studies cited by the articles obtained in our search were also included in our synthetic review if they fulfilled the requirements. The search

generated a total of 1164 articles. After the exclusions following the criteria mentioned above, 197 articles were evaluated.

Results and Discussion

1. Clutch size

Clutch size is one of the best-studied life-history traits in birds, and its variation throughout the latitude gradient is well known, with larger clutch size in higher latitudes (Lack 1947; Skutch 1949; Ashmole 1963; Ricklefs 1980; Evans et al. 2005; Jetz et al. 2008). As expected, studies that assess clutch size are focused on birds and have been carried out mainly in the temperate region (Table 1). Birds that inhabit temperate and tropical areas adopt different life-history strategies to respond to climate change through other mechanisms (Table 1).

Clutch size is related to species fecundity; thus, it indicates the population ability to recruit. Species with smaller clutch size present low reproductive potential and consequently a slower response to risk factors, which would make them more vulnerable to decline and extinction (Smith and Quin 1996; Pimm 1991; Hero et al. 2005). On the other hand, species with larger clutch size may present a higher ability to respond to climate change, for they present shorter life cycles (Mckinney 1997). Larger clutch size is related to the probability of occupying broader geographic areas, higher dispersal ability and higher ability to colonise changing habitats and explore new opportunities (Duncan et al. 2001; Hero et al. 2005).

Some studies have found a significant relationship between clutch size and environmental variables. In temperate regions (with severe winter), studies with birds have shown that temperature increases have led to larger clutch sizes (Jarvinen 1996; Przybylo et al. 2000; Møller 2002; Husek and Adamík 2008; Table 1). The mechanism involved in this physiological adjustment seems to be related to resource availability. In these regions, the cold climate imposes food shortage (Jarvinen

1986, 1996), and higher temperatures lead to higher food availability, allowing species to have a higher number of broods. Annual variation in temperature, which reflects the seasonality of resources, was the most crucial variable to explain clutch size in a global assessment (Jetz et al. 2008). For example, the clutch size of owls in Finland is strongly determined by the abundance of their prey (voles): warmer years, with thinner snow cover, favour a higher abundance of voles, allowing larger clutch size (Lehikoinen et al. 2011). Such a positive relationship between food availability and mean clutch size in birds is well-known (Lack 1947; Price 1985; Gibbs and Grant 1987). Correlation between clutch size and climatic variables was also confirmed for other groups such as lizards (Smith et al. 1995; Abell 1999) and butterflies (Karlsson and Wiklund 2005; Saastamoinen 2007). In this sense, for species that live in temperate regions, where the cold is a limiting factor for population regulation, climate change may positively impact environmental conditions, increase resource availability, and allow larger clutch size.

In the tropical region, resource seasonality is less intense, and the reproductive season is longer, which allow species to attempt reproduction more frequently per season (Martin, 1996). A higher number of attempts to reproduce may lead to smaller clutch size, as the parents need to save energy to invest in the next clutch (Slagsvold 1984; Farnsworth and Simons 2001). This seems to be a good strategy in the tropics since nest predation is higher than in the temperate region, which would allow the spread of predation risk in numerous reproduction attempts (Cody 1966; Kulesza 1990; Martin 1995; Griebeler et al. 2010; Table1). If clutch size depends on nest predation rate, as proposed by Skutch (1949), if larger broods attract more predators, natural selection will favour smaller clutch sizes in the tropics (Martin et al. 2000). Considering that, a possible consequence of climate change to species that inhabit the tropics is that temperature increase and rainfall decrease might shorten the reproductive season, leading to a reduction in the number of reproduction attempts, which could force species to compensate by increasing clutch size (Lovette and Fitzpatrick 2016).

Table 1. Possible mechanisms that explain how clutch size may influence species responses to climate change and their respective studies.

Pattern	Mechanism	Reference	Taxon	Location
In temperate and boreal regions, temperature increase may favour larger clutches	In cold regions, temperature increase leads to abundance of feeding resources	Jarvinen, 1996	Bird	Finland
		Przybylo et al., 2000	Bird	Sweden
		Moller, 2002	Bird	Denmark
		Husek and Adamik, 2008	Bird	Czech Republic
In the tropics, temperature increase and rainfall decrease may shorten reproductive season, decreasing the number of reproduction attempts and consequently reproductive success	In the tropics, reproductive season is longer and species may have more clutches with fewer eggs to spread predation risk, which is high.	Skutch, 1949	Bird	Central America
		Cody, 1966	Bird	Global
		Slagsvold, 1984	Bird	Norway
		Kulesza, 1990	Bird	Americas
		Martin, 1995	Bird	North America
		Martin, 2000	Bird	America
		Farnsworth and Simons, 2001	Bird	Theoretical model
		Griebeler et al., 2010	Bird	Theoretical model
Aridity may lead to reduction of clutch size	Lack of water may jeopardise egg production	Grant et al., 2000	Bird	Galápagos islands
		Coe and Rotenberry, 2003	Bird	Mojave desert
In the tropics, temperature increase may reduce viability of the first eggs	Temperatures higher than 24-26ºC induce embryonic development before incubation	Deeming and Ferguson, 1992	Bird and reptile	Theoretical model
		Stoleson, 1999	Bird	Venezuela
		Stoleson and Beissinger, 1999	Bird	Venezuela

That would represent a risk for species since the tropics nest predation rate is relatively high, reaching 80-90% (revised by Stutchbury and Morton 2001).

In regions where climate change will cause temperature increase and significant rainfall decrease, making the areas arider, species tend to reduce the clutch size (Grant et al. 2000; Coe and Rotenberry 2003; Table 1). A study in the California desert has shown that, in territories that received water supplementation (treatment), a desert sparrow had a significantly larger clutch size than in non-supplemented territories (control) (Coe and Rotenberry 2003). This result shows that environment variables have an indirect effect (regulating food availability) and act directly on physiology, so that supplemented females can allocate more water to egg production. During the reproductive period, females need a significantly higher amount of water to produce eggs since they contain a high percentage of water (Bartholomew and Cade 1963; Reynolds and Waldron 1999).

Another hypothesis used to explain smaller clutch size in the tropical region than the temperate region is the egg-viability hypothesis (Stoleson and Beissinger 1999; Table 1). According to this hypothesis, in the tropics, where the temperature is higher, extended exposure of the eggs to temperatures higher than 24-26ºC (physiological zero) may trigger embryonic development even when the eggs are not incubated. Such premature development of the embryos below optimum incubation temperature (36-38ºC) results in abnormal growth of some tissues and consequent embryo death (Deeming and Ferguson 1992; Stoleson 1999). Therefore, birds that live in the tropics may lay smaller clutches to start active incubation earlier to keep the viability of the first eggs instead of waiting until many eggs are laid (Stoleson and Beissinger 1999). Based on this hypothesis, in a scenario of temperature increase, it is expected that species initiate incubation earlier and earlier to avoid loss of the first eggs, which can lead to smaller clutch size, since premature incubation or contact with the eggs may interrupt follicular growth and egg-laying (Haywood 1993).

Available evidence shows that species can adjust to climate change through phenotypic plasticity instead of altering their genetic constitution through microevolutionary adaptation (Gienapp et al. 2008). There seems to be low, or no additive genetic variation to clutch size and most intrapopulation variation is due to transitory environmental effects (Gibbs 1988). Species may present fast physiologic responses adjusting the clutch size to environmental changes (Gibbs 1988; Baker 1995; Coe and Rotenberry 2003). For example, the mean clutch size for sparrows in New York was 4.7 eggs, while in Costa Rica, it was two eggs (reviews in Baker 1995). When sparrows captured in Costa Rica were raised in aviaries in New York, their clutch size was 3.50 (+ 0.46) eggs in the first year and 4.62 (+ 0.55) in the second year. Sparrows from New York raised in nearby aviaries under the same feeding conditions, and same pressures had a mean clutch size of 4.89 (+ 0.48) eggs (Baker 1995). This example shows that species do not need several generations to adjust their clutch size to climatic conditions. Therefore, negative impacts on species that will be forced to reduce their clutch size, such as low population recruitment, could occur at a somewhat accelerated pace, thus increasing their vulnerability.

2. Diet breadth

In general, studies that assess climatic effects on diet are not focused on a specific taxon, but there is a prevalence of studies with vertebrates living in the temperate region (Table 2). Diet is an important trait that summarises distinct morphological, physiological and behavioural characteristics of a given organism, determining how it interacts with the biotic and abiotic environments (Donnell et al. 2012; Abrahamczyk and Kessler 2014). It is expected that species with specialised diets present narrow niches, low local abundance and restricted geographic distribution (Mckinney 1997). On the other hand, generalist species have flexible behaviour and can change their feeding habits to adapt to changes in resource availability (O'Donoghue et al. 1998). Therefore, the diet breadth of a given species may influence its extinction risk

Table 2. Possible mechanisms that explain how diet may influence species responses to climate change and their respective studies.

Pattern	Mechanism	Reference	Taxon	Location
Climate change may alter resource availability to species in the environment.	Generalists may increase the diversity of ingested items to include new options when their preferred resources are scarce	Folks et al. 2014	Mammal	Texas, USA
		Gray et a. 2016	Mammal	Australia
		Robinson et al. 2018	Mammal	California, USA
		Rubolini et al. 2003	Bird	Northern Italy
		Bojarska and Selva 2012	Mammal	Holarctic
	There might be population decline when preferred food items are scarce	Pearce-Higgins et al. 2010	Bird	United Kingdom
		Fancourt et al. 2018	Mammal	Tasmania
		Víkingsson et al. 2014	Aquatic mammal	Iceland coast
Climate change may force species to alter their phenology and distribution	Species with more flexible diets can change their phenology more easily to follow modifications induced by the climate.	Altermatt 2010	Lepidoptera	Central Europe
	Generalist species can easily change their distribution areas following climate change	Braschler and Hill 2007	Lepidoptera	Great Britain
		Angert et al. 2011	Bird	North America
Alter omnivore diets	In higher temperatures, animals increase herbivory to maximise energy intake	Floeter et al. 2005	Sea fish	Atlantic ocean
		Boersma et al. 2016	Copepoda	North Sea
		Carreira et al. 2016	Tadpole	Iberian Peninsula
		Espinoza et al. 2004	Reptile	South America
		Clarke and O'Connor 2014	Bird and mammal	Global

(Boyles and Storm 2007). Species with a more specialised diet are associated with higher probabilities of negative response to climate change (Pacifici et al. 2017). We will discuss three main mechanisms species may respond to climate change through their diets (Table 2).

Climate change may affect the availability of feeding resources. In regions where these resources will decrease, species with specialised diets will become more sensitive, presenting a higher extinction risk than generalist species (Chessman 2013). Species with broader diet breadth can avoid hunger by changing their diet to the available food item during adverse climatic conditions (Brändle et al. 2002). Such plasticity in the diet is a mechanism that has allowed species to deal with climate-related fluctuations in availability and abundance of resources (Furness 1996; Ancona et al. 2012). Generalist species can increase diet diversity in response to unfavourable changes in the weather when their preferred resources are scarce. They are led to supplement their diets with available resources at the moment (Folks et al. 2014; Gray et al. 2016; Table 2). For example, temperature increase in North Pacific waters alters the availability of sea lion preys, making them change their diet, increasing the diversity of consumed preys (Robinson et al. 2018). In Northern Italy, owls have become more generalist under adverse climatic conditions: increased rainfall and decreased temperature increased the breadth of owls' diets. (Rubolini et al. 2003). Alternatively, species with specialised diets may not respond to resource fluctuation and therefore experience higher extinction risk. For mountain birds, temperature increase can result in population decrease caused by the abundance of preys, insects from the Tipulidae family adapted to cold weather (Pearce-Higgins 2010). Temperature and rainfall increase during winter caused a significant decrease in the Eastern quoll population due to a reduction in the abundance of moth larvae (Fancourt et al. 2018).

Diet type may influence species ability to change their phenologic events (Altermatt 2010) and their distribution area (Angert et al. 2011) to follow climate change. Species that are not able to change their distribution areas fast enough to follow their adequate climatic conditions are at higher risk of extinction (Devictor et al. 2008), as well as those species that cannot change phenology to match species that they depend on for survival (Visser and Both 2005). Generally, diet generalists are expected to be more likely to find adequate resources in new areas. They should, therefore, present a greater ability to change their distributions than specialists, which could be more limited by the phenology of species they depend on (Angert et al. 2011; Buckley and Kingsolver 2012). Broader diets can facilitate the expansion of distribution areas driven by climate (Braschler and Hill 2007) and the establishment and persistence of species in new environments (Estrada et al. 2016). However, a specialist may have a greater probability of following spatial changes if its host species or prey also changes (Betzholtz et al. 2013; Auer and King 2014). Generally, diet specialists could be more affected by climate change since they present narrower distribution, are less likely to leave their habitats (Caldas 2014) and alter their phenologic events (Altermatt 2010) to track adequate climatic conditions.

The temperature increase may cause omnivore species to change their diet, becoming more herbivores and fewer carnivores (Table 2). For ectotherms, low body temperature makes herbivory energetically unfavourable, as it constrains the rate at which energy can be extracted from the diet (Floeter et al. 2005; Boersma et al. 2016). For marine herbivorous fishes, herbivory is only possible above a threshold of 15°C

(Floeter et al. 2005). There seems to be a consensus that due to better digestion of vegetal material at high temperatures, ectotherms might maximise energy intake and maintain high metabolic rates in higher temperatures by increasing herbivory (Carreira et al. 2016). This idea is supported by studies that have found that herbivory increases in response to higher temperatures in several groups, such as Copepoda (Boersma et al. 2016), fish (Floeter et al. 2005), tadpoles (Carreira et al. 2016) and reptiles (Espinoza et al. 2004). Even amongst endotherms, herbivores maintain higher body temperature than carnivores (Clarke and O'Connor 2014). Although omnivores can regulate their diet to deal with temperature increase caused by climate change, changing to a more herbivore diet and its adaptive value is variable among species (Carreira et al. 2016). Besides, an increase in herbivory in response to global warming can alter food chains, species interactions, and ecosystems' functioning.

3. Dispersal ability

Birds and lepidopterans are the best-represented taxa in studies regarding climatic effects on dispersal ability, and no studies were carried out in the tropical region (Table 3). Understanding species ability to respond to climate change is a fundamental point to identify species that experience higher risk (Møller et al. 2008; Hurlbert and Liang 2012). Species that cannot change their annual cycles and their distributions to follow their suitable climatic conditions will be prone to higher extinction risk (Møller et al. 2008; Corlett and Westcott 2013). In this sense, dispersal ability is a crucial attribute for species. It is expected that those with higher dispersal ability respond more quickly to climate change, presenting lower extinction risk (Pöyry et al. 2009; Angert et al. 2011).

Climate change can affect the dispersal processes of organisms both directly and indirectly (Travis et al. 2013; Table 3). Indirect mechanisms (e.g. altering resource availability and climatic suitability of the habitat) may lead species to change their distribution areas. Their annual cycles will be discussed in the following paragraphs (Table 3). On the other hand, climate change may directly interfere with behaviour, affecting the organisms' decisions to stimulate or inhibit dispersal (Table 3). Higher temperatures increase the dispersal of moths (Battisti et al. 2006), butterflies (Cormont et al. 2011) and birds (Møller et al. 2006) and decrease dispersal of lizards (Massot et al. 2008). Flooding increases the dispersal of an aquatic bird in Canada (Roche et al. 2012), and the reduction of snow cover decreases the dispersal of wolverines in the USA (Schwartz et al. 2009). These examples indicate that climatic variables may increase or reduce dispersal depending on the system and the species (Travis et al. 2013). Moreover, species response may depend on weather and landscape configuration (Delattre et al. 2013). In more fragmented landscapes, dispersal distance is longer at lower temperatures, while in continuous landscapes, dispersal distance is longer at higher temperatures.

Recent climate change is quickly altering the location of areas with a suitable climate for certain species (Loarie et al. 2009). To survive, species must move fast enough to follow such changes (Chen et al. 2011; Lenoir and Svenning 2015). Therefore, as expected for the future, climate change might be a significant threat to species persistence since rates of distribution changes should be much higher than those observed in the past (Williams and Blois 2018). Some studies show that many organisms will not be able to disperse fast enough to follow their climatic

Table 3. Effects and possible mechanisms that explain how dispersal influences species responses to climate change and their respective studies.

Effect	Pattern	Mechanism	Reference	Taxon	Location
Direct	Affecting decision to disperse	Increasing/ stimulating dispersion	Battisti et al. 2006	Moth	Europe
			Cormont et al. 2011	Butterfly	Netherlands
			Roche et al. 2012	Bird	Canada
			Møller et al. 2006	Bird	Denmark
			Pärn et al. 2012	Bird	Norway
			Delattre et al. 2013	Butterfly	France
		Decreasing/ inhibiting dispersion	Schwartz et al. 2009	Mammal	USA
			Massot et al. 2008	Lizzard	France
			Bullock et al. 2012	Plant	Great Britain
Indirect	Changing the distribution area	Higher dispersal ability, higher probability of tracking suitable environmental conditions	Pöyry et al. 2009	Butterfly	Finland
			Angert et al. 2011	Plant	Switzerland
			Hill et al. 2002	Butterfly	Great Britain
			Warren et al. 2001	Butterfly	Great Britain
			Krause et al. 2015	Plant	USA
			Methorst et al. 2017	Bird	Palearctic
			Williams and Blois 2018	Mammal	North America
	Changing phenological responses	Short-distance migrants respond more quickly to climate change than long-distance migrants.	Butler 2003	Bird	North America
			Swanson and Palmer 2009	Bird	USA
			Tryjanowski et al. 2002	Bird	Poland
			Tøttrup et al. 2010	Bird	Europe
			Hurlbert and Liang 2012	Bird	North America
			Rubolini et al. 2010	Bird	Germany
			Végvári et al. 2010	Bird	Europe
			Rubolini et al. 2007	Bird	Europe
			Thorup et al. 2007	Bird	Europe

niches, even highly mobile species (Pearson 2006; Devictor et al. 2008, 2012; Schloss et al. 2012). Species with low dispersal ability might lose significant parts of their distribution areas in the future (Krause et al. 2015), hence facing higher extinction risk (Pearson 2006; Corlett and Westcott 2013). Therefore, dispersal ability is a good predictor of species vulnerability to climate change. Both empirical observations (Warren et al. 2001; Hill et al. 2002; Pöyry et al. 2009; Angert et al. 2011) and model projections (Krause et al. 2015; Methorst et al. 2017; Williams and Blois 2018) evidence that higher dispersal ability indicates higher ability to change distribution to follow climate displacement (Table 3).

Recent global warming has already caused significant changes in many species' life cycles (Walther et al. 2002; Parmesan and Yohe 2003). Generally, plants and animals have advanced their phenologies in response to temperature increase (Parmesan and Yohe 2003; Parmesan 2006). However, consumers and predators at higher trophic levels in the food chain might not respond in the same proportion, leading to a mismatch between reproductive period and resource availability (Visser et al. 1998, 2004; Visser and Both 2005). Species that cannot advance their arrival to reproduction sites to match the peak of food abundance may suffer population declines and, consequently, be more prone to extinction (Both et al. 2006; Møller et al. 2008).

Migratory birds should advance the beginning of the migration to follow the phenology of plants and invertebrates in their reproduction areas (Sparks et al. 2005). Indeed, as a response to temperature increase in the last years, migratory birds have arrived earlier in their reproduction sites (Butler 2003; Hurlbert and Liang 2012). However, literature shows that long-distance migrants cannot respond to climatic change as quickly as short-distance migrants do and arrive later (Table 3). This happens because long-distance migrants experience slower temperature increase in wintering areas than their reproduction areas, while short-distance migrants are exposed to warm weather throughout the year (Lehikoinen et al. 2004). Therefore, short-distance migrants have more and better cues to match their phenology with resource phenology (Jones and Cresswell 2010). Thus, long-distance migratory behaviour can represent an essential constraint to responses to climate change, contributing to the decline of some species (Berthold et al. 1998; Møller et al. 2008; Jones and Cresswell 2010; Rubolini et al. 2010).

4. Climatic tolerance

Studies assessing species climatic tolerance are focused on ectotherms, and most of them were carried out on a global scale (Table 4). Tolerance to climatic conditions is one of the most critical factors determining how species are distributed around the globe (Thomas 2010). A variation in climatic tolerance among species is an important characteristic to determine their responses to climate change, as it can alter distribution and survival (Deutsch et al. 2008; Huey et al. 2012; Caldwell et al. 2015; Rugiu et al. 2018). Species with higher thermic tolerance occupy broader geographic areas (Bozinovic et al.

2011) and will deal better with global warming (Calosi et al. 2008; Buckley et al. 2012; Huey et al. 2012). In general, the thermic tolerance of an organism is proportional to the magnitude of temperature variation experienced in its habitat, steeply increasing with latitude (Deutsch et al. 2008). Thus, species from the tropics, which inhabit environments with lower temperature variation throughout the year, have narrower thermic tolerance than species from temperate regions (Deutsch et al. 2008; Huey et al. 2009, 2012; Duarte et al. 2012; Khaliq et al. 2014; Table 4). Deutsch et al. (2008) have reported that heat tolerance in tropical insects is, on average, only one-fifth of the tolerance of insect species from temperate regions. Besides that, tropical species already live in warmer environments, close to their critical temperature, compared to species from the temperate areas, which live in colder environments, far from their critical temperature (Sunday et al. 2012; Araújo et al. 2013; Khaliq et al. 2014). Therefore, even slight temperature increases might be a threat to tropical species.

Heat tolerance is more conserved amongst lineages than cold tolerance, implying that many species might have lost their evolutionary potential to respond to global warming (Addo-Bediako et al. 2000; Huey et al. 2009; Araújo et al. 2013). When organisms are exposed to temperatures close to their upper thermal limit, biological activity suffers from several limitations and might compromise survival (Somero 2011). Furthermore, it is unlikely that species can persist under conditions that surpass their physiological tolerance limits (Calosi et al. 2010). Thus, climatic conditions expected in the future might negatively affect population abundance and potentially compromise their persistence (Rugiu et al. 2018). However, while tropical species might be severely affected, species from temperate regions might benefit from temperature increase, responding with higher population growth rates and aptitude (Deutsch et al. 2008; Caldwell et al. 2015; Carrascal et al. 2016; Table 4).

Such pattern of greater physiological vulnerability to climatic changes in tropical species, when compared to species from temperate areas, has been shown to ectotherms, especially reptiles (Deutsch et al. 2008; Tewksbury et al. 2008; Huey et al. 2009, 2010; Diamond et al. 2012; Duarte et al. 2012; Sunday et al. 2012; Hoffmann et al. 2013; Caldwell et al. 2015). For endotherms, on the other hand, the relationship between higher thermic tolerance in species that experience higher climatic variability was observed in birds but not in mammals (Khaliq et al. 2014). Even though most ectotherms, particularly those from the temperate region, might tolerate projected temperature increases across significant ranges of their distributions, potential vulnerability to projected temperatures increases from polar regions to tropical areas (Khaliq et al. 2014). Unlike the observed pattern for ectotherms (Addo-Bediako et al. 2000; Deutsch et al. 2008), endotherms present low phylogenetic conservatism regarding climatic tolerance to respond to temperature increase through physiological adaptation (Khaliq et al. 2015). In temperate regions, endotherms distribution is limited by extremes of low temperature via physiological cold tolerance of species (Khaliq et al. 2017). Global warming scenarios might benefit species living in those regions, increasing their abundance (Carrascal et al. 2016). In the tropics, endotherms (especially mammals) seem limited by other factors, such as biotic interactions, rather than climatic conditions (Khaliq et al. 2017).

Overall, species that present the lowest climatic tolerances will be more affected by climate change. Species from the tropical region and mainly ectotherms will be more vulnerable to projected temperature increases in the future (Table 4). Endotherms can keep high and constant body temperature, which is generally independent of ambient climatic conditions (MacNab 2012). On the other hand, ectotherms might be more vulnerable as their physiology, locomotion, growth and

Table 4. Possible mechanisms that explain how climatic tolerance may influence species responses to climate change and their respective studies.

Pattern	Mechanisms	Reference	Taxon	Location
Species from tropical regions are more vulnerable to climatic change than species from temperate regions	Species from tropical regions have narrower thermic tolerance and live in environments where the temperature is close to their upper thermal limit	Deutsch et al. 2008	Ectotherms	Global
		Tewksbury et al. 2008	Lizard	Global
		Huey et al. 2009	Lizard	Neotropics
		Sunday et al. 2012	Ectotherms	Global
		Huey et al. 2012	Ectotherms and endotherms	Global
		Diamond et al. 2012	Ant	Global
		Hoffmann et al. 2013	Ectotherms	Global
		Khaliq et al. 2014	Bird and mammal	Global
		Caldwell et al. 2015	Lizard	Tasmania
Species from temperate regions are less vulnerable and may benefit from climate change	Species present broader thermic tolerance and live in environments where the temperature is far from their upper limits	Deutsch et al. 2008	Ectotherms	Global
		Sunday et al. 2012	Ectotherms	Global
		Huey et al. 2012	Ectotherms and endotherms	Global
		Khaliq et al. 2014	Bird and mammal	Global
		Caldwell et al. 2015	Lizard	Tasmania
		Carrascal et al. 2016	Bird	Spain
Ectotherms are more vulnerable to climate change than endotherms	Ectotherms present higher niche conservatism and lower capacity to adjust their physiology	Addo-Bediako et al. 2000	Insect	Global
		Deutsch et al. 2008	Ectotherms	Global
		Sinervo et al. 2010	Lizard	Mexico
		Khaliq et al. 2015	Bird and mammal	Global
		Khaliq et al. 2017	Bird and mammal	Global

reproduction are strongly influenced by ambient temperature (Deutsch et al. 2008). Moreover, warmer temperatures may force ectotherms to spend more time in shelters to avoid lethally high temperatures, restricting the time available for other vital activities such as foraging, territory defence and mating (Sinervo et al. 2010). Due to their low ability to respond to climate change, several ectotherm populations were locally extinct in recent decades, and temperature increase might lead to the extinction of almost 40% of lizard populations and 20% of lizard species globally 2080 (Sinervo et al. 2010).

Conclusions

Overall, the literature review performed regarding the four chosen traits enabled us to present and discuss mechanisms that might explain species responses to climate change. As shown here, response to climate change is highly variable among species and regions. Some species may exhibit a critical response to a specific climate variable. In contrast, others may have a minimal response, and some might even present a contradictory response from what is expected, depending on the region they inhabit. Explaining such variation has become a significant challenge to conservationists in this century. Such explanation would allow the identification of species at higher extinction risk, the definition of the best conservation strategies, and the resources' strategic direction. It was also possible to verify bias concerning region and taxa in the evaluated studies. The tropical region, which holds more sensitive species, was weakly represented, while most studies have focused on the temperate region. For some traits, studies concentrate on a specific group and neglect others; for example, most studies assessing climatic tolerance have concentrated on reptiles.

Species exposed to a higher magnitude of climate warming should present more pronounced biological responses (Chen et al. 2011). However, intrinsic differences between species' life-history traits, physiology and other ecological characteristics are fundamental to determine their vulnerability (Williams et al. 2008; Foden et al. 2013). Assessments of climate change vulnerability that consider both exposure and traits that define sensitivity and adaptive ability could be helpful tools (Foden et al. 2013; Böhm et al. 2016). However, trait choice should be based on empirical evidence that shows the relevance of such traits in determining the vulnerability of assessed species.

This review shows that the four evaluated traits are significant predictors of species responses to climate change, and we present the main mechanisms involved in each response. Therefore, clutch size, diet breadth, dispersal ability and climatic tolerance are essential traits for vulnerability assessments. Even though some evidence might lead us to conclude that species with smaller clutch size, with specialised diets, low dispersal ability and lower climatic tolerance would experience higher risk due to climate change, the set of studies evaluated here indicates that the risk depends on the region and the species group considered. While species from the temperate region could benefit from temperature increase with greater resource availability, increasing clutch size and expanding the distribution area through dispersal, species from the tropics could be severely affected. They have lower climatic tolerance and already live close to their limits of heat tolerance. Vulnerability is higher for ectotherms because, unlike endotherms, they cannot control body temperature and their biological activities depend on the climatic conditions of the environment. Ectotherms from the tropical region

will not escape from temperature increase through dispersal (Buckley et al. 2013).

The lack of response in a trait may interfere with the response of another feature. In the temperate region, temperature increase causes advanced flowering in plants and an abundance of insects. Thus, birds that spend the winter in other areas should advance their arrival so that the reproductive period matches food availability. Species that cannot advance their arrival might face food scarcity during reproduction, leading to smaller clutch size. In the tropics, species present lower thermic tolerance, affecting their dispersal ability to follow suitable climatic conditions if they have to cross warmer areas.

As we understand the mechanisms involved in the response of other traits, we will enhance our ability to predict climate change impacts, enabling conservation practices that are more adequate to protect species. The increase of this type of studies could facilitate understanding which characteristics are more informative to each species group within each region. Besides that, understanding the mechanisms through which traits influence species responses to climatic changes may help justify the traits included in vulnerability assessments, improving their results and making them more useful. For that, CCVAs need to be more integrated with the ecology literature to assess how species traits respond to changes in the climate.

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Author Contributions

Fábio Júlio Alves Borges: Originally formulated the idea, performed the literature search, data analysis and wrote the first version of the manuscript.

Rafael Loyola: Commented and revised the manuscript, substantially improving the final version.

Conflict of Interest

The authors declare that they have no conflict of interest.

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