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Beyond migration: How landscape composition and heterogeneity sustain stationary honey bee colony productivity across biogeographical regions

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ABSTRACT

Migratory beekeeping provides honey bees with abundant floral resources, but migration imposes ecological and physiological costs. We investigated whether landscape composition and heterogeneity can support stationary colony productivity comparable to migratory colonies. We quantified productivity from daily weight changes in 2313 hives from 2020–2024, comparing management strategies and assessing landscape relationships in stationary colonies overall and by biogeographical region. Landscape models included year, mean seasonal temperature, and cumulative precipitation. Migratory and stationary colonies showed similar frequencies of productive days, but migratory colonies had higher mean seasonal productivity and larger daily weight gains and losses. In stationary colonies, mean seasonal productivity decreased with pasture cover and increased with landscape heterogeneity, whereas daily weight gains and losses increased with forest cover and decreased with urban cover. Higher temperatures were associated with smaller daily gains and losses, and cumulative precipitation with larger daily losses. Predicted daily gains were lower than those of migratory colonies only above 43.5% urban cover. In the Continental region, urban cover was negatively associated with mean seasonal productivity and daily gains and losses, whereas industrial, commercial and transport cover was positively associated with mean seasonal productivity. In the Mediterranean region, mean seasonal productivity decreased with permanent crops and pastures and increased with landscape heterogeneity and cumulative precipitation. No landscape relationships were significant in the Alpine region. Overall, stationary colonies reached productivity comparable to migratory colonies depending on landscape attributes, with greater heterogeneity of natural and semi-natural habitats associated with higher mean seasonal productivity.

1. Introduction

Migratory beekeeping is a long-established form of traditional colony management, characterised by the seasonal movement of colonies to overwinter and increase honey production (Mavrofridis et al., 2024). Since the introduction of movable-frame hives in the mid-nineteenth century (Crane, 1999), migratory beekeeping has been a defining feature of large-scale intensive beekeeping. Today, migratory beekeeping is driven by multiple, partly overlapping motivations related to pollination services, honey production strategies, and the need to cope with spatial and temporal variability in floral resources.

In modern intensive beekeeping, colonies are often relocated to provide pollination services to monocultures of cultivated plants that depend on animal pollination for fruit set (Martínez-López et al., 2022). The expansion of monocultures has intensified cropping systems' reliance on managed honey bees. This is because agricultural intensification is associated with landscape simplification, leading to the erosion of wild pollinator communities (Maurer et al., 2024), whose reduced abundance and diversity cannot sustain reliable fruit set (Narjes and Lippert, 2019). The resulting dependence on managed pollination services has become a primary driver of seasonal colony migration to follow the spatiotemporal distribution of crop flowering. In this context, colony migration may often be decoupled from the maximisation of honey production (Bond et al., 2021). Almond pollination systems provide a representative example, because the honey produced has low market desirability due to its organoleptic properties and therefore is not

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Table 1
Main environmental and land-use features of the Alpine, Continental, and Mediterranean biogeographical regions, including morphology, climate regime, potential natural vegetation, and current landscape structure (Fratianni and Acquaotta, 2017; Blasi, 2010; Tasser et al., 2007; Garbarino et al., 2011; Della Bella et al., 2021; Lorenzato et al., 2024).

Biogeographical region	Morphology	Climate regime	Potential natural vegetation	Main land use	Current landscape structure
Alpine	Complex orography; high mean elevation; steep altitudinal gradients	Low mean temperatures; high precipitation; marked seasonal snow cover persistence	Montane and subalpine conifer forests (*Picea abies*, *Larix decidua*, *Pinus cembra*); mixed or pure *Fagus sylvatica* stands; dwarf shrub communities and alpine grasslands above treeline	Long-term forest management; livestock grazing in alpine and subalpine pastures; transport infrastructure development	Heterogeneous mosaic of natural and semi-natural forest stands; extensive managed forests; natural and semi-natural grasslands; fragmented wetlands and riparian habitats confined to valley floors
Continental	Predominantly lowland and alluvial plains (Po Plain), bordered by mountain systems; limited topographic variation	Strong seasonal temperature contrasts; cold winters; warm summers; frequent thermal inversions in lowland areas	Mixed deciduous broadleaf forests (*Quercus robur*, *Carpinus betulus*); riparian forests along major river systems	Intensive agriculture; industrial and urban expansion; large-scale hydrological regulation	Agricultural matrix dominated by monocultures; dense urban and industrial centres and widespread low-density urbanisation; remnant semi-natural habitats mainly along rivers and foothills
Mediterranean	Morphologically heterogeneous: Coastal plains and lowlands interspersed with extensive hilly and mountainous inland sectors	Mild winters; pronounced summer aridity; autumn–winter precipitation maxima	Evergreen sclerophyllous forests (*Quercus ilex, Quercus suber*); thermophilous oak forests; *Fagus sylvatica* stands in mountains; shrublands; grasslands above treeline	Perennial crops (e.g., olive groves, vineyards); mixed and extensive agriculture; land abandonment in uplands; coastal tourism development	Heterogeneous mosaic of agricultural land and fragmented natural and semi-natural vegetation; urban and tourism-oriented coastal settlements

a primary production objective (Goodrich et al., 2019).

Alongside pollination services, diversification strategies in honey production, particularly those targeting monofloral honeys, are a significant driver of seasonal colony migration, especially in regions such as Europe, Australia and China (Martínez-López et al., 2022). Seasonal colony migration reflects the need to access spatially and temporally distinct nectar flows associated with specific plant species, enabling the differentiation of honey production (Persano Oddo and Piro, 2004). Among the most produced monofloral honeys are those derived from monocultures (e.g. *Brassica napus* L. and *Helianthus annuus* L.) or from plant species widespread and abundant in natural and semi-natural habitats, such as *Castanea sativa* Mill., *Robinia pseudoacacia* L., *Taraxacum officinale* F.H.Wigg., and *Tilia* spp. Their extensive and predictable flowering enables relatively stable and repeated production (Persano Oddo and Piro, 2004). In contrast, rare monofloral honeys are generally produced from nectar sources with restricted geographical distributions, short or irregular flowering periods, or ecological conditions that limit honey bee density (Crane, 1999), including alpine (e.g. *Rhododendron* spp. honey; Leoni et al., 2021) or coastal habitats (e.g. *Limonium* spp. honey; Fantinato and Buffa, 2019).

Beyond product differentiation, colonies are also moved to secure continuous and abundant floral resources, particularly under conditions of landscape simplification and climate change (Le Féon et al., 2010; Neumann and Straub, 2023). Landscape simplification, driven by urban expansion and agricultural intensification, has progressively reduced the density, diversity, and phenological continuity of floral resources for honey bees, resulting in recurrent foraging gaps during the production season (Tscharntke et al., 2005; Requier et al., 2015). In addition to agricultural intensification, the abandonment of marginal, less productive areas has further contributed to floral resource depletion through processes of vegetation succession and shrub encroachment, reducing the availability of open, flower-rich habitats (Fantinato et al., 2023). Climate change interacts with landscape simplification, increasing inter-annual variability in resource availability and amplifying seasonal resource fluctuations (Vanbergen et al., 2013). The ongoing impacts of landscape simplification and climate change on floral resource availability are already prompting adaptive strategies in beekeeping practices, including increased reliance on supplemental artificial feeding and more frequent seasonal colony migration (Neumann and Straub, 2023).

Importantly, colony migration often involves long-distance travel under variable environmental conditions that can harm colony health (Melicher et al., 2019). Transportation can disrupt the development of food glands of worker bees, resulting in downstream effects on brood nursing and colony-level functioning (Ahn et al., 2012). Reduced lifespan and increased oxidative stress observed in migratory adult honey bees indicate cumulative physiological costs from repeated colony movements, while transport-related thermal stress has been identified as an additional factor contributing to annual colony losses (Simone-Finstrom et al., 2016; Melicher et al., 2019). Colony migration is also associated with increased parasite loads and pathogen infections, as well as greater transmission between managed honey bees and wild pollinators, thereby raising the likelihood of spillover and spillback events (Zhu et al., 2014; Martínez-López et al., 2022). Collectively, these phenomena decrease colony health, resulting in unpredictable honey productivity and unreliable economic returns for beekeepers. The abrupt introduction of high densities of managed honey bees into new sites can also intensify competition for floral resources with wild pollinators, contributing to the simplification and weakening of local networks of pollination interactions (Davis et al., 2025).

The balance between the benefits and costs of migratory beekeeping raises the question of whether, and under which landscape conditions, stationary colonies can achieve honey productivity comparable to that of migratory colonies. Landscape attributes may be a key factor influencing the density, diversity and phenological continuity of floral resources, potentially enabling stationary beekeeping to be a valuable alternative to seasonal migration (Lecocq et al., 2015). As honey productivity depends on the balance between production gains and losses, as well as on the continuity of productive periods, disentangling these components is essential to understand how landscape can promote honey production for stationary colonies, and make them as advantageous as migratory colonies. Furthermore, the effects of landscape attributes are likely to differ across distinct biogeographical regions, because the unique environmental and ecological characteristics of each region result in differences in the density, diversity, and phenological availability of floral resources (Templ et al., 2017).

Accordingly, in the present study we addressed the following questions: (i) What is the contribution of the frequency of productive days, mean seasonal productivity, and the magnitude of production gains/losses to making migratory colonies more advantageous than stationary colonies? (ii) Which landscape attributes influence mean seasonal productivity and production gains/losses of stationary colonies? (iii) Under which landscape attributes do mean seasonal productivity and

production gains/losses of stationary colonies become comparable to those observed in migratory colonies? (iv) Do the effects of landscape attributes on mean seasonal productivity and production gains/losses vary among biogeographical regions?

2. Materials and methods

2.1. Study site

The study was conducted in Italy, covering a broad latitudinal and altitudinal gradient encompassing the Alpine, Continental, and Mediterranean biogeographical regions. Biogeographical regions are large-scale geographical units defined by coherent patterns of climate, geomorphology, and potential natural vegetation, providing a framework for capturing broad-scale environmental and ecological differences across Italy (Metzger et al., 2005; European Environment Agency, 2017). The proportional distribution of the Italian terrestrial surface among the three regions is 18% for the Alpine region, 29% for the Continental region, and 53% for the Mediterranean region (Zivkovic et al., 2017). The key climatic, geomorphological, potential natural vegetation, and dominant land-use features of the three biogeographical regions are summarised in Table 1.

2.2. Data collection

Colony productivity was assessed using hive weight data from electronic hive monitoring systems deployed in 7100 hives. Hive weight is widely used in monitoring due to its strong relationship with colony health and productivity (Lecocq et al., 2015; Czekońska et al., 2023). Data were collected using smart hive monitoring devices (3Bee srl, Italy), which integrate load-cell-based scales installed beneath individual hives, allowing non-invasive and continuous measurement of total hive weight. The weight-measurement device had a stated instrumental error of 0.05 kg and a maximum capacity of 300 kg. Weight was recorded every three hours from midnight. Although the monitoring systems can record multiple hive parameters (e.g. internal temperature, relative humidity, and acoustic activity), this study used only hive weight data as an indicator of colony productivity (Liu and Lin, 2025). Analyses were performed on data collected during the production season (21 March to 21 December), over five consecutive years (2020–2024). Winter records (22 December–20 March) were excluded because colony weight dynamics during winter primarily reflect food consumption and reduced foraging activity rather than honey production (Meikle and Holst, 2015). Each monitoring device was equipped with a GPS module, providing geographic coordinates that enabled the identification of hive locations. We classified hives as stationary or migratory based on whether they were relocated by a distance greater than 7 km during the production season, adopting a conservative threshold to distinguish migratory movements from local relocations, consistent with previous distance-based approaches to classifying migratory beekeeping (Pavlin et al., 2025).

Landscape composition around each stationary hive was characterised using CORINE Land Cover (hereafter CLC) level 2 data within a 1 km radius buffer centred on the modal hive geographic coordinate. The 1 km buffer was selected to characterise the immediate landscape context surrounding each hive, as this is expected to exert the strongest influence on daily colony weight dynamics and provides a biologically meaningful approximation of the honey bee foraging area (Beekman et al., 2004; Hollands et al., 2025; Mahdizadeh Gharakhanlou et al., 2025). To capture ecologically meaningful variation in the proportion of land-cover and land-use types relevant to floral resource availability, we quantified landscape heterogeneity using the Shannon diversity index, calculated for natural and semi-natural land CLC classes (i.e., classes 3, 4, and 5) using CLC level 3 data to better reflect fine-scale differences in habitat types relevant to floral resource availability (Lorenzato et al., 2024).

Each hive was assigned to one of three biogeographical regions (Alpine, Continental, Mediterranean) based on its geographic coordinates (European Commission, 2013). For migratory colonies, the spatial distribution of hive locations across biogeographical regions was determined by the annual proportion of recorded coordinates in each region.

For each hive, climatic covariates were obtained from the E-OBS daily gridded observational dataset (version 33.0e; 0.1° regular grid; Copernicus Climate Change Service; Cornes et al., 2018). For each year, daily mean temperature (TG) and daily precipitation sum (RR) from 21 March to 21 December were aggregated over the production season to obtain mean temperature and cumulative precipitation.

2.3. Data analysis

Hive weight data were processed to derive daily weight change values. Weight records, originally collected at three-hour intervals, were converted to daily weight changes (kg day^{-1}) by calculating the difference between successive midnight measurements. This approach minimises the influence of short-term diurnal fluctuations associated with forager departure and return and provides a robust proxy for net daily colony weight change (Liu and Lin, 2025). To limit the influence of honey harvests, hive manipulations, measurement artefacts, and other non-biological disturbances known to affect continuous hive-weight records (Meikle et al., 2018), daily weight changes with absolute values exceeding 6 kg day^{-1} were excluded from subsequent analyses. The proportion of daily observations excluded based on the 6 kg day^{-1} threshold was comparable between stationary and migratory colonies, with annual mean proportions of 0.6% and 0.7%, respectively. To ensure temporal consistency and reduce biases associated with discontinuous time series, we considered only hives retaining at least 90% of daily observations during the production season. Consequently, of the 7100 hives initially monitored, 2313 hives met the data-quality and temporal-coverage criteria and were included in the final dataset.

For each hive and production season, four productivity variables were derived: (i) The occurrence of a positive daily weight change, coded as a binary variable (1 = daily weight gain; 0 = daily weight loss or no gain) to quantify the probability of productive days (hereafter, *positive day probability*); (ii) the *mean daily change* (kg day^{-1}), calculated by averaging all daily weight change observations to quantify mean seasonal productivity; (iii) the *mean daily gain* (kg day^{-1}), calculated by averaging only positive daily weight changes to quantify the magnitude of production gains; and (iv) the *mean daily loss* (kg day^{-1}), calculated by averaging only the absolute magnitudes of negative daily weight changes to quantify the magnitude of production losses.

Differences between stationary and migratory colonies were analysed using mixed-effects models fitted in R (R Core Team, 2024) with the lme4 package (Bates et al., 2015). The probability of observing a positive daily weight change was analysed using a generalised linear mixed-effects model (GLMM) with binomial error distribution and logit link function, fitted using the *glmer* function. Mean daily change was analysed using a linear mixed-effects model (LMM) fitted with the *lmer* function, whereas mean daily gains and mean daily losses were analysed using GLMMs with Gamma error distribution and log link function, also fitted using the *glmer* function. In all models, colony management strategy (stationary vs migratory) was included as a binary fixed effect, coded 0 for stationary and 1 for migratory, while year was included as a categorical fixed effect and hive identity was specified as a random intercept to account for repeated observations of the same hive across the five production seasons. Accordingly, the coefficient of colony management strategy represents the expected change in the response variable associated with migratory management relative to stationary management, after accounting for interannual variation.

We investigated the effects of landscape composition and heterogeneity on the three mean daily variables (change, gain, loss) only for stationary colonies. Relationships between the response variables and

the percentage cover of CLC classes and landscape heterogeneity were first analysed using global models including all stationary colonies, and then separately for each biogeographical region (Alpine, Continental and Mediterranean). Specifically, three response variables were modelled: (i) Mean daily change, (ii) mean daily gain, and (iii) mean daily loss. To account explicitly for temporal and climatic variation, year was included as a categorical fixed effect, whereas mean temperature and cumulative precipitation during the production season were included as continuous covariates.

Mean daily change was analysed using LMMs fitted with the *lmer* function, whereas mean daily gains and losses were analysed using GLMMs with Gamma error distribution and log link function, fitted using the *glmer* function. Initial models included the percentage cover of CLC classes, landscape heterogeneity, year, mean temperature, and cumulative precipitation as fixed effects, while hive identity was specified as a random intercept to account for repeated observations of the same hive across years. All continuous predictors, including landscape attributes, mean temperature, and cumulative precipitation, were standardised to zero mean and unit variance prior to model fitting to improve numerical stability. Year was not standardised and was entered as a factor. Gamma GLMMs were fitted using the BOBYQA optimiser, with a maximum of 200,000 function evaluations. Prior to model fitting, multicollinearity among landscape predictors was assessed using variance inflation factors (VIFs), calculated with the *vif* function of the R package car (Fox and Weisberg, 2019). Predictors with VIF values ≥ 3 were excluded (Zuur et al., 2009). Model selection was performed by backward elimination of non-significant landscape predictors. Year, mean temperature, and cumulative precipitation were specified a priori as control covariates and retained in all models irrespective of their statistical significance. The significance of fixed effects in Gamma GLMMs was evaluated using likelihood ratio tests (LRTs) comparing models with and without the predictor of interest (Zuur et al., 2009), whereas significance in LMMs was assessed using Satterthwaite-approximated F tests. Model assumptions were evaluated by inspection of residual distributions and diagnostic plots. Residual spatial autocorrelation in the final global models of stationary colonies was assessed using Moran's I, calculated separately for each year. Response residuals were used for the LMM fitted to mean daily change, whereas Pearson residuals were used for the Gamma GLMMs fitted to mean daily gains and losses. Hive coordinates were projected to ETRS89-LAEA (EPSG:3035), and hives located within 10 km of each other, corresponding to the upper range of reported honey bee foraging distances (Steffan-Dewenter and Kuhn, 2003), were considered spatial neighbours. Statistical significance was assessed using 999 permutations of model residuals within each year. P-values were adjusted across years separately for each response variable using the Benjamini–Hochberg procedure, with adjusted P-values < 0.05 considered statistically significant. For mixed-effects models, the variance explained by fixed effects alone and by fixed and random effects combined was quantified using marginal (R^2_m) and conditional (R^2_c) coefficients of determination, calculated with the *r.squaredGLMM* function of the R package MuMIn (Bartoń, 2020).

For the global models fitted to mean daily change and mean daily gain, sensitivity analyses were conducted by iteratively excluding stationary colonies with the lowest mean daily change and mean daily gain values to determine the productivity level at which stationary colonies exhibited mean daily change and mean daily gain comparable to those observed in migratory colonies. For each landscape predictor retained in the corresponding global model, we then assessed whether the fitted response crossed the response level identified by the sensitivity analysis within the observed range of predictor values. A landscape threshold was identified only when such an intersection occurred within the observed predictor range.

Complete model outputs, including fixed-effect estimates, confidence intervals, random-effect variance components, and model fit statistics, are provided in Supplementary material 1.

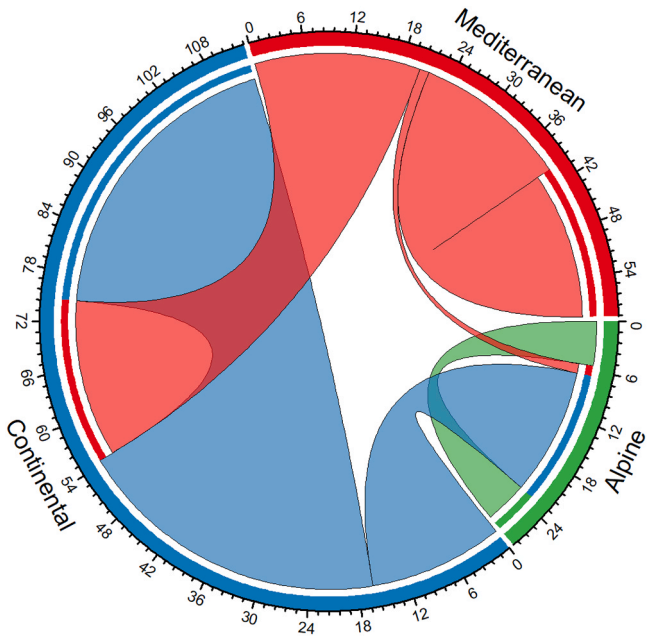


Fig. 1. Chord diagram illustrating movements of migratory honey bee colonies among biogeographical regions during the production season. Self-links indicate movements of migratory honey bee colonies within the same biogeographical region.

Table 2
Annual descriptive statistics of colony productivity for stationary and migratory honey bee colonies from 2020 to 2024. Values are mean ± SD. Mean daily loss is expressed as the absolute magnitude of negative daily weight changes.

Year	Management	N	Productive days	Mean daily change (kg day^{-1})	Mean daily gain (kg day^{-1})	Mean daily loss (kg day^{-1})
2020	Stationary	54	123.26 ± 27.59	0.07 ± 0.08	0.44 ± 0.17	0.24 ± 0.10
2020	Migratory	66	121.52 ± 27.93	0.07 ± 0.10	0.55 ± 0.23	0.32 ± 0.15
2021	Stationary	189	117.17 ± 22.96	0.03 ± 0.11	0.40 ± 0.18	0.25 ± 0.16
2021	Migratory	192	122.01 ± 26.28	0.06 ± 0.09	0.48 ± 0.20	0.28 ± 0.11
2022	Stationary	423	123.56 ± 26.07	0.08 ± 0.09	0.46 ± 0.21	0.24 ± 0.14
2022	Migratory	444	121.77 ± 23.22	0.11 ± 0.10	0.61 ± 0.22	0.28 ± 0.15
2023	Stationary	669	121.54 ± 26.72	0.04 ± 0.11	0.40 ± 0.18	0.24 ± 0.12
2023	Migratory	611	122.29 ± 21.16	0.08 ± 0.09	0.51 ± 0.20	0.28 ± 0.14
2024	Stationary	713	119.55 ± 26.45	0.04 ± 0.08	0.39 ± 0.17	0.23 ± 0.10
2024	Migratory	579	119.16 ± 24.99	0.06 ± 0.17	0.49 ± 0.21	0.28 ± 0.21

3. Results

The final dataset comprised 3940 production-season observations from 2313 hives, with each observation representing the time series of a single hive during one production season. Of these, 2048 observations from 1326 hives were from stationary colonies, while 1892 observations from 987 hives were from migratory colonies. The distribution of stationary colonies across biogeographical regions was as follows: 302 observations from 189 hives in the Alpine region, 947 observations from 604 hives in the Continental region, and 799 observations from 533

Table 3
Results of mixed-effects models comparing stationary and migratory honey bee colonies.

Response	β management	95% CI	Test statistic	P	R^2_m	R^2_c
Positive day probability	0.003	-0.013–0.020	$\chi^2 = 0.167$	0.683	0.005	0.903
Mean daily change	0.024	0.017–0.031	$F = 46.043$	< 0.001	0.043	0.160
Mean daily gain	0.142	0.110–0.174	$\chi^2 = 58.941$	< 0.001	0.037	0.677
Mean daily loss	0.115	0.085–0.146	$\chi^2 = 50.408$	< 0.001	0.016	0.633

Table 4
List and description of CORINE Land Cover classes significantly related to the response variables in the context of the study area. Descriptions were modified from Kosztra et al. (2017).

Landscape metric	Description
CLC 1.1 (urban fabric)	Areas mainly occupied by dwellings and buildings used for administrative or public utilities, including their associated lands, approach roads, and parking lots. Urban areas are typically characterised by low availability and diversity of floral resources, due to the prevalence of impervious surfaces and intensive vegetation management. However, urban green spaces, such as parks, gardens, and roadside plantings, often composed of ornamental species with staggered flowering phenologies, may provide a quantitatively limited, yet temporally continuous, supply of floral resources for honey bees.
CLC 1.2 (industrial, commercial and transport units)	Areas primarily occupied by industrial activities such as manufacturing, trade, financial services, and transport infrastructure for road and rail networks, airport facilities, river and sea port installations, including their associated land and access infrastructure. This includes industrial livestock rearing facilities. Industrial and commercial areas, typically located at city boundaries, can provide valuable floral resources for pollinators, as vegetated margins, embankments, brownfields, and remnant semi-natural habitats may support diverse flowering plants that contribute to honey bee foraging.
CLC 2.1 (arable land)	Land under a rotation system used for annually harvested crops, including fallow land, under rain-fed or irrigated conditions. This class also includes flooded crops such as rice fields and other inundated croplands. Agricultural practices generally reduce the availability and diversity of floral resources for honey bees by limiting the establishment and persistence of spontaneous herbaceous vegetation.
CLC 2.2 (permanent crops)	Land occupied by permanent crops not included in a rotation system, including vineyards, fruit tree and berry plantations, and olive groves.
CLC 2.3 (pastures)	Permanent grassland characterised by agricultural use or significant human disturbance. The floral composition is dominated by graminoids and influenced by human activity. Typically used for grazing (pastures) or mechanical harvesting of grass (meadows).
CLC 3.1 (forest)	Areas occupied by forests and woodlands with vegetation composed of native or exotic coniferous and/or broad-leaved trees, suitable to produce timber or other forest products. Under normal climatic conditions, forest trees are taller than 5 m with a canopy closure of at least 30%. For young plantations, the minimum threshold is 500 individuals per hectare. In addition to their productive role, forested areas can provide valuable floral resources for honey bees, particularly where diverse tree species, forest edges, understory vegetation, and flowering shrubs contribute to sustained nectar and pollen availability.

hives in the Mediterranean region. Among migratory colonies (Fig. 1), most recorded movements during the production season occurred within a single biogeographical region, particularly in the Continental region (38.22% of movements) and the Mediterranean region (18.79%), while movements confined to the Alpine region were less frequent (5.39%). Movements between biogeographical regions were mainly between the Continental and Mediterranean regions (19.57% of movements), followed by the Alpine and Continental regions (15.75%) and the Alpine and Mediterranean regions (0.65%). Movements spanning all three biogeographical regions (Alpine–Continental–Mediterranean) accounted for a small fraction (1.63%).

3.1. Differences between stationary and migratory colonies

Productivity variables showed interannual variation in both stationary and migratory colonies (Table 2). The number of productive days varied relatively little across years, whereas mean daily change, mean daily gain, and mean daily loss showed more pronounced interannual variation.

Mixed-effects models indicated no significant difference in the probability of experiencing positive daily weight changes between stationary and migratory colonies (Table 3). In contrast, mean daily change was significantly higher in migratory colonies, indicating higher mean seasonal productivity (Table 3). Moreover, both mean daily gains and mean daily losses were significantly higher in migratory colonies than in stationary colonies (Table 3).

3.2. Influence of landscape on stationary colonies

Both landscape composition and heterogeneity varied widely among landscape buffers of stationary colonies. Details are in Supplementary material 1, while the description of CLC classes significantly related to the response variables is in Table 4. Multicollinearity analysis led to the exclusion of CLC class 2.1 (arable land) from the global models of mean daily change and mean daily loss, because it was strongly and negatively correlated with CLC class 3.1 (forests). No landscape predictor was excluded because of multicollinearity from the mean daily gain model.

Mean daily change was significantly related to both landscape composition and heterogeneity after accounting for interannual and climatic variation. Mean daily change decreased with increasing cover of CLC class 2.3 (pastures) and increased with higher landscape heterogeneity of natural and semi-natural land-cover classes (Fig. 2; Table 5). Year was significantly associated with mean daily change ($P < 0.001$), whereas mean temperature and cumulative precipitation were not ($P = 0.215$ and $P = 0.082$, respectively). Sensitivity analysis indicated that a mean daily change of -0.02 kg day^{-1} was the level at which stationary colonies were no longer significantly different from migratory colonies. We then evaluated whether the fitted relationships with landscape predictors crossed this response level within their observed ranges. Neither the fitted relationship with pasture cover nor that with landscape heterogeneity crossed -0.02 kg day^{-1}. Consequently, although some individual observations fell below this value, model-predicted mean daily change remained at levels comparable to those of migratory colonies throughout the observed ranges of both predictors. Mean daily gain showed a significant relationship with landscape composition, decreasing with increasing cover of CLC class 1.1 (urban fabric) and increasing with higher cover of class 3.1 (forests) (Fig. 2; Table 5). Year was significantly associated with mean daily gain ($P < 0.001$), and mean temperature showed a negative relationship with

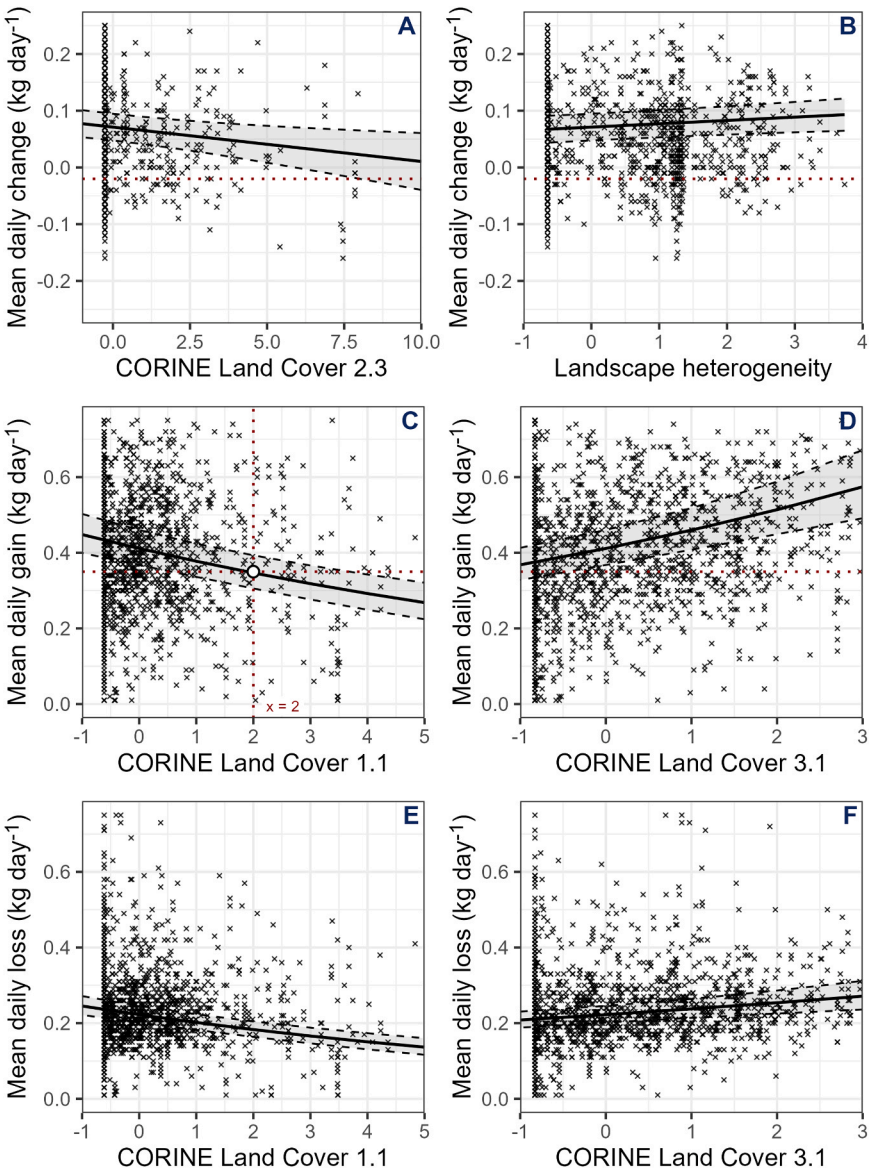


Fig. 2. Relationships derived from mixed-effects global models between landscape composition, landscape heterogeneity, and colony weight-change variables for stationary colonies. Dashed lines represent 95% confidence intervals. Red dotted horizontal lines indicate the response levels identified through sensitivity analyses at which stationary colonies were no longer significantly different from migratory colonies. In panel C, the vertical dotted line and circle indicate the urban fabric cover value (CLC class 1.1; z = 2; 43.5%) at which the fitted relationship crosses the corresponding response level; above this value, model-predicted mean daily gains were lower than those of migratory colonies. Panels A–B show mean daily change in relation to CLC class 2.3 (pastures) and landscape heterogeneity, respectively; panels C–D show mean daily gain in relation to CLC class 1.1 (urban fabric) and CLC class 3.1 (forests), respectively; panels E–F show mean daily loss in relation to CLC class 1.1 and CLC class 3.1, respectively. Landscape predictors are expressed as standardized values (z-scores) on the x-axes.

mean daily gain (P = 0.027), whereas cumulative precipitation was not significant (P = 0.466). Sensitivity analysis showed that a mean daily gain of 0.35 kg day^{-1} represented the level at which production gains of stationary colonies were no longer significantly different from those of migratory colonies. The fitted relationship with cover of class 1.1 (urban fabric) crossed this response level at a z-score of 2, corresponding to 43.5% urban cover. In contrast, the fitted relationship with forest cover (CLC class 3.1) did not cross 0.35 kg day^{-1} within the observed range, and model-predicted gains therefore remained comparable to those of migratory colonies throughout the observed forest cover range. Mean daily loss was associated with the same landscape attributes, with lower absolute daily losses at higher cover of class 1.1 (urban fabric) and higher absolute daily losses at higher cover of class 3.1 (forests) (Fig. 2; Table 5). Year was significantly associated with mean daily loss (P = 0.002). Mean temperature was negatively related to mean daily loss (P = 0.045), whereas cumulative precipitation showed a positive relationship (P = 0.009).

Residual spatial autocorrelation was generally not detected in the global models. After adjustment for multiple comparisons, Moran's I was not significant in any year for mean daily gain or mean daily loss. For mean daily change, significant positive residual spatial autocorrelation was detected only in 2024 (Moran's I = 0.129, adjusted P = 0.025), whereas no significant spatial autocorrelation was detected in the other years.

3.3. *Biogeographical variation in landscape influence on stationary colonies*

Both landscape composition and heterogeneity varied widely among landscape buffers of stationary colonies across biogeographical regions

Table 5
Landscape predictors retained in the final mixed-effects models of stationary honey bee colony productivity at the global and biogeographical-region levels. Complete outputs for all final models, including year and climatic covariates, random-effect variance components, and model fit statistics, are reported in Supplementary material 1.

Response variable	Landscape predictor	β	95% CI	Statistic	P	Hive variance	R^2_m	R^2_c
Mean daily change (Global)	CLC 2.3 (pastures)	-0.006	-0.010 to −0.002	$F = 7.412$	0.007	0.001	0.037	0.215
	Landscape heterogeneity	0.006	0.002–0.010	$F = 7.227$	0.007			
Mean daily gain (Global)	CLC 1.1 (urban fabric)	-0.086	-0.123 to −0.048	$\chi^2 = 20.046$	< 0.001	0.214	0.119	0.735
	CLC 3.1 (forests)	0.111	0.064–0.158	$\chi^2 = 21.604$	< 0.001			
Mean daily loss (Global)	CLC 1.1 (urban fabric)	-0.098	-0.130 to −0.065	$\chi^2 = 34.488$	< 0.001	0.178	0.095	0.744
	CLC 3.1 (forests)	0.066	0.026–0.107	$\chi^2 = 10.238$	0.001			
Mean daily change (Continental)	CLC 1.1 (urban fabric)	-0.007	-0.012 to −0.001	$F = 5.735$	0.017	0.001	0.056	0.191
	CLC 1.2 (industrial, commercial and transport units)	0.008	0.002–0.014	$F = 7.951$	0.005			
Mean daily gain (Continental)	CLC 1.1 (urban fabric)	-0.225	-0.285 to −0.165	$\chi^2 = 50.508$	< 0.001	0.246	0.171	0.757
	CLC 3.1 (forests)	0.079	0.003–0.156	$\chi^2 = 4.169$	0.041			
Mean daily loss (Continental)	CLC 1.1 (urban fabric)	-0.193	-0.244 to −0.142	$\chi^2 = 52.718$	< 0.001	0.200	0.129	0.766
Mean daily change (Mediterranean)	CLC 2.2 (permanent crops)	-0.011	-0.019 to −0.003	$F = 7.655$	0.006	0.001	0.070	0.185
	CLC 2.3 (pastures)	-0.015	-0.023 to −0.008	$F = 15.689$	< 0.001			
	Landscape heterogeneity	0.012	0.004–0.020	$F = 8.843$	0.003			
Mean daily gain (Mediterranean)	CLC 1.2 (industrial, commercial and transport units)	-0.086	-0.143 to −0.028	$\chi^2 = 8.685$	0.003	0.190	0.133	0.716
	CLC 3.1 (forests)	0.117	0.052–0.181	$\chi^2 = 12.705$	< 0.001			
Mean daily loss (Mediterranean)	CLC 1.2 (industrial, commercial and transport units)	-0.065	-0.116 to −0.014	$\chi^2 = 6.413$	0.011	0.165	0.099	0.714
	CLC 3.1 (forests)	0.086	0.028–0.143	$\chi^2 = 8.551$	0.003			

(Supplementary material 1). Multicollinearity analysis led to the exclusion of CLC class 3.1 (forests) from the Alpine region analyses because of its strong negative correlation with CLC class 2.4 (heterogeneous agricultural areas). In the Continental and Mediterranean regions, CLC class 2.1 (arable land) was excluded because of strong negative correlations with CLC classes 2.4 (heterogeneous agricultural areas) and 3.1 (forests).

In the Alpine region, mean daily change, mean daily gain and mean daily loss (expressed as absolute values) showed no significant relationships with the percentage cover of the CLC classes or with landscape heterogeneity of natural and semi-natural land-cover classes after accounting for interannual and climatic variation. Year was significantly associated with mean daily change ($P < 0.001$), mean daily gain ($P < 0.001$), and mean daily loss ($P = 0.035$), whereas mean temperature and cumulative precipitation were not significantly related to any of the three response variables.

In the Continental region, mean daily change decreased significantly with increasing cover of CLC class 1.1 (urban fabric) and increased significantly with increasing cover of class 1.2 (industrial, commercial and transport units) (Fig. 3; Table 5). Mean daily gain decreased significantly with increasing cover of class 1.1 (urban fabric) and increased significantly with increasing cover of class 3.1 (forests) (Fig. 3; Table 5), while mean daily loss (absolute values) decreased significantly with increasing cover of class 1.1 (urban fabric) (Fig. 3; Table 5). Year was significantly associated with mean daily change and mean daily gain (both $P < 0.001$), but not with mean daily loss ($P = 0.071$). Neither mean temperature nor cumulative precipitation was significantly associated with any of the three response variables.

In the Mediterranean region, mean daily change decreased significantly with increasing cover of CLC class 2.2 (permanent crops) and CLC class 2.3 (pastures) and increased significantly with increasing landscape heterogeneity of natural and semi-natural land-cover classes (Fig. 3; Table 5). Mean daily gain decreased significantly with increasing cover of CLC class 1.2 (industrial, commercial and transport units) and increased significantly with increasing cover of CLC class 3.1 (forests). Mean daily loss showed the same directional relationships, decreasing with increasing cover of CLC class 1.2 and increasing with increasing cover of CLC class 3.1 (Fig. 3; Table 5). Year was significantly associated with mean daily change ($P = 0.003$), mean daily gain ($P < 0.001$), and mean daily loss ($P = 0.002$). Mean temperature was not significantly related to any response variable, whereas cumulative precipitation was positively associated with mean daily change ($P = 0.008$) but showed no significant relationship with mean daily gain or mean daily loss.

4. Discussion

Our comparison of stationary and migratory colonies indicates that migratory management was associated with higher mean seasonal productivity and greater production gains, rather than with a higher probability of productive days. Higher productivity likely reflects repeated colony relocation towards spatially and temporally concentrated nectar flows associated with short flowering periods, particularly for the production of monofloral honeys (Persano Oddo and Piro, 2004; Requier et al., 2015; Martínez-López et al., 2022). Migratory colonies, however, also exhibited higher mean daily losses. Periods of high floral resource availability may support larger colony populations and intensified brood rearing, increasing energetic demands and honey consumption when foraging conditions subsequently become unfavourable (Debnam et al., 2024; Vincze et al., 2025). Additional losses can also arise from colony transport and post-relocation reorganisation. Experimental and field studies have shown that repeated colony movement disrupts worker physiology, impairs hypopharyngeal gland development, and increases oxidative stress, resulting in higher colony-level maintenance costs (Ahn et al., 2012; Simone-Finstrom et al., 2016; Melicher et al., 2019).

In stationary colonies, mean daily change was significantly related to both landscape composition and heterogeneity, indicating that seasonal productivity varies with the surrounding landscape. Mean daily change decreased with increasing pasture cover (CLC class 2.3), a land-cover class encompassing permanent grasslands used for grazing or fodder production. Under intensive management, floral resources can be abundant during certain periods, but frequent mowing and the dominance of anemophilous grasses may reduce their temporal continuity (Plantureux et al., 2005; Cong et al., 2020; Hassan and Wang, 2024; Harris et al., 2024). As a result, floral resources may be concentrated within short periods of the production season, potentially explaining the negative association between pasture cover and seasonal colony productivity, despite pastures being commonly selected as hive locations in agricultural landscapes. In contrast, mean daily change increased with greater landscape heterogeneity of natural and semi-natural land-cover classes. Greater heterogeneity suggests the co-occurrence of multiple habitat types that may provide floral resources at different times during the productive season, thereby promoting temporal complementarity in resource supply (Fantinato et al., 2019a, b). Nevertheless, across the full observed ranges of pasture cover and landscape heterogeneity, predicted productivity for stationary colonies never fell below the threshold of comparability with migratory colonies, indicating that even

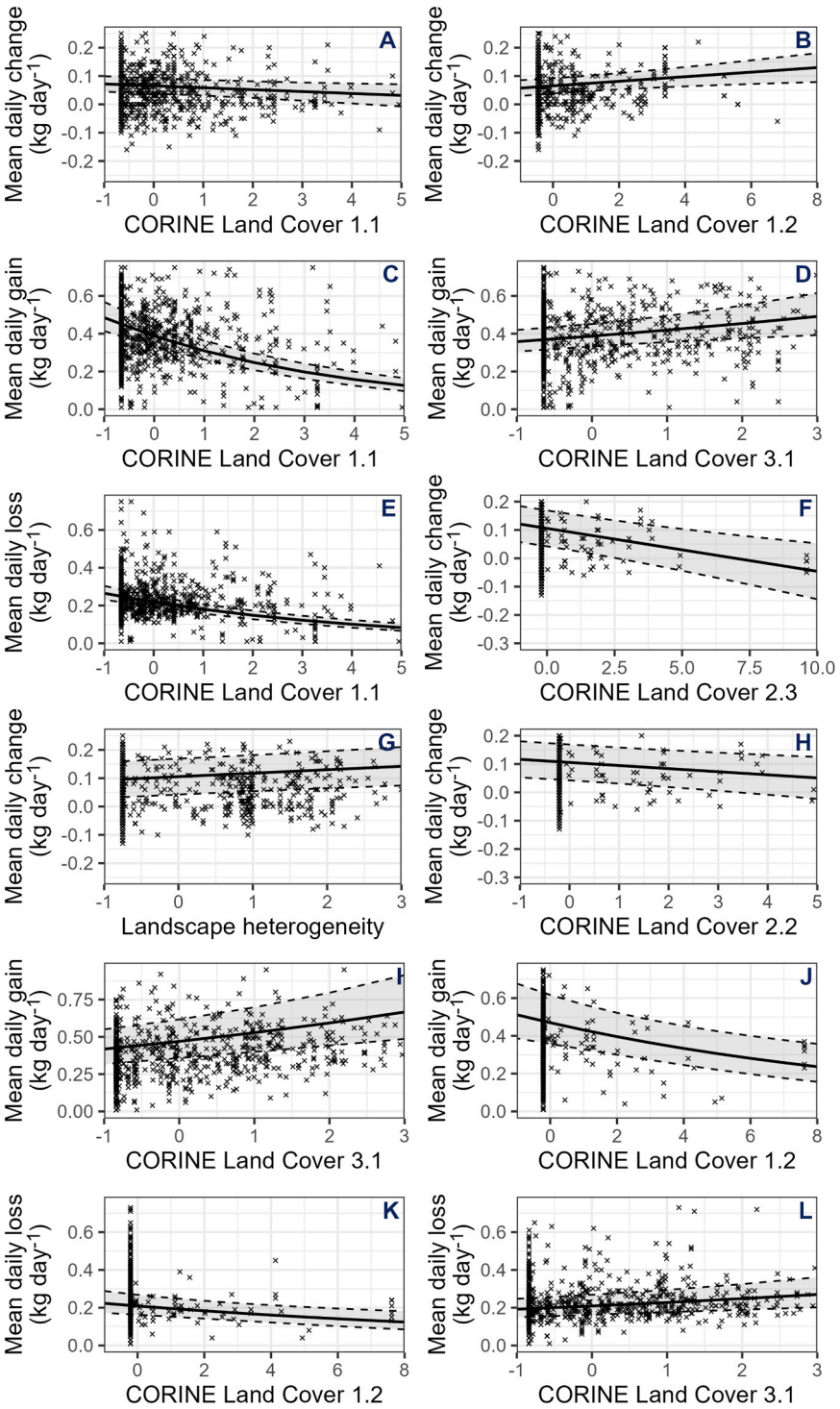


Fig. 3. Relationships derived from mixed-effects regional models between landscape composition, landscape heterogeneity, and colony weight-change variables for stationary colonies. Panels A-E correspond to the Continental region, while panels F-L correspond to the Mediterranean region. Dashed lines represent 95% confidence intervals. In the Continental region, panels A–B show mean daily change in relation to CLC class 1.1 (urban fabric) and CLC class 1.2 (industrial, commercial and transport units), respectively; panels C–D show mean daily gain in relation to CLC class 1.1 and CLC class 3.1 (forests), respectively; and panel E shows mean daily loss in relation to CLC class 1.1. In the Mediterranean region, panels F–H show mean daily change in relation to CLC class 2.3 (pastures), landscape heterogeneity, and CLC class 2.2 (permanent crops), respectively; panels I–J show mean daily gain in relation to CLC class 3.1 and CLC class 1.2, respectively; and panels K–L show mean daily loss in relation to CLC class 1.2 and CLC class 3.1, respectively. Landscape predictors are expressed as standardized values (z-scores) on the x-axes.

landscapes with high pasture cover can maintain seasonal productivity comparable to migratory management.

Landscape composition was also associated with mean daily gains and losses, both of which decreased with increasing urban fabric cover (CLC class 1.1). Reduced density and diversity of floral resources in urbanised landscapes may constrain colony growth and the development of large worker populations, thereby limiting weight accumulation during favourable periods as well as weight losses when foraging

conditions become unfavourable (Richardson et al., 2023). Specifically, sensitivity analysis identified a critical threshold at 43.50% urban fabric cover, above which daily weight gains of stationary colonies fell significantly below migratory levels. Forest cover (CLC class 3.1) showed the opposite relationship, being positively associated with both mean daily gains and losses. Larger gains may reflect temporally concentrated nectar flows from tree species such as *Castanea sativa*, *Tilia* spp. and *Robinia pseudoacacia*, whereas larger losses may follow the decline in resource availability after flowering peaks. In contrast to urban cover, forest cover revealed no threshold effect, maintaining daily weight gains comparable to migratory colonies across its entire observed range.

Mean daily gains and losses were associated with climatic covariates. Higher mean temperature was related to smaller mean daily gains and losses, whereas greater cumulative precipitation was related to larger mean daily losses. Higher temperatures may reduce nectar availability and shorten flowering periods (Takkis et al., 2015), thereby limiting daily weight gains, while lower resource accumulation and associated colony growth may also constrain subsequent weight losses. Greater precipitation, in contrast, may increase daily losses by restricting foraging activity and reducing resource intake. Neither climatic covariate was significantly related to mean daily change. Because mean daily change integrates both the frequency and magnitude of positive and negative daily weight changes, associations with individual components of daily weight dynamics do not necessarily translate into a detectable relationship with mean seasonal productivity.

Landscape relationships differed among biogeographical regions. In the Alpine region, the lack of significant relationships between productivity and landscape attributes may reflect the widespread presence of natural and semi-natural habitats and extensively managed land-cover types, which may ensure floral resource availability across the landscape throughout much of the production season (Wang et al., 2024).

In the Continental region, urban fabric was negatively associated with mean daily change, mean daily gain, and mean daily loss, indicating lower seasonal productivity together with smaller positive and negative daily weight changes in more urbanised landscapes. This combination is consistent with resource limitation in intensively modified landscapes (Naug, 2009; Donkersley et al., 2014; Threlfall et al., 2015). By contrast, industrial, commercial and transport units (CLC class 1.2) were positively associated with mean daily change, possibly because vegetated margins and linear features associated with industrial and transport infrastructure may provide floral resources, as highlighted by Phillips et al. (2020). Forest cover was positively associated with mean daily gain, consistent with the global relationship.

In the Mediterranean region, mean daily change decreased with increasing cover of permanent crops (CLC class 2.2) and pastures and increased with greater heterogeneity of natural and semi-natural land-cover classes. Permanent crops, including vineyards, orchards and olive groves, provide limited floral resources under intensive management, particularly where herbaceous vegetation between or beneath crop rows is strongly reduced (Favarin et al., 2024). Resource limitations associated with permanent crops and pastures may become particularly relevant under Mediterranean summer aridity, where drought can rapidly reduce nectar availability and shorten flowering periods (Flo et al., 2018). Accordingly, the positive relationship between cumulative precipitation and mean daily change suggests that greater water availability may partly alleviate resource limitation during the production season. Greater landscape heterogeneity may further contribute by providing complementary floral resources across habitat types and periods of the season. Forest cover showed the same positive relationships with mean daily gain and loss as observed in the global models, whereas industrial, commercial and transport units were negatively related to both responses, indicating smaller positive and negative daily weight changes. Overall, the Mediterranean relationships are consistent with limited continuity of floral resources across the production season as a key constraint under Mediterranean summer aridity (Satta et al., 2024).

Beyond differences among biogeographical regions, most productivity responses were associated with year in both the global models and those fitted separately by biogeographical region, after accounting for mean temperature and cumulative precipitation. Landscape composition and seasonal climatic covariates provide only indirect information on floral resource availability and may not capture inter-annual variability in flowering phenology, the timing of favourable and unfavourable conditions during the production season, or variation in initial colony strength. Local colony density was also unavailable and could not be included in the models. Because the monitored hives do not necessarily represent the total number of colonies present, potential density-dependent competition for floral resources could not be quantified. The recurrent association with year may therefore reflect interannual variation in the timing and availability of floral resources not represented by the environmental predictors included in the models. Consistently, the relatively low marginal R^2 values indicate that the fixed effects explain only a limited fraction of the overall variation in colony productivity, whereas the substantially higher conditional R^2 values highlight the importance of persistent colony-level heterogeneity captured by the random effects.

Taken together, our results indicate that although migratory colonies achieved higher mean seasonal productivity overall, stationary colonies can reach comparable productivity depending on landscape composition. Within stationary colonies, mean seasonal productivity increased with the heterogeneity of natural and semi-natural habitats, while associations with individual land-cover classes differed among biogeographical regions. Greater heterogeneity of natural and semi-natural habitats may therefore increase the productive potential of stationary beekeeping, although associations with landscape composition differ among biogeographical regions.

CRediT authorship contribution statement

E. Fantinato: Writing – original draft, Visualization, Validation, Supervision, Methodology, Conceptualization. **A. Della Bella:** Writing – original draft, Methodology, Formal analysis, Data curation. **A. Fiorese:** Visualization, Data curation. **M.E. Mancino:** Writing – original draft, Visualization, Validation, Resources, Project administration, Funding acquisition. **M. LiCalzi:** Writing – original draft, Visualization, Validation, Supervision, Resources, Funding acquisition. **G.V. Lombardi:** Writing – original draft, Visualization, Validation, Resources, Funding acquisition. **F. Maglione:** Writing – original draft, Visualization. **G. Toscano:** Writing – original draft, Visualization. **G. Buffa:** Writing – original draft, Visualization, Validation, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110859.

Data availability

The data supporting this study are proprietary, provided by 3Bee (www.3bee.com), and obtained under a commercial agreement; they are not publicly available. Access is subject to approval by 3Bee.

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