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ORIGINAL RESEARCH

Wind energy infrastructures drive habitat loss and fragmentation for threatened Orthoptera: spatial planning needed in developed landscapes

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Abstract

Renewable energy expansion is essential for achieving climate goals but threatens biodiversity without proper spatial planning. This study assesses the impacts of renewables on threatened Orthoptera fauna and suggests mitigation solutions. Using geospatial analysis and habitat connectivity metrics, we quantified the impacts of wind power stations on three globally threatened and endemic Orthoptera species. *Parnassiana tymphrestos*, *Parnassiana coracis* and *Oropodisma willemsei* are projected to lose 9.1%, 6.6% and 4.3% of their total suitable habitat, respectively. Local impacts can be severe, with habitat loss (11–49%), reduced connectivity (12–99%), and population declines (12–53%). Population on Mt Oxia will be at risk of local extinction. Nationally, 62% of the distribution of threatened Orthoptera already overlaps with RES infrastructure (mainly wind and solar), and this figure is projected to rise to 79%. Mountains and islands, key centers of endemism, are disproportionately affected: 26% of wind energy is planned for mountainous areas (12% of Greece: >1000 m), and 35% for islands (19% of Greece), threatening narrowly distributed species. We applied a sustainable spatial planning scenario that excludes Natura 2000 sites, low-fragmentation zones, and roadless islands and roadless areas larger than 5 km². This approach fully protects the habitats of the three target species, exceeds the 2050 national wind energy target (13 GW) by 30%, and reduces the overlap between wind facilities and threatened species distributions by 0.9% (±2.1%). Our findings highlight the urgent need for biodiversity-inclusive energy planning to prevent local extinctions while meeting climate goals, offering a scalable model for biodiversity hotspots globally.

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Introduction

Renewable Energy Sources (hereafter RES**)** are leading the clean energy transitions towards electrification and decarbonization of the global economy. They are rapidly expanding to cut greenhouse gas emissions and keep global warming to less than 2 C^{o}, in the frame of the Paris Agreement (Baruch-Mordo et al. 2019). RES are expected to account for 45.6% of electricity generation by 2030, with the share of wind power stations (hereafter WPS) globally anticipated to reach 13.4% (IEA 2024). The clean energy transition is faster in the European Union (EU), aspiring to achieve climatic neutrality by 2050 under the European Green Deal (EC 2019). The ambitious targets involve a 55% reduction of greenhouse gas emissions and a 42.5–45% share of RES in the gross final energy consumption by 2030 (EU 2023). Wind energy stands at the forefront of European electrification, and a massive speed-up of RES is encouraged by the REPowerEU Plan (EC 2022). Nowadays, wind provides about 20% of electricity in Europe, and the total installed capacity is projected to double by 2040 (210 GW in 2024 vs. 440 GW in 2040) (WindEurope 2025). However, a significant conflict emerges for land resources required to accommodate RES and protect biodiversity at global (Díaz et al. 2019), national (Kati et al. 2023b; Serrano et al. 2020) and local (Kati et al. 2025a) levels. Onshore wind development will impact about 400,000 km^2 of natural and agricultural lands in Europe by 2050 (Kiesecker et al. 2024). There is an urgent need for policy frameworks and spatial planning schemes that guide onshore energy investments in a way that reconciles the clean energy, climate action and life on land goals of the Sustainable Development Goals (UN 2015) and aligns with the first target of a “biodiversity inclusive spatial planning” of the Global Biodiversity Framework (CBD 2022).

The environmental impact of WPS is comparatively low in most sectors, such as pollution and human health, but considerable in others, such as habitat loss and biodiversity degradation (Adeyeye et al. 2020; Bošnjaković et al. 2024; Gasparatos et al. 2017; Wang and Wang 2015). The most well-documented impact of WPS on species is the direct mortality and population declines in flying species (birds, bats, flying insects (Thaxter et al. 2017; Voigt 2021; Weschler and Tronstad 2024). However, WPS-driven land take has been overlooked in global and European policies as a major threat to biodiversity and ecosystems (Kati et al. 2023a). It refers to direct habitat loss due to the conversion of land to artificial land and sealed surfaces, which is associated with vegetation removal for wind tower bases, auxiliary facilities, new access roads and disposal areas. Studies have investigated mainly the indirect habitat loss associated with vertebrate avoidance patterns of WPS (Tolvanen et al. 2023), but a research gap exists for insects (Voigt 2021). The direct insect habitat loss caused by WPS-driven land take has not yet been explicitly quantified, even though habitat loss is recognized as the main driver of insect declines worldwide (Hochkirch et al. 2023; Sánchez-Bayo and Wyckhuys 2019). Covering this knowledge gap is essential, as insects account for the largest proportion of organisms worldwide (5.5 million species estimated, with one million of them described) (Bánki et al. 2025; Stork 2018) and are experiencing unprecedented extinction risks and abundance declines (Cardoso et al. 2020; Dirzo et al. 2014; Goulson 2019; IUCN 2025).

Orthoptera is one of the insect orders most threatened globally, with more than one-third of their species being red-listed (IUCN 2025; Sánchez-Bayo and Wyckhuys 2019). These insects have an important role in food webs and ecosystem function (Samways 1997) and are fine-scale indicators of environmental change, given their dependence on vegetation structure and microclimatic conditions (Ogan et al. 2022; Thorn et al. 2022). According to the European report for red-listed grasshoppers (Hochkirch et al. 2016), Europe hosts 1082 Orthoptera species, with one-fourth of them being threatened by habitat loss, degradation and fragmentation, coupled with wildfires, climate change and invasive species. Many human pressures driving habitat loss were captured in the report, but only biofuels concerned entomologists in the energy production domain a decade ago. The ongoing expansion of the wind energy sector under recent EU policy frameworks underscores the need to assess its land-use impacts on Orthoptera habitats and populations, which remain insufficiently studied.

This need is even more pronounced in Greece, a global biodiversity hotspot (Myers et al. 2000) and a typical conflict terrain of European policies for green energy transition vs. biodiversity and wilderness conservation (Kati et al. 2021, 2025a). The country is particularly rich in Orthoptera fauna; it hosts 380 species (35% of European fauna), out of which 84 threatened species and 141 endemics (67 threatened endemics) that inhabit ecological islands such as the Greek islands, mountain tops or caves (Willemse et al. 2018). These centers of endemism and zones of high ecological significance may be affected by future wind energy developments, although the magnitude and direction of such impacts remain uncertain. Kati et al. (2021) proposed a sustainable spatial planning scenario for wind facilities with substantial benefits for biodiversity, but without explicitly addressing Orthoptera. This scenario succeeded in achieving the national energy targets by 2030 exclusively in a zone of lower ecological significance, setting aside protected areas of the Natura 2000 network and more natural landscapes of lower fragmentation degree. It is still unknown whether the suggested scenario will be considered within the Strategic Environmental Assessment (EC 2001) for RES in Greece, which is under preparation. The wind energy sector continues to expand in the absence of comprehensive spatial planning, raising concerns regarding potential impacts on protected species and habitats, as highlighted by the infringement procedure of the European Commission against Greece for non-compliance with the Habitats Directive (case 2014/4073). In this study, we provide the first quantitative evaluation of wind-driven habitat loss, fragmentation and population decline for threatened Orthoptera, while testing biodiversity-inclusive spatial planning solutions. We assessed the impact of WPS on three globally threatened and endemic Orthoptera species with available habitat suitability maps (Stefanidis et al. 2025b) as data limitations prevented assessment of other grasshoppers. We considered three high-altitude species: *Parnassiana tymphrestos* (Endangered) (Kati et al. 2025b), *Parnassiana coracis* (Vulnerable) (Willemse et al. 2016), and *Oropodisma willemsei* (Critically Endangered) (Kati and Willemse 2025). We incorporated unpublished phylogenetic and morphometric data of ongoing research for *Parnassiana* (Nefeli Kotitsa, *pers. comm.*) and *Oropodisma* (Trillo and Ortego 2025), naming the species that inhabit seven mountains in central Greece (Stefanidis et al. 2025b). We focused on the impact of WPS on habitat loss and fragmentation, given the crucial importance of habitat connectivity in species of restricted distribution range (Haddad et al. 2015; May et al. 2019). We further attempted to depict the potential impact of WPS on all threatened species of the country under the current policies (business-as-usual scenario) and explore the potential benefits of

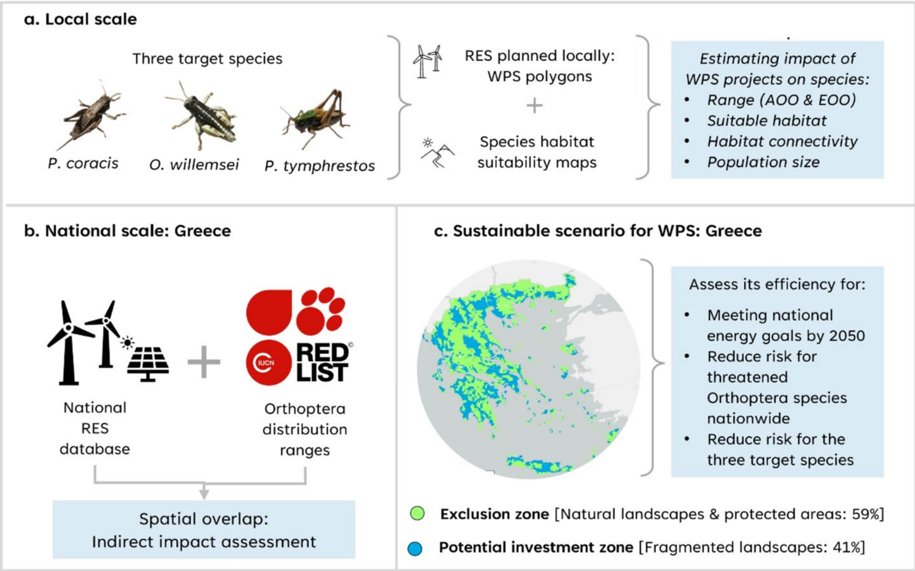

Fig. 1 Conceptual flowchart of the study. RES: Renewable Energy Sources. WPS: Wind Power Stations. AOO: Area of Occupancy. EOO: Extent of Occurrence, after IUCN red list criteria for species risk assessment

the sustainable scenario to them using distribution range data. Our objectives were to: (a) To predict the impact of the planned wind energy projects on the populations of the three target Orthoptera species in terms of habitat loss and fragmentation and assess whether these impacts would alter their conservation status under IUCN Red List criteria (Fig. 1a); (b) to compare the potential impact of different renewable energy sources in terms of their spatial overlap with the distribution range of all globally threatened Orthoptera species of Greece (Fig. 1b); (c) to evaluate the effectiveness of the business-as-usual scenario in meeting the national energy target for 2050, analyze its spatial configuration with respect to Natura 2000 sites, islands, and mountain regions, and assess its potential impact on threatened Orthoptera species; (d) to refine the sustainable scenario for wind development and assess the same parameters in comparison with the business-as-usual scenario (Fig. 1c). Our study can serve as a paradigm of the local and national conservation actions needed to avert global extinctions.

Methods

Study area

The area considered for the target species spanned 186 km^2 across the mid to high-altitude zone (over 1260 m a.s.l.) of seven mountains (Pindos Mountain Range) in central Greece (Fig. 2). It covered the total suitable habitat area for the three target species, based on Species Distribution Modeling across their global range (Stefanidis et al. 2025b). It is characterized by high naturalness: 94% cover of forests and semi-natural areas according to the

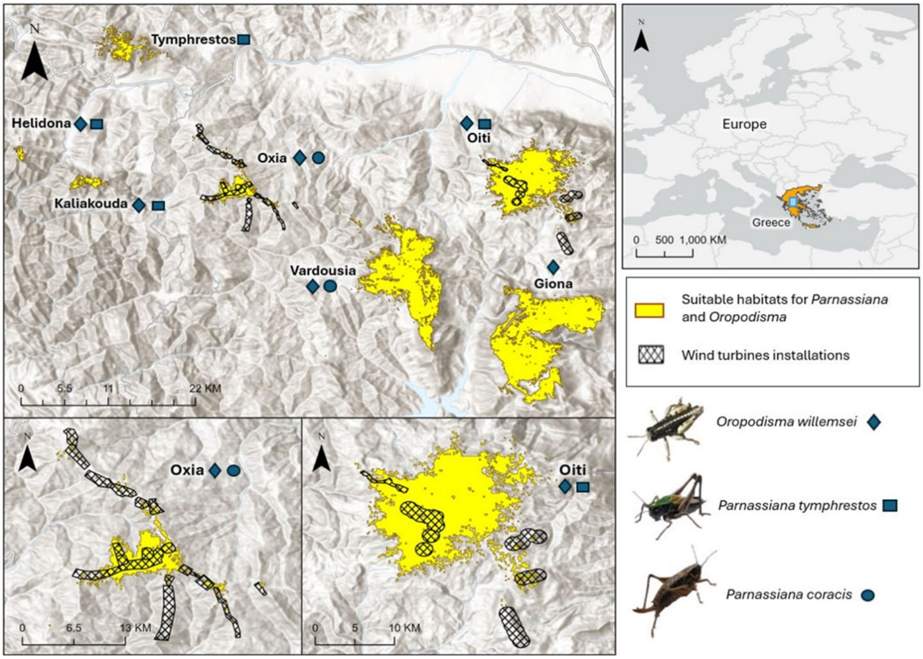

Fig. 2 Installation polygons of wind power stations (RAE 2025) within the area of suitable habitats (merged) for the three target species, across their global distribution range (Stefanidis et al. 2025b). Symbols indicate the species' presence across the seven mountains. See Fig. S2 for the presence points (172 records) and the current Extent of Occurrence (EOO) for the three target species

Corine European typology (Kosztra and Büttner 2019) (Fig. S1) and 42% cover of roadless areas (Kati et al. 2023b). The greatest part (91%) is protected under the Natura 2000 network across four mountains – Tymphrestos (GR2430001), Vardousia (GR2450001), Giona (GR2450002), Oiti (GR2440007) - while the mountains Oxia, Kaliakouda, and Helidona are not protected (Fig. S1). Based on field observations, livestock farming is the main human activity above the tree line, with ski centers (Mt Tymphrestos) and bauxite mining (Mt Giona) as additional uses. The area considered for all threatened Orthoptera covered all Greek land (mainland and islands: 130,891 km^2).

Orthoptera dataset

The three target species database consisted of 172 point records and their habitat suitability maps, considering their updated distribution pattern: *P. coracis* (two mountains), *P. tymphrestos* (four mountains) and *O. willemsei* (six mountains) (Stefanidis et al. 2025b) (Fig. 2, Fig. S2).

For the national species database, we considered all Orthoptera species in Greece classified as globally Vulnerable (VU), Endangered (EN) or Critically Endangered (CR) (IUCN 2025), noting their endemism (Cigliano et al. 2024), their known elevation range and main habitat category (mainland, islands, mountains, caves) (Willemse et al. 2018). We downloaded (15/1/2025) the species distribution range maps from the IUCN Red List portal

(IUCN 2025). The final dataset included 84 globally red-listed species, out of which 67 species were endemic to Greece (Table S1).

Renewable energy sources dataset

We collected geospatial data on the installation sites for all RES types (installation polygons, except points for hydroelectric stations, as well as wind turbine coordinates (point data) and their installed power (MW) from the online database of the National Regulatory Authority for Energy (downloaded at 15/1/2025) (RAE 2025). The dataset includes all applications for RES across four successive licensing stages (rejected stations excluded): (1) under evaluation (preliminary technical evaluation), (2) production license (evaluation for obtaining a Decision Approving Environmental Terms), (3) installation license (under construction) and (4) operational license (the station currently operates). We classified as "current" the stations that operate now or are going to operate soon (stages 3 and 4), "planned" the stations under production or evaluation (stages 1 and 2) and as "total" all stations (stages 1–4), including both current and planned investments. The dataset included 5,929 records on 15/1/2025 as follows: wind power (1,976 polygons, 12,547 onshore turbines), geothermal (3 polygons), solar thermal (3 polygons), biomass (60 polygons), hybrid stations (183 polygons), photovoltaics (2,142 polygons), and hydroelectric stations (1,562 points).

Impact of wind energy infrastructures on the target species

We performed all statistical analyses in the R software environment, version 4.5.1. (R Core Team 2024) and geospatial data analysis in ArcGIS Pro v.3.2.2. (ESRI 2025). We used the target species database (Stefanidis et al. 2025b) to calculate the Area of Occupancy (AOO), as the area occupied by the species in terms of the number of occupied cells of 2 × 2 km, and the Extent of Occurrence (EOO), as the spatial species spread (including non-suitable habitats). We employed the "Con" 1.3 R package and the 'AOO.computing()' and 'EOO.computing()' functions to compute the two metrics before and after filtering out presence points inside WPS installations (Dauby and Ferreira de Lima 2024).

We assessed habitat loss in each mountain from wind energy facilities (RAE 2025), excluding the area of WPS polygons from each species' suitable habitat area. We estimated the habitat connectivity within each mountain before and after the construction of the WPS by calculating the patch cohesion index and the effective mesh size using the "landscapemetrics" 2.0.0 R package (Hesselbarth et al. 2019). The patch cohesion index quantifies the physical connectedness of habitat patches within a specific landscape in terms of their aggregation and proximity (McGarigal 2002). It considers the proportion of patch edges that are physically connected and evaluates the structural integrity of patches and their ability to remain cohesive and not isolated despite fragmentation. Effective mesh size is a metric of landscape fragmentation, representing the average size of unfragmented habitat patches; larger values indicate greater habitat connectivity by quantifying the probability that two randomly selected points lie within the same, unobstructed patch (Jaeger 2000).

We applied a species abundance-area relationship approach to estimate the impact of habitat loss on population size, following established modeling frameworks (Yamaura et al. 2016a, b). We fitted a negative binomial generalized linear model that allows for overdispersion in the abundance data, adopting the log-linear model structure described in (Taki et al. 2018). We assumed that the expected number of individuals (abundance) of species i in mountain j (λ_{ij}) was the function of suitable habitat area (A_j km^2): $\log(\lambda_{ij}) = \beta_0 + \beta_1 \log(A_j)$, where β_0 is the logarithmically transformed expected abundance at $A_j = 1$. The slope coefficient β_1 expresses the area dependence of population density (Connor et al. 1997), and when this value exceeds 1, density increases with habitat area, and vice versa. We estimated a single scaling exponent across species–mountain combinations to avoid overparameterization given the limited number of independent abundance–area observations (Yamaura et al. 2016b). After fitting the model, we estimated population sizes before and after habitat loss caused by wind energy infrastructures. We then calculated the relative population reduction percentage for each species in each mountain $\left(\frac{original\ population - population\ after\ WPS\ construction}{original\ population}\right)$.

Potential impact of renewable energy sources on Orthoptera

We used the distribution ranges of threatened Orthoptera species (IUCN 2025) and the polygons of the RES database (RAE 2025) to calculate their spatial overlap. We calculated the percentage of threatened Orthoptera species (CR, EN, VU) whose distribution ranges overlap with RES infrastructures by RES type that operate now and, in the future, (categories “current” and “future” respectively).

Scenarios for WPS spatial planning

The scenarios

We considered two scenarios for WPS spatial planning: The business-as-usual scenario reflects the current energy policies and corresponds to all wind turbines (and respective polygons) under all licensing stages from the RES dataset. The suggested sustainable scenario consists of two zones for wind turbine installation. The exclusion zone comprises: (a) The area proposed by Kati et al. (2021) disqualifying wind energy deployment inside the Natura 2000 network and the landscapes of higher naturalness in terms of very low and low landscape fragmentation, using the European Landscape Fragmentation Index (LFI: effective mesh density values < 10) (EEA 2019); (b) the merged polygon of roadless areas larger than 5 km^2, roadless islands and islets (Kassara et al. 2022), because LFI overestimates fragmentation on small islands (Kati et al. 2023a). The potential investment zone comprises the remaining Greek land. The scenario assumes that the current WPS (operating and under-construction) will continue operating, while only the planned WPS applications within the potential investment zone should be considered in the licensing process.

Scenarios’ effectiveness for energy goals

We considered the database of turbines’ wind power from RES dataset in Gigawatts (GW). We calculated the cumulative wind power of the wind energy investments across the four licensing stages for each scenario to test their effectiveness in achieving the national onshore wind harnessing targets by 2030 and 2050 (8.9 GW and 13 GW, respectively) (MEE 2024).

Scenarios' spatial configuration

We divided the country into three zones: (a) islands, including all islands regardless of their size (large islands such as Crete and Evvoia included), (b) mountains in the mainland (zone above 1,000 m), and (c) lowlands in the mainland (zone below 1,000 m). Each zone was further subdivided based on inclusion in the Natura 2000 network of protected areas. We then calculated the number of turbines and cumulative turbine wind power installed within each zone for each scenario, considering the current, planned and total (current and planned) wind turbines.

Potential impact of WPS on Orthoptera

We calculated the number of threatened Orthoptera and the percentage overlap of their distribution range with WPS polygons now and in the future for the two zones of the sustainable scenario (exclusion zone and potential investment zone). We also calculated the number of threatened Orthoptera inhabiting islands, mountains and lowlands (species occupying both mountains and lowlands are considered in both categories).

Results

Impact of wind energy infrastructures on the target species

From all RES planned in the study area, only wind energy facilities coincided with the suitable habitats of the three targeted species in two out of the seven mountains, namely Mt Oiti (five WPS, 28 wind turbines, 120.6 GW, 9.7 km^2) and Mt Oxia (six WPS, 58 wind turbines, 179.6 GW, 10.4 km^2) (Table S2).

While all target species experience quite high physical connectivity (Cohesion) among habitat patches, the amount of suitable habitat and degree of patch connectivity vary substantially across the mountains they occupy (Table S3). *Parnassiana tymphrestos* shows a restricted distribution in four mountains and is going to experience 9% loss of its total habitat area and 6% reduction in the Area of Occupancy (AOO), due to WPS deployment on Mt Oiti, but no change in the Extent of Occurrence (EOO) **(**Table 1; Fig. 2**)**. *Parnassiana coracis* inhabits only two mountains, and it is the most vulnerable species severely affected by the WPS deployment on Mt Oxia. It shows the lowest distribution metrics in terms of AOO and EOO, which are going to be substantially reduced (27% and 23%, respectively), along with a reduction of the total suitable habitat area of 7%. Two out of the six mountainous populations of *O. willemsei* will be affected by WPS infrastructures. The species is anticipated to lose 4% of its total suitable habitat area, with a decline of AOO of 11%, without a change in EOO **(**Table 1, Fig. S2).

At the local scale, the model showed a strong positive scaling of population size with suitable habitat area (β_1 = 1.13 ± 0.07 SE), indicating decreasing population density with decreasing habitat extent (Table S4). The planned WPS on Mt Oiti are projected to substantially impact populations of *P. tymphrestos* and *O. willemsei*, causing 11–17% loss of suitable habitat, medium population reductions of 12–18%, a significant decrease in patch connectivity (12–55%), and a slight decline in cohesion (< 0.2%) **(**Table 1**)**. The planned

Table 1 Patch cohesion index (Cohesion), effective mesh size (Connectivity), suitable habitat area (Habitat) and population decline for the three target species in two mountains before and after the installation of Wind Power Stations and distribution metrics for their total range

Species Mountain		*P*. tymphrestos			*P*. coracis			O. willemsei		
		Before	After	*R*. (%)	Before	After	*R*. (%)	Before	After	*R*. (%)
Oiti	Cohesion (%)	99.86	99.68	0.18	-	-	-	99.97	99.96	0.01
	Connectivity (km^2)	16.50	7.48	54.67	-	-	-	34.51	30.48	11.65
	Habitat (km^2)	27.10	24.18	10.77	-	-	-	35.70	30.00	17.35
	Population decline (%)	12.1			-			17.9		
Oxia	Cohesion (%)	-	-	-	98.83	96.11	2.72	99.87	94.60	5.27
	Connectivity (km^2)	-	-	-	0.65	0.08	88.13	5.63	0.03	99.43
	Habitat (km^2)	-	-	-	2.74	1.40	48.94	6.15	3.88	36.91
	Population decline (%)	-			53.2			40.6		
Total range	Habitat (km^2)	35.34	32.11	9.13	20.44	19.09	6.58	164.85	157.84	4.25
	AOO (km^2)	64	60	6.25	44	32	27.3	76	68	10.50
	EOO (km^2)	647	647	0	87	67	23	758	758	0.00

R (%): Rate of decline, AOO: Area of Occupancy. EOO: Extent of Occurrence

WPS on Mt Oxia are expected to have a devastating impact on *O. willemsei* and *P. coracis*, causing 37–49% loss of suitable habitat, severe population declines of 41–53%, severe patch connectivity reduction by 88–99%, and a 3–5% decline in patch cohesion (Table 1).

Potential impact of renewable facilities on Orthoptera

The Renewable Energy Sources polygons (data as of January 2025) currently overlap with the distribution range of 62% of the threatened Orthoptera species of Greece (52 species), and this number will reach 79% (66 species) in the future. They will potentially affect 7 out of the 11 Critically Endangered Species, 28 out of 29 Endangered species, 31 out of 44 Vulnerable species, as well as 51 endemic species in total (Table S5). RES polygons will occupy 2.2% (±2.2%) of the distribution area of the red-listed species on average (Table S1).

Among all RES types, the WPS polygons overlap with a greater number of red-listed Orthoptera species of Greece than photovoltaic stations, biomass, hybrid and solar thermal stations in descending order, and the same trend applies for future investments (Table S5). The land impact of photovoltaic stations in terms of their polygon cover is currently limited but is projected to increase sixfold, within the distribution range of 27 species. Fewer species might be affected by the deployment of other RES and none by solar thermal stations.

Many small hydroelectric stations are planned within the distribution range of the species, but their spatial impact cannot be assessed (point data across rivers, no data on auxiliary infrastructures cover).

The business-as-usual scenario

Under the business-as-usual scenario, the national wind power installation goals will be largely achieved (Fig. 3). The power installed or to be soon installed (operation and construction permits) in January 2025 was 7.48 GW, corresponding to 84% and 58% of the 2030 and 2050 national targets (8.9 and 13 GW installed wind power, respectively). The total investment interest for onshore wind harnessing was threefold higher (323%) than the 2050 national target, reaching 41.97 GW. It corresponded to 12,547 wind turbines, out of which 3,663 turbines were inside the Natura 2000 network of protected areas (27% of total wind power). Figure S3 presents the localities of WPS as 1 × 1 km grid cells in relation to the Natura 2000 protected areas in Greece. If all investments are to be approved for construction, 9,059 more wind turbines will be planted, out of which 2,649 turbines will be located inside the Natura 2000 network of protected areas (Fig. S3).

The percentage of threatened Orthoptera species accommodating WPS in their distribution range is going to rise from 52% to 79% (52 to 66 of the 84 threatened species), with the total occupied area of WPS polygons rising from 373 km^2 to 3,087 km^2 (Table S5).

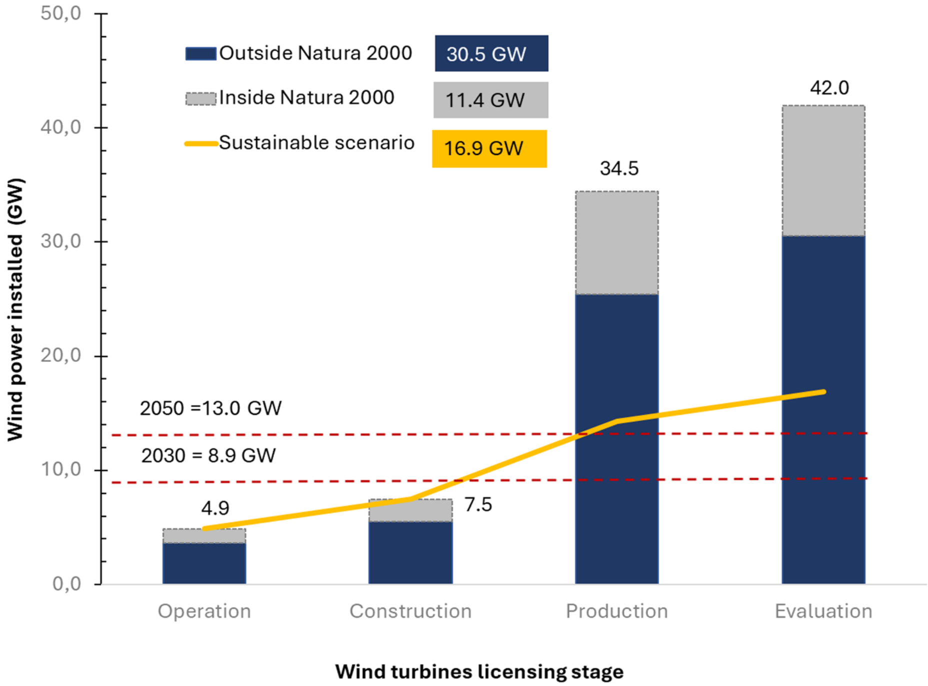

Fig. 3 Cumulative wind power (GW) installed across the successive permission stages of Wind Power Stations applications (wind turbine data of 15/1/2025) according to the business-as-usual scenario (inside and outside the Natura 2000 network) and the sustainable scenario, in relation to the national targets (NT) for onshore wind power installed by 2030 (8.9 GW) and 2050 (13 GW)

Table 2 Geography of wind power harnessed in Greece and percentage of threatened Orthoptera species whose distribution overlaps with WPS polygons across three geographical categories, after the business-as-usual scenario and the sustainable scenario (potential investment zone)

Geographical categories	Business-as-usual scenario					Sustainable scenario		
	Inside N2000 (GW %)	Outside N2000 (GW %)	Total (GW %)	Species (%Nt, Ne|Nt)	Over-lap (km^2)	Out-side (GW %)	Species (%Nt, Ne|Nt)	Over-lap (km^2)
Current power of WPS (7.48 GW)								
Islands	11	11	22	20% (15|17)	13	-	-	-
Mountains	9	25	34	38% (21|32)	181	-	-	-
Lowlands	7	37	44	23% (9|19)	184	-	-	-
Planned power of WPS (34.49GW)								
Islands	16	22	37	27% (21|23)	287	40	14% (12|12)	95
Mountains	6	18	24	57% (33|48)	803	13	37% (21|31)	250
Lowlands	5	33	38	40% (20|34)	1665	47	35% (16|29)	732
Total power of WPS (41.97 GW)								
Islands	15	20	38	27% (23|23)	300	33	14% (12|12)	97
Mountains	6	20	26	61% (36|51)	984	22	38% (22|32)	281
Lowlands	6	33	39	42% (21|35)	1848	45	35% (16|29)	768

Islands are foreseen to accommodate disproportionally more turbines in their area: 35% of the total wind power (5,245 wind turbines) in 19% of Greek land (25,333 km^2) (Table 2). They host 23 threatened Orthoptera species (27%) that are all endemics to the Greek islands (100% of distribution range in insular Greece) (Table 2, Table S1). The mountainous zone above 1,000 m in the Greek mainland (16,266 km^2) is also foreseen to accommodate disproportionally more turbines: 26% of the total wind power (2,920 wind turbines) in 12% of Greek land. This zone hosts 43% of all threatened species: 32 species (27 endemics) inhabit the mountainous zone, with 24% of their total distribution range falling in this zone. Most species (32 species, 27 endemics) are high-altitude species inhabiting exclusively this zone (22% of their total distribution). The lowland zone below 1000 m in the mainland (90,482 km^2) is foreseen to accommodate disproportionally less wind power in its area: 39% of wind power and 4,382 turbines in 69% of the country (Table 2, Table S5, Fig. S4-S5). The zone hosts 35% of all threatened species (29 species out of which 17 are endemics), with 77% of their total distribution range falling in this zone.

Sustainable scenario

According to the sustainable scenario, the national wind harnessing goals can be met exclusively in the potential investment zone. The zone covered 40.94% of Greece (53,584 km^2) (Fig. S4), and the power of the WPS applications in January 2025 overcame the 2050 national target for installed wind power by 30% (16.9 vs. 13 GW) (Fig. 3). The scenario allowed the installation of a further 2,439 wind turbines (1,086 in the islands, 300 in the mainland above 1,000 m and 1,053 in the remaining mainland), all outside the Natura 2000 network, adding 9.4 GW of wind harnessing. A great number of 6,620 new turbines in areas of high ecological value and natural landscapes would be rejected, including 2,873 turbines in the islands and 1,722 turbines in the mountainous zone above 1,000 m in the mainland (Table 2, Fig. S5).

The suitable habitat of the four target species would be fully protected, as 100% of their suitable habitat area fell outside the potential investment zone (Fig. S4). The percentage of threatened Orthoptera species accommodating WPS in their distribution range is going to rise from 52% to 68% (44 to 57 species out of 84 threatened species), with the total occupied area of WPS polygons rising from 373 km^2 to 1,075 km^{2,} corresponding to 0.9% (±2.1%) of the species distribution ranges (Table S5). This percentage was significantly lower than the respective proportion in the business-as-usual scenario (Wilcoxon signed-rank test, $p<0.05$).

Discussion

Impact of wind facilities on the target species

Our findings showed that wind energy facilities could cause substantial loss (4.3–9.1%) of the suitable habitats of the three endemic and red-listed Orthoptera species, leading to local population declines. Land use change is the primary threat to grasshopper communities (Pernat et al. 2024), often exceeding the negative effects of climate change (Dey et al. 2021), with the two drivers acting synergistically (Löffler et al. 2019). Land conversion to artificial land, known as land take, is its most detrimental form. It can cause direct habitat loss through soil sealing and rapid degradation of habitat quality in terms of plant biomass reduction (Gao et al. 2023) and alteration of vegetation composition (Urziceanu et al. 2021). Therefore, it can impact grasshoppers more severely than other land uses that still pose significant threats to their communities, such as mowing, grazing, and fertilization (Chisté et al. 2016; Hochkirch et al. 2016).

Impact on local populations

Our results underlined the devastating impact of WPS on a local scale. *P. coracis* will be the most severely affected species by WPS. This flightless species will lose almost half of its habitat and population on Mt Oxia, hosting the largest population of the two mountains in which it occurs. Wind facilities could trigger even its local extinction in the future, when considering additionally the eight-fold time fragmentation increase and the decline of physical patch cohesion that were not considered in the population model. The population of *O. willemsei* might also face an extinction risk on Mt Oxia. The species is also flightless and is going to undergo a substantial habitat loss, population decline, severe habitat fragmentation (176-fold fragmentation increase) and decline of patch cohesion. Habitat loss and fragmentation can lead to immediate or time-delayed species loss, known as the extinction debt (Krauss et al. 2010), through a gradual process of hampering inter-population dispersal and reducing local genetic pools (Ortego et al. 2015). The response of grasshoppers depends on their life history traits, such as dispersal ability and feeding strategies (Nufio et al. 2011). It is not known if and when the two species will be locally extinct in this mountain, but it is possible to happen in few decades, depending on the initial population size, the critical threshold of habitat patch area required for the species, the habitat quality within the patch remnants (Pasinelli et al. 2013; Poniatowski and Fartmann 2010), as well as the rate of genetic erosion process, being faster in species with limited dispersal ability (Kaňuch et al.

2012), and other pressures that could accelerate the extinction process. Assuming the extinction of the two species on Mt Oxia, a decline in the Extent of Occurrence will follow for *P. coracis* but not for *O. willemsei* inhabiting six mountains. However, a second population of *O. willemsei* will be affected by WPS, raising concerns about the cumulative impact of WPS on its global population. Similarly, the planned WPS on Mt Oiti is going to cause a moderate population decline for *P. tymphrestos*. This mountain supports the largest known population of the species, highlighting risks for the global population amid the rapid wind developments in the mountains of the country.

Other threats

Besides land artificialization and the consequent habitat loss and fragmentation from the planned WPS in the study area, other pressures can act synergistically in the seven mountains and increase the species' global extinction risk, such as wildfires, climate change and land use practices. The frequency and severity of extreme wildfires are increasing in Greece, leading to unprecedented natural disasters (OECD 2024). For species with limited distribution, such as most red-listed endemics, a single or a few wildfire events can result in the loss of entire populations and potentially cause global extinction. Climate change is another major threat. Projections indicate that global warming will profoundly impact the Mediterranean region (Lionello and Scarascia 2018), including shifts in the elevational ranges of montane insects (Menéndez et al. 2014). In the case of the target species, climate change is expected to impact their climate niche through altered precipitation and evapotranspiration patterns (Stefanidis et al. 2025b). Other pressures for the target taxa involve further habitat loss from mining activities expansion on Mt. Giona or touristic infrastructure expansion on Mt Tymphrestos, while the impact of grazing on high-altitude species can be positive, hampering forest encroachment, or negative, depending on the grazing regimes and livestock type [IUCN assessments: *P. coracis* (Willemse et al. 2016), P. *tymphrestos* (Kati et al. 2025b)d *willemsei* (Kati and Willemse 2025)].

Red-list assessment

If the WPS projects are to be constructed, they may increase the extinction risk of the species, but this is not going to be reflected in the status of the red-list assessments, remaining the same before and after the construction of the WPS. The red-list status of the species is suggested to change based on the updated distribution pattern of the species (Stefanidis et al. 2025b; Trillo and Ortego 2025) and our findings. The assessment of *P. tymphrestos* remains Endangered, considering the restricted distributions (criteria B1, B2), the fragmented distribution pattern and the continuing decline inferred. The same criteria apply to the other two species, with *P. coracis* being upgraded from Vulnerable to Critically Endangered and *O. willemsei* being downgraded from Critically Endangered to Endangered.

Potential impact of renewables on Orthoptera

At the national level, we found that RES facilities fall within the distribution range of most red-listed species in Greece (52 species), potentially affecting 66 of the 84 threatened species in the future, if all planned projects are implemented **(Table S5).** However, RES polygons cover only a small percentage of species' distribution ranges, indicating a low likelihood of significant impact. These findings underscore the potential, rather than the actual, impact of RES on the species. The species distribution ranges are much broader than the occupied habitat of the species, reflecting the "current known limits of distribution of a species, accounting for all known, inferred or projected sites of occurrence" (IUCN Spc 2024), including non-suitable habitats as well. Nonetheless, such overlaps signal emerging threats for Orthoptera with very restricted ranges, increasing their extinction risk, as captured by criterion B of the IUCN Red List, commonly used in the absence of population trend data (Le Breton et al. 2019; Maes et al. 2015). For instance, land industrialization stemming from a WPS project in the mountains of central Evvoia island in Greece might affect 23 red-listed species, including two mountainous short-winged endemic grasshoppers: the Endangered Lucas' Dark Bush-cricket (*Pholidoptera lucasi*) and the Vulnerable Dirphys Greek Bush-cricket (*Parnassiana dirphys*) (Kati et al. 2025a). If and how much the species will be impacted is a matter of chance. As demonstrated by the case study of the three target species, the incidental placement of renewable energy facilities within suitable habitats can have moderate to detrimental impacts, depending on the localities of the investments and the spatial configuration of the subpopulations. The uncertainty derives from the large knowledge gaps on Orthoptera distribution patterns and habitat preferences, filled so far for only eight species in Greece (*Chorthippus lacustris* (Kati et al. 2006), P. *parnassica*, *O. parnassica* (Stefanidis et al. 2025a), P. *coracis*, *P. gionica*, *P. tymphrestos*, *O. tymphrestosi* and *O. willemsei* (Stefanidis et al. 2025b). Unless species habitat mapping is completed, the actual impact of RES on grasshopper populations cannot be predicted. Greater conservation efforts are needed to establish baseline knowledge for insect distributions, habitats and population trends to halt their global decline (Wagner et al. 2021), under the new conditions of land artificialization (Winkler et al. 2021) accelerated from the fast green energy developments (Kiesecker et al. 2019).

The business-as-usual scenario

Our results underscored that the wind industry poses a great threat to threatened Orthoptera, as under the business-as-usual scenario, it is anticipated to potentially affect most species, converting 3,087 km^2 of land to artificial surfaces inside their distribution ranges. Some red-listed species, such as cave-dwelling ones, are unlikely to be directly affected by onshore WPS. Nonetheless, the biodiversity-wind energy conflict is severe for mountains and islands. On one hand, these areas are preferred wind investment grounds, and on the other hand, they harbor the most threatened and endemic grasshopper species (Table 2, Table S1).

Furthermore, our results showed that the implementation of the Natura 2000 legislation under the business-as-usual scenario has not efficiently impeded land-consuming projects that can undermine its ecological integrity and harm biodiversity. With a protected area accounting for 27.2% of the Greek mainland, the network already accommodates 29% of current onshore wind harnessing (1,014 turbines) and is expected to accommodate 2,649 more turbines if all projects are going to be approved. The business-as-usual scenario has allowed so far disproportionally more wind harnessing in mountains and natural forested land, against the general European trend of avoiding such areas, and has generated a large land take footprint due to wind planting in remote, undeveloped mountainous areas with steep slopes (Kati et al. 2023a).

The business-as-usual scenario is expected to swiftly reach and largely exceed the national energy goals. Greece is among the most attractive global markets for wind energy investments (RECAI 2024), aspiring to become a green energy hub in Southeast Europe. This is reflected in our results by the impressive investment interest, being threefold higher than the national wind energy target set for 2050. Nowadays, the country has achieved more than half of its national wind harnessing goal by 2030 (operating WPS) without adequate spatial planning. The scenario reflects the national policies and procedural contexts that speed up the deployment of the wind energy sector under poor spatial planning and environmental impact assessment processes at the expense of nature and biodiversity (Kati et al. 2021, 2025a). This tendency will continue to affect species, as also illustrated in the case study of the three target species, despite the relevant national legislation for the protection of red-listed and endemic species (Biodiversity Law 3937/31-3-2011). Beyond Orthoptera, the scenario comes with important losses for nature, including the fragmentation and loss of many wilderness areas in Greece (Kati et al. 2023a, 2025a), increased species extinction risks (Bounas et al. 2025), degradation of landscape qualities coupled with substantial social oppositions (Skiniti et al. 2022; Vlami et al. 2020).

The sustainable scenario

The sustainable scenario was initially developed as a horizontal spatial planning guideline for WPS, banning them as land-consuming projects from ecologically sensitive areas, protecting the Natura 2000 network and natural landscapes with low fragmentation values from artificial land conversion (Kati et al. 2021). It offered multiple benefits for biodiversity by better protecting habitats and species covered by European legislation (EC 1992, 2009), Important Bird Areas now recognized as Key Biodiversity Areas, and the roadless areas of the country. However, it was criticized for falling short of the more ambitious 2050 wind energy targets, which had not yet been established at the time. Our study presents the improved scenario version, slightly increasing the windfarm banning zone by including roadless islands and roadless patches over 5 km^2 to better protect natural landscapes. The sustainable scenario identified 41% of Greek land as a suitable zone for potential wind project licensing, and it enables the country to meet and even exceed its 2050 wind energy targets by 30%, allowing flexibility for potential project rejections.

If implemented, the scenario will succeed in fully protecting the habitats of the three target species and hence halt local population declines and potential local extinctions from wind energy infrastructures. It also seems to contribute to the maintenance of threatened Orthoptera in Greece, with fewer species being potentially affected by WPS developments and WPS polygons occupying significantly lower land areas in the species distribution ranges. It is going to primarily benefit high-altitude species in the mainland, as it would allow only 300 wind turbines vs. the six-fold higher number of the business-as-usual scenario, as well as island species, allowing 1088 wind turbines vs. the three-fold higher number of the business-as-usual scenario. Mountains and islands are centers of endemism for grasshoppers, hosting 79 mountain endemics (mainland) and 78 island endemics (Willemse et al. 2018). Beyond grasshoppers, they are the most ecologically valuable areas of the country, harboring rare and endemic biodiversity (Kougioumoutzis et al. 2021; Spiliopoulou et al. 2021), while mountains can also act as climate refugia in Greece (Doxa et al. 2022). Although mountain ecosystems are among the most vulnerable to climate change

(Schmeller et al. 2022), RES developments to mitigate global warming should not compromise their essential roles in ecosystem functioning and the provision of ecosystem services (EEA 2010).

Methodological limitations and future directions

This study was subject to inherent uncertainties in population decline and species range estimates. We considered the area of WPS installation polygons unsuitable Orthoptera habitats. This assumption might have overestimated habitat and range loss because WPS polygons do not correspond to fully sealed permanently unsuitable habitats (Kati et al. 2023a), and grasshoppers could still occupy the remaining vegetated patches inside them. However, this would depend on the degree of habitat degradation during the construction phase, vegetation recovery and whether the quality of the remaining microhabitat patches could satisfy the specific ecological requirements of the target species. All species have a narrow and specialized ecological niche in terms of vegetation composition and structure; they depend on specific plant species (e.g., *Festuca jeanpertii*, *Astragalus creticus*, *Thymus longicaulis*), and require substantial cover of grass/herb height above 33% with a height above 25 cm (Stefanidis et al. 2025b). On the other hand, we might have underestimated habitat loss and fragmentation by not considering the area outside the WPS polygons, where vegetation clearance and habitat destruction also take place to support the wind turbine operation with complementary infrastructures (electricity pylons, meteorological towers, operational buildings, transmission lines, new access roads and road widening). The amount of land take outside the installation polygons is estimated to be 26% of the total artificial land generated in Greece (Kati et al. 2023a). The WPS impact on the target species might extend beyond direct land impacts. Wind facilities can alter local microclimates, which may have pronounced effects on invertebrates (Elzay et al. 2017). Turbine-induced wake effects can influence precipitation, temperature, and evaporation rates (Fiedler and Bukovsky 2011; Zhou et al. 2013). The climatic niche of the target species is narrow and shaped by specific climatic variables, such as precipitation during the driest quarter, annual temperature range, and potential evapotranspiration (Stefanidis et al. 2025b). Given the limited knowledge of the ecological requirements of threatened grasshopper species, the precautionary principle should be applied when assessing and interpreting the estimated range population declines.

The sustainable scenario considers the officially submitted WPS applications and assumes that developers have pre-assessed wind resource adequacy and basic sitting constraints (e.g. settlements, archaeological sites and military zones) to ensure the technical viability, economic profitability and regulatory admissibility of their investment. Under this assumption, the land in the potential investment zone satisfies and overcomes the national energy goals of 2050 by over 30%. The sustainable scenario is not intended to replace the pending national RES strategic planning or project-level environmental impact assessments; rather, it provides a spatial guideline that prioritizes investment areas with less biodiversity cost, as illustrated here for globally threatened grasshoppers. Strategic planning for RES deployment should consider wind-harnessing efficiency and address the full range of environmental components required by the Strategic Environmental Assessment (SEA) Directive, including biodiversity, soil, air, water, landscape, cultural heritage, and human well-being, while accounting for cumulative and landscape-scale impacts. Within this framework, species-specific analyses, such as those presented here provide complementary evidence that strengthens biodiversity-sensitive RES spatial planning. We underline the need for field surveys, species distribution modeling, and habitat connectivity analyses to quantify the land impact of renewable energy infrastructures on grasshopper populations and guide conservation efforts (Jackson and Robertson 2011; Thomaes et al. 2008), focusing on the species with restricted distributions and dispersal abilities that are more vulnerable to local extinctions (Cardoso et al. 2020). Further research is also required to support the integration of other important biodiversity components alongside cultural, social, and landscape values in forthcoming national strategic renewable energy spatial planning, enhancing broad public acceptance.

Conclusion

Our study provided a first insight into the potential devastating land impacts of wind energy infrastructures on insect populations at the local scale and discussed their potential threats posed to the globally threatened and endemic Orthoptera of Greece. As local extinctions precede global extinctions, early warning signals for species declines should be considered in conservation action (Kempel et al. 2020).

We proved that sustainable spatial planning by sitting in wind turbines outside protected areas and landscapes of high naturalness would halt population declines of the three Orthoptera species studied. It would also better protect mountains and islands as the most ecologically valuable areas of great endemism while succeeding in meeting and exceeding the ambitious national wind harnessing targets by 2050. The recommended sustainable scenario aligns with the growing scientific consensus advocating for selecting sites for planting renewables away from ecologically sensitive zones (Kiesecker et al. 2024; Rehbein et al. 2020; Serrano et al. 2020; Wang et al. 2025), and such solutions should be adopted in the strategic spatial planning process and relevant policies.

However, global and European policies have not efficiently addressed the land take problem, and the European policies for green energy development and nature conservation are largely conflicting (Kati et al. 2023a). We propose a more effective reconciliation of these two conflicting policies through sustainable spatial planning approaches, in line with European (EC 2020) and global guidelines (Bennun et al. 2024).

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Data availability All data supporting the findings of this study are available within the paper and its Supplementary Information. Geospatial data are openly available in Mendeley Data (v4) at https://doi.org/10.17632/kh3fjww93t.4

Declarations

Competing interests The authors declare no competing interests.

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