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A case of spatial coexistence among Black Wheatear *Oenanthe leucura*, Black-eared Wheatear *Oenanthe hispanica* and Blue Rock Thrush *Monticola solitarius* in the Western Mediterranean

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Abstract - The coexistence of similar species is determined by resource partitioning, while the exploitation of the same resource could lead to competitive exclusion scenarios. The breeding distribution of birds like the Black Wheatear *Oenanthe leucura*, the Black-eared Wheatear *Oenanthe hispanica*, and the Blue Rock Thrush *Monticola solitarius* overlaps in open, rocky areas of the Western Mediterranean but so far, the degree of spatial segregation/overlap is poorly understood. Here, we used MAXENT to build species distribution models and investigate how the habitat preferences of those three species shape coexistence patterns in a coastal protected area of the Western Mediterranean. Within the study area the Black Wheatear is completely restricted to quarries with a predicted distribution of 162 ha. We found that the Black and Black-eared Wheatears responded to a vegetation-vigour gradient that limits their interspecific territorial overlap (145.3 ha) to sunny slopes. The Blue Rock Thrush presence is mostly affected by slope gradient, although tolerating different vegetation-vigour levels, but overlapping with the Black Wheatear (32.1 ha) in quarry areas and with the Black-eared Wheatear (62.8 ha) in steep, rocky slopes. Within the studied area, quarries appear as a key habitat favouring the coexistence of sympatric breeding species.

Keywords: Coexistence, Spatial Ecology, GIS, MAXENT, Western Mediterranean

INTRODUCTION

Understanding how species with similar requirements coexist is a major question in ecology (Valladares et al. 2015; Hart et al. 2017). Knowledge about species distribution, overlap with closely related species, and habitat preference is essential in order to understand coexistence or subsequent competitive dynamics established in bird communities (Wiens 1989, Fletcher & Fortin 2018). Coexistence of similar species is generally consistent with some degree of spatial segregation, often conditioned by environmental gradients (Hassell et al. 1994). In addition, divergence in response to spatial change dynamics (for example, faster or slower colonization of perturbed areas) is considered a potential characteristic promoting coexistence by avoiding direct competition (Hart et al. 2017). On a broader scale, coexistence can be possible due to colonization-extinction patch dynamics explained by stochastic events and fitness of each involved species (Amarasekare & Nisbet 2001). Previous statements are consistent with the existence of specialist species linked to specific stages of vegetal succession, as the highest fitness for each species can be reached in different vegetation stages after some perturbations (Real 2000, Zozaya et al. 2012).

This short study aims at increasing our knowledge about the habitat preference and the potential distribution of three sympatric bird species in a Western Mediterranean protected area: the Black-eared Wheatear *Oenanthe hispanica*, the Black Wheatear *Oenanthe leucura* and the Blue Rock Thrush *Monticola solitarius*. Specifically, the objectives are to study the importance of environmental variables for the distribution of each species as well as the characteristics of the areas where the three species overlap. The Black Wheatear population of this region has been already studied, but there is lack of information on the Black-eared Wheatear and the Blue Rock Thrush populations along with their coexistence dynamics (Noguera et al. 2014). These species are of particular interest as they are suffering important population declines across Europe because of the transformation of traditional Mediterranean landscapes (Keller et al. 2020). In order to understand how the habitat preferences of those three species shape their coexistence patterns and to predict their distributions in a coastal protected area of the Western Mediterranean I used the MAXENT software.

MATERIALS AND METHODS

The survey was conducted at Garraf Park protected area, a 12,377 ha reserve located in Catalonia, Eastern Iberian Peninsula. It is a Mediterranean, limestone coastal massif ranging from sea level to 594 meters above. This protected area is mostly occupied by maquis, garrigues and other Mediterranean shrublands, followed by holm oak *Quercus ilex* and Aleppo pine *Pinus halepensis* forests, as well as dry meadowlands, quarries, and rocky slopes. Moreover, a small coverage of farmland and urban areas is present in the area.

In order to detect the breeding territories of the three species, the study area was divided into a grid of 1x1 kilometre cells. In 2020, 3.5 km transects (n=35) were performed in the early morning (7:30 – 10:30) from May 5 to June 10 and from June 15 to July 30, using available paths and roads and covering the largest number of cell grids. Target species were searched using 10x42 binoculars, recording each breeding evidence and the corresponding location in geographical coordinates. Transects were always performed by the same observer. Following the European Breeding Bird Atlas 2 code, observed reproductive evidence was classified into three categories: possible, probable, or sure territories (Herrando et al. 2013). I recorded and then used 61 Blue Rock Thrush, 20 Black-eared Wheatear and 11 Black Wheatear records to build their distribution models. Agonistic interactions (i.e. persecution and aggression) among the three species were also recorded.

I operated with eight environmental layers corresponding to topographic, climatic, land cover and vegetation variables characterizing Garraf Park protected area and having a spatial resolution of 15x15m (Tab. 1). Topographic variables correspond to elevation (meters above sea level), slope, aspect, and solar radiation (WH/m2) available as raster files. Elevation was obtained from open databases downloading available DTM (Digital Terrain Model) (see Tab. 1).

Slope, aspect, and solar radiation raster files were obtained by performing geospatial operations using the previously mentioned DTM layer. Aspect was reclassified to its North – South component while Eastern – Western component was removed. Previous operation was followed in order to focus on the North – South component, a significant topographic concern for Mediterranean habitats (Kutiel 1992). Climatic variables were obtained from open databases (Fick & Hijmans 2017). Those climatic variables correspond to mean annual precipitation and temperature, transformed along with other available data by conducting kernel interpolation operations to obtain required spatial resolution (Hoerl & Kennard 1970, Environmental Systems Research Institute 2012). Land cover layer was first

Table 1. Environmental variables used to model species distribution within the Garraf Park protected area including layer, group, type of variable (continuous vs. categorical) and data source.

Layer	Group	Type of variable	Source
Elevation	Topographic	Continuous	Cartographic and Geological Institute of Catalonia (https://www.icgc.cat/ca/Descarregues/Elevacions/Model-d-elevacions-del-terreny-de-15x15-m)
Slope	Topographic	Continuous	Cartographic and Geological Institute of Catalonia (https://www.icgc.cat/ca/Descarregues/Elevacions/Model-d-elevacions-del-terreny-de-15x15-m)
Aspect	Topographic	Continuous	Cartographic and Geological Institute of Catalonia (https://www.icgc.cat/ca/Descarregues/Elevacions/Model-d-elevacions-del-terreny-de-15x15-m)
Solar radiation	Topographic	Continuous	Cartographic and Geological Institute of Catalonia (https://www.icgc.cat/ca/Descarregues/Elevacions/Model-d-elevacions-del-terreny-de-15x15-m)
Precipitation	Climatic	Continuous	World Clim v 2.1 (https://www.worldclim.org/data/worldclim21.htm)
Temperature	Climatic	Continuous	World Clim v 2.1 (https://www.worldclim.org/data/worldclim21.htm)
Land Cover	Land Cover	Categorical	Centre for Research in Ecology and Forestry Applications of Catalonia (https://www.creaf.uab.es/mcsc/)
NDVI	Vegetation vigour	Continuous	Copernicus OAH (https://scihub.copernicus.eu/dhus/#/home)

downloaded in shapefile format and converted to raster conducting geospatial operations. Land cover data consists of 66 categories, with predominance of Mediterranean scrublands, Aleppo pine forest habitats, and quarries within the studied area. Moreover, in order to obtain a vegetation variable reflecting the vegetation vigour, I calculated the Normalized Difference Vegetation Index (NDVI). This index required a set of satellite imagery (Sentinel 2A level) of the studied area available in Copernicus Open Access Hub, recovered by Sentinel II satellite in spring 2019. NDVI index is obtained by conducting raster operations with near-infrared (IRP, band 8 = 0.78 – 0.9 µm) and visible red (RV, band 4 = 0.65 – 0.68 µm). NDVI values range from 0 to 1, with most values within the studied area ranging from 0.4 to 0.8 (highest values correspond with forest patches), and scarce areas with values under 0.2 (mostly quarries).

The correlation between quantitative variables was measured using Band Collection Statistics Analysis available in ARCGIS Spatial Analyst tool extension. Precipitation and temperature were excluded from further analysis as being highly correlated with elevation (r> 0.6). Minimizing the correlation between variables increased the robustness of further maximum entropy analysis (Merow et al. 2013). All GIS operations and geospatial analyses were performed with QGIS v 3.4.14 (QGis Development Team 2017) and ARCGIS v 10.7.1 (Environmental Systems Research Institute 2019) software.

Distribution models of the three species were developed using MAXENT v 3.4.1 (Phillips et al. 2019), a presence-background method not requiring absence data (Baldwin 2009). Maximum entropy modelling only demands presence data and environmental layers for the study area (Kumar & Stohlgren 2009). I performed results output in logistic, ascii format, maximum number of background points fixed in 10000, and 10 replications. I used all records and the cross-validation form of replication. Cross-validation techniques have a great advantage over test split: all data is used for validation, so this technique is particularly suitable for small datasets (Phillips et al. 2006). I also used Jackknife tests to identify the most informative variables for each species. Moreover, in order to evaluate the predictive capacity of the spatial distribution models I used mean AUC (Area Under the receiver-operator curve with ranging values between 0 and 1), that is a decisive statistic since it is positively correlated to model sensitivity (Fielding & Bell 1997, Merow et al. 2013). The output of the predictive models was transformed to raster, and then reclassified in ArcMap by using Arc Toolbox Spatial Analyst and Conversion Tool extensions (Environmental Systems Research Institute 2012). Finally, they were converted to obtain binary maps (threshold for the probability of occurrence was set at 0.5). It is worth noting that using a threshold 0.5 can overestimate species distribution (Jiménez-Valverde & Lobo 2007). Despite that, it was used in order to prioritize accuracy in predicted distributions. TIFF files were vectorised in order to conduct geospatial operations. I intersected binary TIFF files of each species using Arc Analysis Toolbox, Geoprocessing tools (Environmental Systems Research Institute 2012) resulting in potential overlap combinations.

RESULTS

Jackknife tests of regularized training gain highlighted the importance of vegetation-vigour (maximum gain with only variable and maximum loss without variable) for both wheatears (Fig.1). In the case of the Blue Rock Thrush slope was the most relevant variable, while land cover was particularly relevant for the Black Wheatear according to its exclusive appearance within surveyed quarries. All species were favoured by low NDVI values (less than 0.5), but the Black Wheatear was limited to areas with

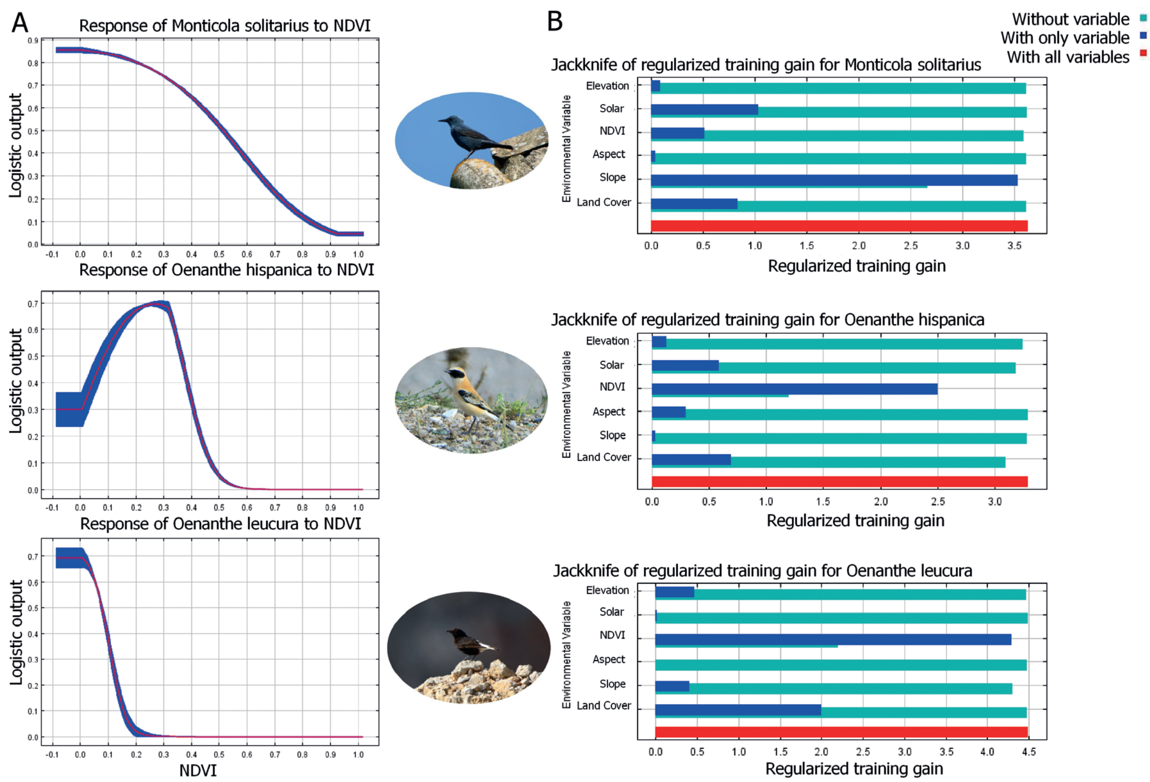

Figure 1. A) Response curve for vegetation-vigour (NDVI) predicted by MAXENT distribution models of the Blue Rock Thrush, the Black Wheatear, and the Black-Eared Wheatear (from top to bottom), and B) Jackknife tests of regularized training gain for each studied species.

extremely low values (less than 0.2). The optimum for the Black-eared Wheatear was between 0.1 and 0.35 NDVI values (Fig. 1).

The MAXENT modelling produced consistent spatial distribution models for studied species, with high AUC values in all cases (Tab. 2). Up to 28.9 ha of Garraf protected reserve (total area of 12,377 ha) potentially involved the coexistence of the three studied species (Fig. 2). The Black-eared Wheatear potentially coexists with the Black Wheatear in 30.7% of its predicted range (145.3 ha), and with the Blue Rock Thrush in 13.3% of its predicted range (62.8 ha). The Black Wheatear potentially coexists with the Black-eared Wheatear in 89.7% of its predicted range (145.3 ha), and with the Blue Rock Thrush in 19.8% of its predicted range (32.1 ha). The Blue Rock Thrush potentially coexists with the Black-eared Wheatear in 19% of its predicted range (62.8 ha), and with the Black Wheatear in 9.7% of its predicted range (32.1 ha).

The potential coexistence of the Black Wheatear and the Black-eared Wheatear mostly occurred in sunny slopes of quarries while the coexistence of the Black Wheatear with the Blue Rock Thrush was restricted to quarry cliffs and nearby steep slopes. The Blue Rock Thrush and the Black-eared Wheatear potentially coexist in areas of steep, rocky slopes with low vegetation-vigour and open landscapes. The potential coexistence of the three species occurred preferably in quarry regions where sunny slopes, cliffs and steep hillsides overlap (Fig. 2).

I recorded 12 agonistic interactions between the Black Wheatear and the Blue Rock Thrush in quarries where the studied species overlap. I also detected 2 agonistic interactions between the Blue Rock Thrush and the Black-eared Wheatear. In both cases the interaction caused the defeated birds to fly away. No agonistic interactions involving the Black-eared Wheatear were detected.

DISCUSSION

Coexisting bird species are expected to differ in resource use (i.e. resource partitioning), in order to avoid fitness costs produced by the exclusion/competition for similar resources in overlapping territories (Martin 1996). In fact, habitat preference of sympatric bird species could be critical in order to ensure coexistence and avoid competitive exclusion (Martin 1998). In the case of the studied bird species, resource partitioning appears to exist, since each species responds to a specific set of environmental variables, indicating that interspecific competition is likely avoided. Previous studies with wheatear species have demonstrated that in some cases geomorphological features can play a critical role in habitat segregation patterns (Kaboli et al. 2013). In this study case, the vegetation-vigour seems to be a key variable determining segregation (for instance, in areas where NDVI values are only suitable for the Black-eared Wheatear) and coexistence (in slopes where NDVI values are suitable for both species) of the Black Wheatear vs. the Black-eared Wheatear (Fig. 1). This result is consistent with previous ecomorphological approaches that set the Black Wheatear as a rock-dwelling species (heavy and compact bird equipped with short claws) perching preferably on rocks and the Black-eared Wheatear as a vegetation-tolerant species (smaller bird equipped with long claws) able to perch on light branches of

Table 2. Results of the spatial distribution models achieved for each studied species within Garraf protected area. Summary statistics include the extension (ha), the number of patches, the mean AUC, and its standard deviation for the MAXENT modelling of each species.

Species	Extension (ha)	N of patches	Mean AUC	Standard deviation
Blue Rock Thrush	330	1805	0.973	0.042
Black-Eared Wheatear	473	2661	0.978	0.024
Black Wheatear	162	389	0.996	0.004

available shrubs (Kaboli et al. 2007). Conversely, the distribution of the Blue Rock Thrush appears to depend more on vertical slopes than on vegetation vigour.

All studied species are particularly linked to the Mediterranean region. The Blue Rock Thrush occupies rocky areas where cliffs are abundant, being favoured by steep slopes (Fig. 1). Some territories were found both in cliffs surrounded by forest habitat (mostly Aleppo pine and holm oak woods) as well as in sparsely vegetated slopes (as quarries), thus showing a certain degree of plasticity in habitat preferences. However, its presence was mainly related to open, rocky habitats with a large availability of cliffs (Fig. 2). The Blue Rock Thrush territory locations range from a few meters above sea level to the highest areas of the massif with highly variable conditions in solar radiation and vegetation vigour.

Both wheatear species preferred areas with less steep slope, but also rocky zones. The Black-eared Wheatear is distributed from highest plateaus to coastal quarries, with notable preference for higher solar radiation, southern orientation, and lower vegetation index values compared to the Blue Rock Thrush (Fig. 1). Thus, most south-faced slopes with low garrigue, rocky areas, and great availability of Mediterranean meadows are clearly favourable to this species, and in line with other studies in other Mediterranean regions (Brambilla et al. 2013). The Black Wheatear seems to avoid habitat with high vegetation vigour values (Fig. 1) being all territories settled in active or under restoration quarries (Fig. 2). Again, our result is consistent with previous exhaustive studies on the same species (Noguera et al. 2014). It is worth to stress that the Black and Black-eared Wheatears have suffered considerable population declines in recent decades (Keller et al. 2020). In fact, both species are particularly sensitive to the increase of vegetation-vigour and the subsequent loss of open habitat. This trend is widespread across the Mediterranean regions and it affects vast areas including the Garraf massif (Feranec et al. 2010, Cervera et al. 2016, Keller et al. 2020). For ground-nesting birds such as the Black-eared Wheatear, parameters like breeding success could be significantly higher in recently burned areas or quarries. These areas are in fact characterized by less vegetation-vigour and thus suitable for the establishment of breeding territories. Low levels of vegetation-vigour are important because favouring the detection of predators (Oswald et al. 2020). Unlike other species, the Black and Black-eared Wheatears can benefit from ecological disturbance as wildfires, since it creates optimal patches for species that show preference for open habitats, while at the same time it mediates species coexistence by favouring the occurrence of different stages of vegetal succession (Harrison 1991, Real 2000, Roxburgh et al. 2004).

Interspecific interactions only partially match with the idea of “larger beats smaller” (Bracho & Prats 2019). Some studies suggested that competition is correlated with similarities in body size of sympatric birds with highly different body masses favouring a decrease in competition and promoting coexistence within communities (Leyequién et al. 2006). In fact, while during interspecific interactions the larger Blue Rock Thrush beat the smaller Black-eared Wheatear, the former was always defeated by the smaller Black Wheatear. In higher altitudes of the Iberian Peninsula (Sierra Nevada) species like the Northern Wheatear *Oenanthe oenanthe* have been described as dominant over other passerine birds during the reproductive period, when agonistic interactions were more frequent (Zamora 1990). Interestingly, even though 89.7% of predicted Black Wheatear distribution overlaps with Black-eared Wheatear distribution I noted more agonistic interactions with the Blue Rock Thrush. This seems to be linked to thrushes exploring the cliffs close to the Black Wheatear nests thus triggering the aggressive reactions of adult wheatears. In addition, the Blue Rock Thrush and the Black Wheatear are resident birds in Garraf massif (increased probability of competition for territories) while the Black-eared Wheatear is a summer visitor. On the other hand, the absence of agonistic interactions between the Black and the

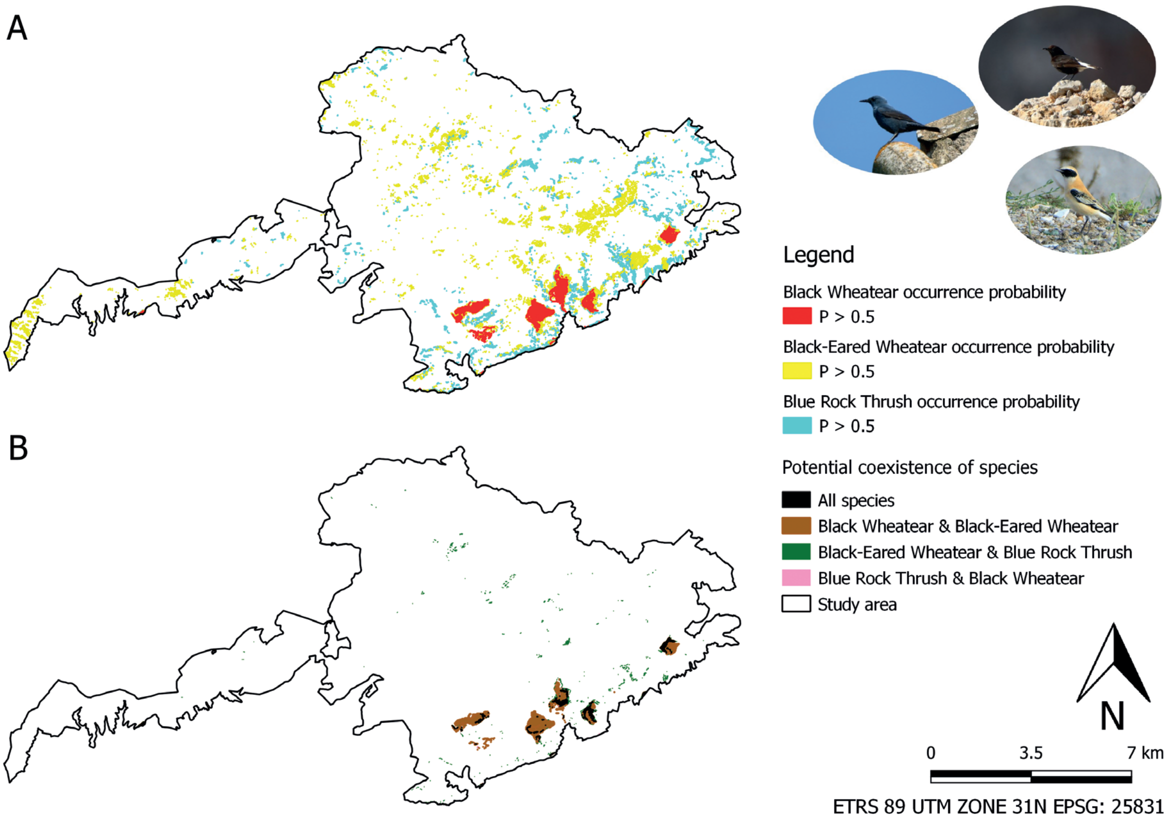

Figure 2. Predicted species distributions (A) and overlap (B) for the three study species within the Garraf protected area (resolution 15x15m). Predicted coexistence among species is mostly restricted to quarries. Further, the Blue Rock Thrush and the Black-Eared Wheatear overlap occurs in some rocky, steep slopes.

Black-eared Wheatears can be partially interpreted by differences in body size. However, the absence of agonistic interactions could be explained by the different degree of vegetation-vigour preference which turns into a reduction of competition among studied wheatears (Fig. 1).

Interspecific coexistence, particularly high in quarries where the three species overlap, could have consequences on their fitness and conservation that should be investigated in future analyses. The fact that a highly modified landscape (quarries) could become a crucial environment for the coexistence and prevalence of endangered species as Black and Black-eared wheatears is particularly important. While vast areas of southern Europe suffer a progressive landscape encroachment by woody vegetation, the maintenance of optimal patches could be critical in order to avoid local extinctions (Prodon, 2020). However, the small number of records, due to the low abundance of the study species within the study area, is the great limitation of this study and it must be taken into account when interpreting the results. This is why further works should aim at understanding how habitat preferences determine the coexistence of the studied species on a wider spatial scale, using a larger dataset and taking into account also the perturbation regime of fires, which are year after year more frequent.

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