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ORIGINAL PAPER

On Madeira, the success of the speckled wood butterfly (*Pararge aegeria*) has coincided with declining populations of the Madeiran speckled wood (*Pararge xiphia*): is the colonist to blame?

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Abstract
The endemic Madeiran speckled wood butterfly (*Pararge xiphia*) was once abundant and widely distributed on the island of Madeira. Declining populations and a range contraction have coincided with the colonisation of Madeira by the speckled wood (*Pararge aegeria*). The colonist has expanded its range and increased in abundance, whereas the opposite is true for *P. xiphia,* where a decline in occurrence and abundance resulted in its current endangered designation. During 3 weeks in July and August of 2018, we assessed the relative abundance, distribution and habitat preferences of the *Pararge* species on Madeira on ten transects, at a range of locations and altitudes, recording all individuals of both species. In addition, we scored percentage cover of several habitat variables per 5-min periods of recording on each transect. Our findings support an ongoing decline in relative abundance of *P. xiphia*, which accounted for 25% of *Pararge* individuals in 2018 compared with historical date from 1986, when *P. xiphia* represented 78% of the *Pararge* population. The endemic species was associated with the native laurel forest and *P. aegeria* with non-native planted forests and agriculture. In addition, we found evidence for an altitudinal range-shift 'uphill' which was particularly evident in *P. aegeria*. Causal reasons for the decline of *P. xiphia* are difficult to pinpoint; however, we surmise that one or more, or a combination of factors ranging from interspecific competition, habitat loss and disturbance resulting from recent environmental events and parasitism may be accountable.

Keywords *Pararge* · Madeira · Competition · Climate change · Habitat loss · Parasitism

Introduction

The Madeiran speckled wood (*Pararge xiphia*) is endemic to Madeira and is one of the island's fourteen resident butterfly species (Owen and Smith 1993). The genus also includes the widely distributed speckled wood (*Pararge aegeria*) and the Canary Island endemic *Pararge xiphioides*.

There is evidence to suggest that the Madeiran speckled wood (*P. xiphia*) diverged first from the common ancestor a maximum of 5 million years ago, whereas *P. aegeria* and *P. xiphioides* diverged later and no more than 3 million years ago (Weingartner et al. 2006).

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In the mid-1970s, the speckled wood (*P. aegeria*) colonised Madeira (Higgins 1977; Oehmig 1977, 1982) from North Africa (Weingartner et al. 2006) and became well established on the island thereafter (Swash and Askew 1982; Oehmig 1982). To this day, Madeira continues to be the only place in the world where two *Pararge* species co-exist (Owen et al. 1986; Weingartner et al. 2006).

On Madeira, both species oviposit on the same host grasses (Gibbs et al. 2004b), notably *Brachypodium sylvaticum, Holcus lanais, Agrostis gigantea* and *Festuca donax* (van Swaay et al. 2010a, b; Aguiar and Karsholt 2006) and on occasion, eggs and larvae of both species are found together on the same plant (Lace pers obs.).

The eggs of the Madeiran speckled wood are larger than those of *P. aegeria* but *P. xiphia* may be less fecund. From data collected in situ on four visits to Madeira between 2000 and 2010 we found that *P. xiphia* females predominantly oviposit a single egg; we only found two instances where two eggs were laid together, and only a single record of a clutch of three eggs. Whereas for *P. aegeria*, although most

eggs were laid singularly, we recorded clutches of two eggs 23% of the time, and on six occasions a clutch size of three and twice a clutch size of four. The number of eggs counted for both species (from the combined studies) was 491; 393 (75%) of the eggs were assigned to *P. aegeria* and the remaining 98 eggs (25%) belonged to *P. xiphia* (Lace pers. obs., Gibbs 2004; O'Farrell 2006; Harris 2010).

Before *P. aegeria* colonised Madeira, the Madeiran speckled wood was reportedly abundant and widely distributed; evidence for this comes from historical records and specimens collected from low-lying southern coastal regions such as the town of Machico and the city of Funchal (Cockerell 1923; De Worms 1964; Wakeham-Dawson et al. 2002a).

Post-colonisation, however, *P. aegeria* has increased in abundance whilst the endemic is experiencing a range contraction and decrease in relative abundance (Lace and Jones 1984; Owen et al. 1986; Jones and Lace 1992). In 1986, Jones and Lace (1992) collected distributional data from twenty-two locations. They recorded highest densities of the colonist at lower elevations and found it to be mostly associated with the non-native plantations of eucalyptus and pine and in agricultural areas; *P. xiphia* was recorded at highest densities at mid to high altitudes and mostly within the native laurel forest. The native Laurisilva forest on Madeira is a mix of relict species from the tertiary such as the laurel (*Laurus azorica*), tree heather (*Erica arborea*) and chain fern (*Woodwadia radicans*) (Wakeham-Dawson et al. 2002b).

Declining populations (of 6 to 30%) and the limited extent of occurrence of *P. xiphia* has warranted a Red Listing status as endangered for the endemic speckled wood (van Swaay et al. 2010b).

The reasons for the decline of *P. xiphia* are unknown and largely speculative but there may be several contributory factors. For example, there is some evidence for interference competition amongst males. Male speckled wood butterflies defend 'sun spot' territories in order to increase their chances of mating where territorial males engage in spiraling flights with intruders (Davis 1978). On Madeira, Jones et al. (1998) recorded both intra and interspecific territorial disputes between male speckled wood butterflies. During these interactions, they found *P. aegeria* to be more aggressive engaging in prolonged spiraling flights, and significantly more likely to 'win' interspecific territorial contests.

Intraspecific competition, within the larvae, may also play a part in the endemic's decline. As both species use the same host-plants and have overlapping life histories, it is possible that *P. aegeria* and *P. xiphia* compete for access to resources at the larval stage (Jones et al. 1998; Owen et al. 1986). This competition may cause both species to disperse to new host-plants.

Gibbs et al. (2004b) found significant differences between the larvae of the two *Pararge* species in their success at locating new host plants. *Pararge xiphia* larvae spent significantly longer searching for host plants and were significantly less likely to locate plants than *P. aegeria*, which could infer a competitive advantage for the colonist.

The recent use of 'natural enemies' such as parasitoid wasps commonly used to combat arthropod pests are known to also parasitise non-target species. For example, the Hawaiian Islands and the island of Guam have experienced significant negative impact of alien parasites on native Lepidoptera (Lozan et al. 2008). Gibbs et al. (2004a) found eggs of both *Pararge* species collected from Madeira were parasitised by the chalcidoid wasp, *Trichogramma gicai.* This is the first known parasitoid of *P. xiphia*, and represents a significant geographical range expansion for *T. gicai.* The levels of parasitism were similar, at 25% for *P. xiphia* and 26% for *P. aegeria* but the consequences could be significant in the less fecund endemic species.

Pararge aegeria is a major model system for insect life history and ecology (Gibbs et al. 2004c; Weingartner et al. 2006). Madeira is the only place where two species of speckled wood co-exist, this provides an ideal opportunity to study the status of a species, which has successfully expanded its range, whilst monitoring the fate of a congeneric endemic species. We have compared our findings with historical data, some from the same locations, allowing an assessment of changes relating to relative abundance, distribution, habitat and altitudinal associations of the two species dating back to 1986.

Methods

We collected the data over 3 weeks from July 12 to 2 August 2018. We established ten transect routes at various locations and altitudes across the island. Five transects, at Ribeiro Frio; Fajã da Nogueira; Santa, Queimadas and Boca do Risco, have been censused on several previous occasions between 1986 and 2014. A further five transects were located at Palheiro Gardens; Camacha; Poiso; Portela and Curral das Freiras (Fig. 1). Many of our transect routes followed walking trails which run alongside levadas, man-made irrigation channels, built to move water from the wetter north side of the island to the drier south side. Although the selection of transects alongside levadas may be biased towards the observation of *P. aegeria* due to the species being more suited to open habitats than the endemic *P. xiphia,* this selection was necessary due to the difficulty of walking through mountain areas. Descriptions and details of each transect are cited in Appendix 1.

A modified 'Pollard walk' method (Pollard 1977; Pollard and Yates 1993) was employed to census the butterflies; we walked at a constant pace along a fixed route and recorded all speckled wood butterflies within 5 m either side of the

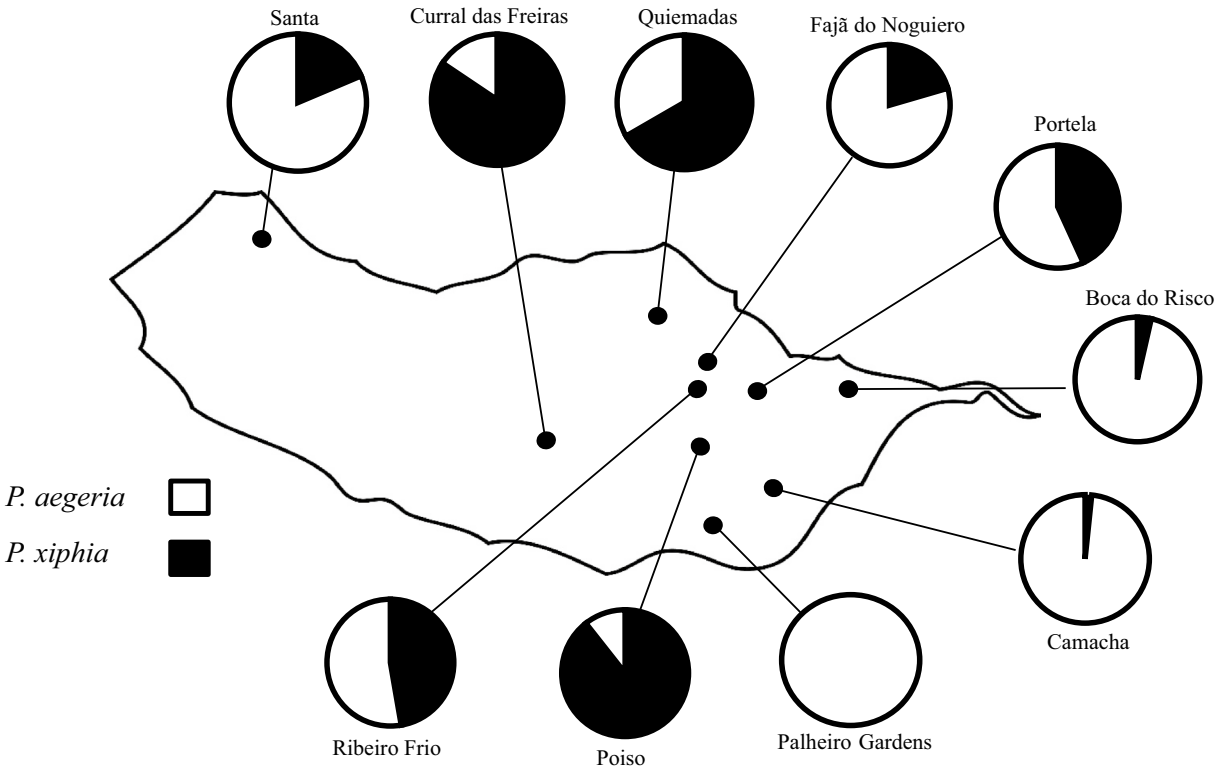

Fig. 1 Locations of the transects on Madeira and the relative abundance of the *Pararge* species

path and 5 m above and in front of the observer. The method requires the temperature to be above 13 °C and sunny, or above 17 °C if the conditions are cloudy. All our recordings took place at temperatures above 19 °C.

All individuals of both *Pararge* species were counted and the abundance of each species on each transect was recorded as the mean number of individuals per 5 min of walking. At each 5-min interval, the habitat was scored by estimating the percentage cover of laurel, pine or eucalyptus, tree heather (*Erica*), agriculture and housing/gardens. Although tree heather and laurel are both components of Laurisilva forest, they were defined separately as some areas are dominated by tree heather. Habitat variables were recorded as zero (0%), one (25%), two (50%), three (75%) or four (100%).

When calculating the densities for each of the speckled wood species in different habitats, only recording periods where the habitat score was a three or a four were included as a means of representing the dominant habitat type.

We noted the altitude of each transect and repeated each transect on more than one occasion when appropriate weather conditions and time permitted (see Appendix 1).

Results

A total of thirty-nine hours was spent walking transects; both species were recorded on all ten transects with the exception of Palheiro Gardens where only *P. aegeria* was encountered (Fig. 1). We counted 720 individual butterflies of both species across all ten transects; *P. aegeria* was recorded 537 times and *P. xiphia* 183 times. Proportionally, *P. xiphia* accounts for 25% of total observations in 2018, whereas in 1986, 78% of records were of the endemic species (Jones and Lace 1992). Over the course of the last 32 years, the relative abundance of *P. xiphia*, compared to *P. aegeria*, has declined dramatically and consistently. Data from the first 10 years (1986 to 1996) suggest a marginal decline, with the relative abundance of *P. xiphia* falling from 78 to 71%, whereas the last decade (2010 to 2018) indicate that the abundance of *P. xiphia* has more than halved, declining to 35% in 2010 and 25% in 2018 (Fig. 2).

In 2018 we found *P. aegeria* was the most abundant of the speckled wood species on seven of the ten transects; namely, Ribeiro Frio; Fajã do Nogueira; Santa, Boca do Risco; Portela; Camacha and Palheiro Gardens (Fig. 1). These are low to mid-altitude locations ranging from 300 to

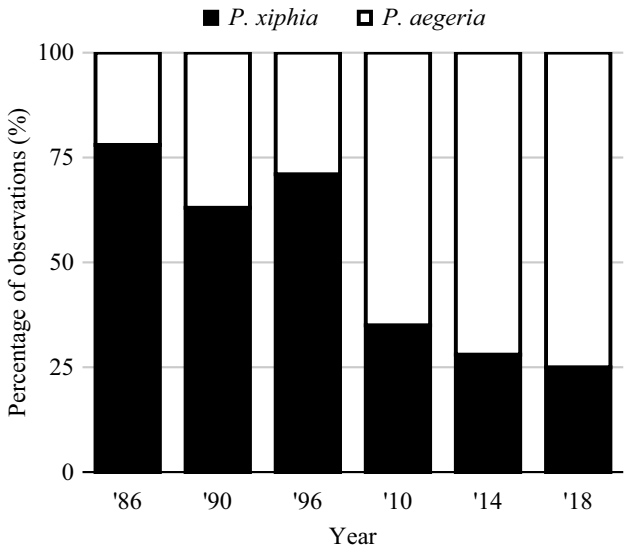

Fig. 2 The relative proportions of the *Pararge* species, shown as a percentage of the total count of individuals, recorded on six occasions from 1986 to 2018

800 m. *Pararge xiphia*, on the other hand, was the dominant species at the remaining three sites: Quiemadas; Curral das Freiras and Poiso (Fig. 1). The latter are locations at higher elevations, from 900 to 1100 m.

Changes in the relative abundance of the *Pararge* species, at five locations where transects have been repeated on six occasions between 1986 and 2018 are shown in Figs. 3 and 4. The most notable change is at Fajã do Nogueira, where *P. aegeria* accounted for 16% of the *Pararge* species recordings in 1986. By 2018, *P. aegeria* was the more abundant of the two species at this location accounting for 80% of *Pararge* observations (Fig. 3, Table 1).

We recorded *P. aegeria* at all altitudinal ranges surveyed (300 to 1100 m) with the highest mean densities recorded between 600 and 800 m (Fig. 5). We also recorded *P. xiphia* across the altitudinal range although it was far more prevalent at altitudes of 1000 m and above (Fig. 5). In 1986, the highest recorded densities of *P. aegeria* were at altitudes of 200 to 300 m and *P. xiphia* at 900 to 1000 m (Jones and Lace 1992). Particularly in the case of *P. aegeria*, which is the dominant species at these low (300 m) to mid-altitude (600 to 800 m) localities there is good evidence for a range shift 'uphill' during the past three decades.

The endemic speckled wood butterfly is most abundant in habitats where the native laurel vegetation and tree heather are dominant, whereas *P. aegeria* is still most frequently recorded in the planted eucalyptus forest and agriculture habitats (Table 2).

Discussion

We began monitoring the *Pararge* species in 1986, 10 years after the first record on Madeira of the European speckled wood (*P. aegeria*). The changing fortunes for the endemic species have seen the reduction in abundance, relative to the colonist, over the past four decades with the decline being most dramatic since 2010, with the endemic species reduced to a quarter of *Pararge* records. We have witnessed the demise of *P. xiphia* at five locations where we have made repeated surveys since 1986, whereas *P. aegeria* is clearly thriving, increasing in both abundance and range across the island. Despite its decline, the endemic speckled wood remains one of Madeira's most abundant species, a study in 2014 (Smith 2015) recorded the relative abundance of eleven of Madeira's resident butterflies and although *P. aegeria* accounted for almost half (49%) of all recorded individual butterflies, *P. xiphia* was the second most abundant of the eleven species, accounting for 19% of records.

We found *P. aegeria* to be the most abundant of the speckled wood species at all altitudes below 900 m, whereas locations at altitudes between 900 and 1100 m, such as Curral das Freiras and Poiso, we found *P. xiphia* to be the dominant species. These high-altitude sites tend also to correspond to those areas supporting the preferred habitat of *P. xiphia*, the native laurisilva and tree heather, now represent areas on Madeira where *P. xiphia* still has a stronghold.

A changing climate increases the frequency, intensity, spatial extent, duration and timing of extreme weather and climate events (IPCC 2018). Annual rainfall on Madeira has been decreasing progressively since the beginning of the twentieth century (Baioni 2011) and temperature has been increasing steadily in phase with average global temperature (Santos et al. 2004), but during the last decade, Madeira has experienced some extreme weather events; flooding in 2010 resulting in mud and landslides; a fire in 2016 and severe storm events in 2017 and 2018. However, Baioni (2011) suggests that the recent increases in damaging events on Madeira are related to human activities such as economic development and population growth rather than natural factors. Climate change may facilitate biological invasions by enabling species to move into new regions, whilst simultaneously causing resident species to become less well adapted to their local environment (Walther et al. 2009).

On Madeira, climate change may be contributing to the demise of the endemic species as well as contributing to the increase in *P. aegeria*. In Britain over the past 150 years, the distribution of *P. aegeria* has witnessed huge fluctuations, probably in response to climate change (Pateman et al. 2016). Following a contraction of its distribution at the end of the nineteenth century, since 1940, *P. aegeria* has subsequently re-expanded its distribution northwards (Hill et al.

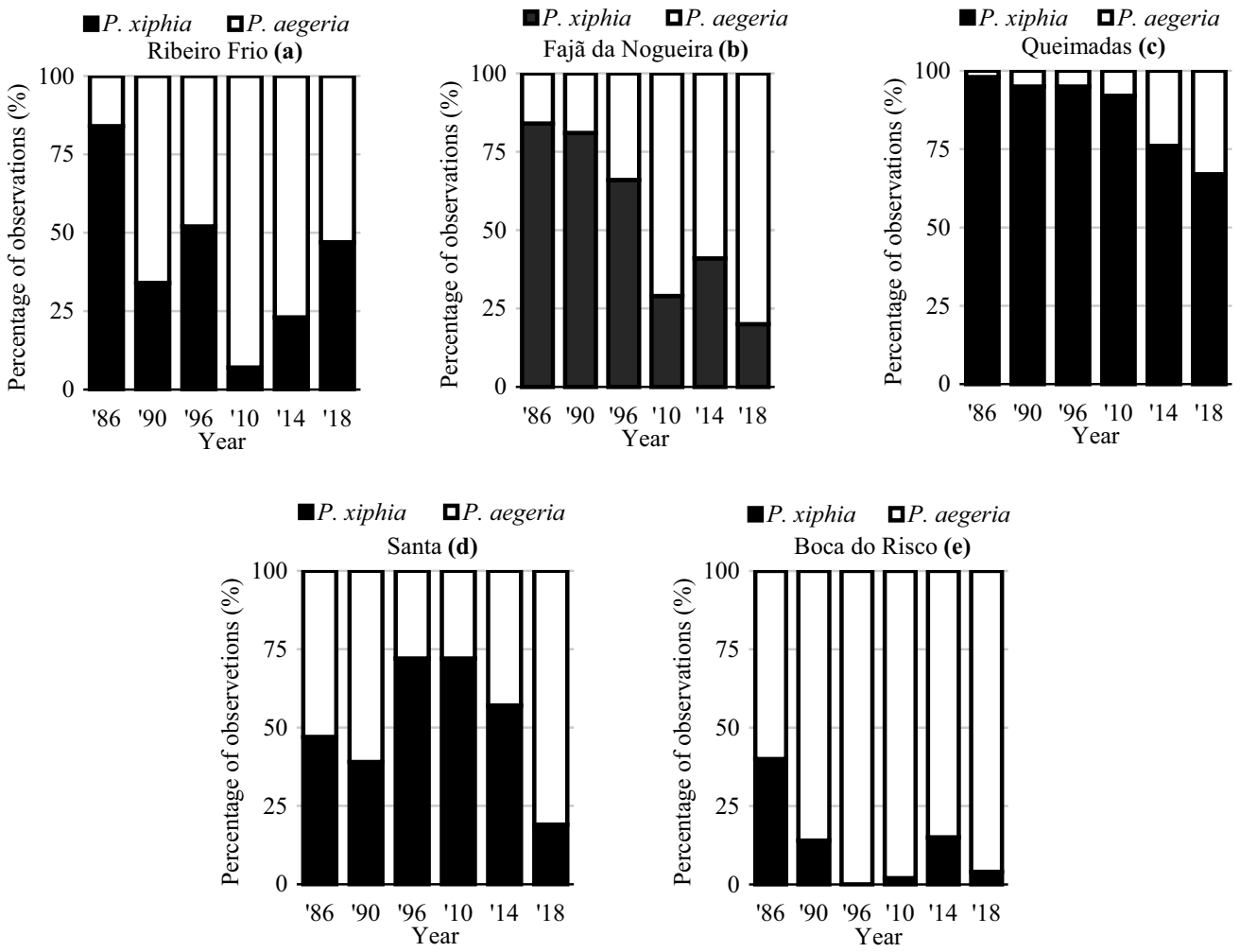

Fig. 3 **a**–**e** The proportions of both *Pararge* species from census data collected on six occasions between 1986 and 2018 at five locations

1999). Karlsson and Van Dyck (2005) found differences in temperature related life history traits within individuals from ancestral woodland populations and populations from novel habitats, indicating *P. aegeria* is adapting to local climatic conditions as it expands its range.

The occurrence of *P. aegeria* on Madeira has been mostly associated with habitat variables such as planted forests of eucalyptus, pine, agriculture and housing that dominate within the lower altitudinal ranges which correspond to the highest recorded densities of *P. aegeria*. Typically, these areas are warmer than higher altitude regions, where *P. xiphia* is now mostly found. Climate-related habitat association may be linked to differences in thermoregulatory biology of the two species. There are morphological differences between the species, which may infer that they are better adapted to thrive at different temperatures. *P. xiphia* is larger and has darker wings; it also has more body and wing hair (Jones et al. 1998). If temperatures on Madeira increase as a result of global warming, the colonist may become better suited to the island's environment, whilst the endemic species, which is active at lower air temperatures than the European species, may become less well adapted (Shreeve and Smith 1992).

Many terrestrial organisms are shifting their range poleward and uphill in response to climate change (Chen et al. 2011; Wilson et al. 2007). Different species range shifts vary greatly, which could suggest there are multiple traits that affect the rate of movement. Chen et al. (2011) estimated that species would shift to high elevations at a median rate of eleven metres per decade.

In 1986, the highest recorded mean densities of *P. xiphia* occurred at altitudes of 900 and 1000 m around 100 m lower than the highest mean densities recorded in this study of 1000 and 1100 m. For *P. aegeria* a range shift is more pronounced; highest mean densities of 200 to 300 m recorded historically (Jones and Lace 1992) and although still abundant at lower altitudes, we found *P. aegeria* dominating at sites of between 600 and 800 m.

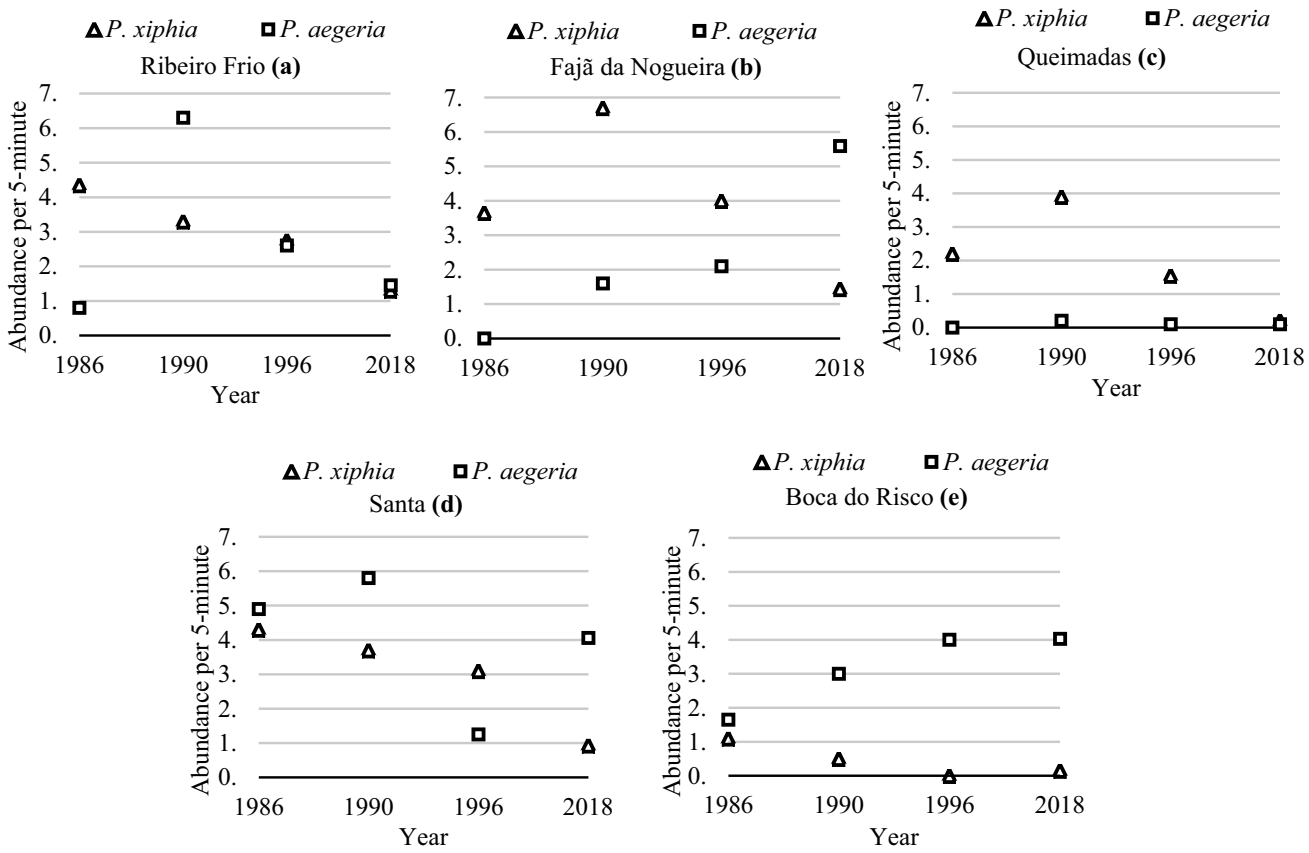

Fig. 4 **a**–**e** Mean abundance of *Pararge* species per 5-mincount at five sites surveyed on four occasions between 1986 and 2018

Table 1 Total number of individual speckled wood butterflies (*n*) recorded between 1986 and 2018 and their relative abundance expressed as a percentage (%)

	Number of transects	Total observations		*P. xiphia*	*P. aegeria*
1986	22	648	*n*	503	145
			%	78	22
1990	6	490	*n*	311	179
			%	63	37
1996	10	460	*n*	325	135
			%	71	29
2010	6	412	*n*	146	266
			%	35	65
2014	10	2114	*n*	588	1526
			%	28	72
2018	10	720	*n*	183	537
			%	25	75

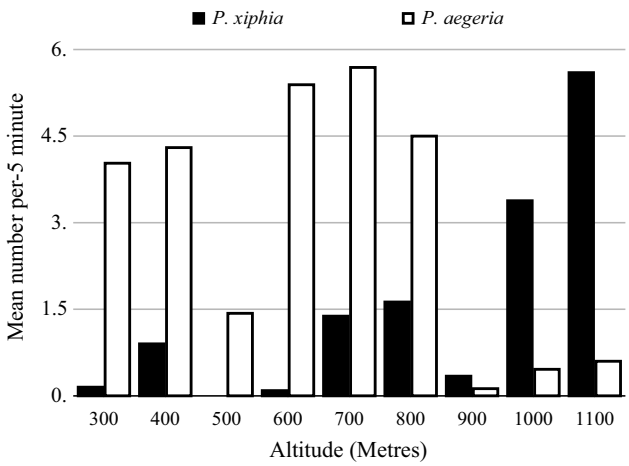

Fig. 5 The altitudinal distribution of the *Pararge* species per 5-minute count per 100 m of altitude

Localisied weather conditions on Madeira, cloud cover in particular, can change rapidly, especially at altitude and is known to affect the activity and occurrence of both *Pararge* species (Shreeve and Smith (1992). Related to this are the differences that exist between the species in thermal tolerance, with *P. xiphia* seemingly better adapted to cooler and

Table 2 The mean number of each *Pararge* species per 5 min of recording in each habitat type

Habitat type	5-min periods	Mean number of individuals per 5-min recording period	
		P. xiphia	*P. aegeria*
Laurel	85	1.7 ± 2.5	1.9 ± 4.0
Tree heather	26	1 ± 1.5	0.7 ± 2.7
Pine	25	0.9 ± 1.8	0.3 ± 0.58
Eucalyptus	11	0.3 ± 1.0	4.9 ± 3.0
Agriculture	16	0.63 ± 1.2	1.63 ± 2.5

overcast conditions. Behavioural differences aside, and the fact that our studies span more than 30 years, we are confident that our data is comparable and accurately reflects the changes we have documented with respect to the occurrence and relative abundance of these congeneric species over three decades. Our methods were consistent, data was only collected when temperatures were above 13 °C when sunny or 17 °C and above when cloudy, and the data was always collected at the same time of year (between July and August) at a range of locations and altitudes.

Parasitism may also be associated with the decline in abundance of *P. xiphia* as there is evidence that invasive parasites are having a negative impact on Macaronesia's endemic butterfly fauna (Lozan et al. 2008). Gibbs et al. (2004a) found that the eggs of both *Pararge* species on Madeira were parasitised by *Trichogramma gicai*, which is the first known parasite of *P. xiphia*. Although both species had similar levels of parasitism, the endemic species, it could be argued, is the more vulnerable, as *P. xiphia* lays many fewer eggs than *P. aegeria* and, additionally, it has evolved in isolation. Another butterfly from Madeira, the endemic large white (*Pieris brassicae wollastoni*) is thought to be extinct; a suggested cause being the introduction of *Cotesia glomerata*, an alien parasitoid wasp, used as a biocontrol agent for agricultural pest control. *Cotesia glomerata* has also been identified as a parasite of the endangered *Pieris cheiranthi*, a species of large white butterfly that is endemic to the Canary Islands (Lozan et al. 2008).

Causal factors affecting the decline of *Pararge xiphia* are difficult to determine but are most likely to be a combination of factors. Habitat loss and disturbance, interspecific competition, at larval and adult life stages between the *Pararge* species, the impacts of climate change and parasitism could all play a part and would negatively impact the less fecund and specialist island endemic.

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Author contributions LL provided the study conceptualisation and design. Material preparation, data collection and analysis were performed by Dr Lesley Lace and Elliot Bland. The first draft of the manuscript was written by Elliot Bland with assistance from Dr Lesley Lace. All subsequent versions were edited and approved of by Dr Lesley Lace and Elliot Bland.

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Compliance with ethical standards

Conflict of interest The authors declare they have no conflict of interest.

Informed consent All authors consent to the submission of this manuscript.

Research involving human and animal participants No butterflies were harmed during the course of this project and no human participants were involved in the work.

Appendix 1: Summary of transect information and abundance of *Pararge* species

Transect	Dates surveyed	Altitude (m)	Length (km)	Repeats	Time (min)	Mean number per 5-min period	
						P. xiphia	*P. aegeria*
1. *Ribeiro Frio*: The transect begins at the EN103 road and follows the Levado do Furado for approximately 1 km to the 'Balcões' viewpoint. This is a mid-altitude area with both native laurel forest and some agriculture and non-native ornamental planting along the path	25/07 29/07	800	1.0	2	100	1.3	1.45
2. *Fajã do Noguiera*: Starting approximately 1 km along the road leading from the EN103 road to the Fajã do Nogueira hydroelectric power station; the transect follows the road past the power station and onto the Levado do Pico Ruivo. Primarily laurel forest and tree heather with some non-native vegetation	15/07	500–800	4.5	3	160	1.44	5.59
3. *Queimadas*: This 7 km transect begins at the Casa das Queimadas and follows the path alongside the Levado do Caldeirão Verde to the Caldeirão Verde waterfall. This is a relatively high-altitude transect of predominantly laurel forest and tree heather but with substantial amounts of pine	19/07 20/07	900	7.0	3	150	0.2	0.1
4. *Santa*: This is the only transect on the western side of the island, despite being a low altitude area this site is surrounded by native laurel forest. The transect starts at the Levada da Ribeira da Janela above Porto Moniz and follows the levada through pine, eucalyptus and laurel forest	16/07	400	4.2	1	75	0.93	4.06
5. *Boca do Risco*: Starting at the beginning of the Vereda da Boca do Risco walk and leading through the Ribeira Seca Valley to the Boca do Risco viewpoint. This area is dominated by agriculture and abandoned terraces; the transect proceeds through planted pine forest with some laurel and tree heather	13/07 17/07	300	2.1	4	170	0.15	4.03
6. *Camacha*: Close to the town of Camacha, on the southern side of the island the transect follows the final section of the Levada dos Tornos towards Gaula. The transect passes through areas of agriculture, as well as planted pine and eucalyptus plantations	18/07	600	6.2	2	115	0.09	5.39
7. *Portela*: The beginning of the transect is close to the bus stop at Ribeiro Frio. Starting at the 'PR10 Portela' signpost, the transect follows the Levada do Furado towards the Lamaceiros waterhouse. The dominant vegetation is the native laurisilva forest with some planted pine	29/07	800	3	1	80	0.19	0.25
8. *Poiso*: This high altitude transect begins at the Casa de Abrigo do Poiso and follows the path towards Pico do Arieiro for approximately 3 km. The start of the transect is dominated by housing with the latter part of the transect being mainly planted pine forest	31/07	1100	3	1	35	1.18	0.14

Transect	Dates surveyed	Altitude (m)	Length (km)	Repeats	Time (min)	Mean number per 5-min period	
						P. xiphia	*P. aegeria*
9. *Curral das Freiras*: Starting at the bus stop outside the Eira do Serrado hotel, a few kilometres north of Câmara de Lobos, this transect follows a steep descent into the town of Curral das Freiros. This transect spans a range of altitudes and consists mainly of laurel and tree heather vegetation, but with some eucalyptus, pine and agriculture	27/07	900–1100	3.5	1	60	5.42	1
10. *Palheiro Gardens*: Located on the hills to the east of Funchal, these gardens are located in the grounds of the Quinta do Palheiro. A short transect around the gardens passes through many exotic, non-native plants, as well as pine and eucalyptus trees	24/07	500	2	1	35	0	1.43

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