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Research article

# Gene flow and genetic connectivity of *Bursera linanoe* (La Llave) Rzed., Calderón & Medina in a fragmented landscape

# Flujo y conectividad genética de *Bursera linanoe* (La Llave) Rzed., Calderón & Medina en un paisaje fragmentado

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**Abstract**

Habitat fragmentation threatens the survival of species by reducing gene flow. *Bursera linanoe*, a tree that is endemic to and of cultural importance in South-Central Mexico, is experiencing a population decline due to harvesting pressure and habitat loss. The genetic structure and population connectivity of this species were analyzed using molecular genetic tools, spatial modeling, and ecological analyses. Four populations were analyzed using ISSR (Inter-Simple Sequence Repeats) markers, and moderate to high genetic differentiation was observed (*FST*=0.31), indicating limited genetic connectivity among locations. Multivariate and Bayesian analyses identified three major genetic groups associated with geographic regions (*Morelos*, *Guerrero*, and *Oaxaca*); this suggests that both physical barriers and habitat fragmentation have influenced genetic structuring. The Mantel test revealed distance-based isolation, while the migration network analysis showed an asymmetric flow, with connectivity between central populations, suggesting possible source-sink dynamics. Landscape genetics models revealed that geographic distance and landscape resistance have similar effects, suggesting that connectivity does not depend on a single factor, but rather on their interaction. In addition, niche modeling revealed spatial overlap between *B. linanoe* and fruit-eating birds (primarily *Myiarchus* and *Tyrannus*), which supports their role as a key disperser. The study highlights the importance of preserving biological corridors and plant-disperser interactions to maintain the species' genetic viability.

**Keywords:** Conservation biology, biotic dispersal, seed dispersal, genetic structure, landscape genetics, deciduous forest.

**Resumen**

La fragmentación del hábitat amenaza la persistencia de las especies, al reducir el flujo génico. *Bursera linanoe*, un árbol endémico y de importancia cultural en el centro-sur de México, presenta declive poblacional debido a la presión extractiva y pérdida de hábitat. Se analizó la estructura genética y la conectividad poblacional de esta especie mediante herramientas de genética molecular, modelación espacial y análisis ecológicos. Se evaluaron cuatro poblaciones con marcadores ISSR (*Inter-Simple Sequence Repeats*) y se determinó una diferenciación genética de moderada a alta (*FST*=0.31), lo que indica una limitada conectividad genética entre localidades. Los análisis multivariados y bayesianos identificaron tres grupos genéticos principales asociados a regiones geográficas (Morelos, Guerrero y Oaxaca); ello sugiere que tanto barreras físicas, como la fragmentación del hábitat han influido en la estructuración genética. La prueba de *Mantel* evidenció aislamiento por distancia, mientras que el análisis de redes de migración mostró un flujo asimétrico, con conectividad entre poblaciones centrales, que indicaron posibles dinámicas fuente-sumidero. Los modelos de genética del paisaje revelaron que la distancia geográfica y la resistencia del paisaje tienen efectos similares, lo que sugiere que la conectividad no depende de un solo factor, sino de su interacción. Adicionalmente, la modelación de nicho evidenció traslape espacial entre *B. linanoe* y aves frugívoras (principalmente *Myiarchus* y *Tyrannus*), lo que respalda su papel como dispersores claves. El estudio destaca la importancia de conservar corredores biológicos y las interacciones planta-dispersor para mantener la viabilidad genética de la especie.

**Palabras clave:** Biología de la conservación, dispersión biótica, dispersión de semillas, estructura genética, genética del paisaje, selva caducifolia.

# Introduction

Habitat fragmentation is one of the main factors threatening the survival of species, as it reduces the connectivity between populations (Fischer & Lindenmayer, 2007). This process is particularly pronounced in South-Central Mexico, where the deciduous forest has been severely altered by land-use change and resource extraction (Miles et al., 2006; Trejo & Dirzo, 2000). It is estimated that more than 70 % of its original coverage has been altered, resulting in a highly fragmented landscape (Portillo-Quintero & Sánchez-Azofeifa, 2010). In this context, woody species endemic to the deciduous forest are facing a reduction in the effective size of their populations and a loss of genetic connectivity (Mesa-Sierra et al., 2022; Rosas et al., 2011).

*Bursera linanoe* (La Llave) Rzed., Calderón & Medina is a tree species of great cultural, ecological, and economic importance. However, its populations have been subjected to intensive exploitation associated with the extraction of essential oil and timber (Cruz-Cruz et al., 2009; Hersch-Martínez et al., 2004; Medina-Tello et al., 2023). Although it is not classified in any risk category in the norm NOM-059-SEMARNAT-2010 (Secretaría de Medio Ambiente y Recursos Naturales [Semarnat], 2010), the International Union for Conservation of Nature (IUCN) classifies it as Vulnerable (VU) due to its restricted range and habitat fragmentation (Fuentes et al., 2019).

The loss of ecological connectivity between fragments where *B. linanoe* persists reduces gene flow and may lead to differentiation, inbreeding, or local extinction (Cushman et al., 2012; Epps & Keyghobadi, 2015). In this regard, assessing genetic connectivity at the regional level among populations of this species is essential for understanding how landscape structure influences gene flow and the long-term viability of populations. The integration of molecular tools with spatial models makes it possible to identify barriers to gene flow, infer dispersal pathways, and detect genetic structures associated with the landscape (Manel et al., 2003; Storfer et al., 2007).

In species with zoochorous dispersal, such as *B. linanoe*, functional connectivity depends not only on the distance between fragments, but also on the permeability of the landscape and the mobility of its dispersers (Cordeiro & Howe, 2003; McRae & Beier, 2007). Assessing the distribution of these dispersers can provide key information about the likelihood of genetic exchange in fragmented landscapes, as their mobility facilitates seed transport among habitat fragments and helps maintain intrapopulation gene flow in spatially isolated populations.

The objective of this study was to analyze the genetic structure and assess the connectivity of *Bursera linanoe* populations in South-Central Mexico using a landscape genetics approach that integrates molecular analyses and spatial modeling, with the aim of providing insights for the design of conservation strategies aimed at preserving regional genetic diversity and protecting habitats that facilitate seed dispersal among populations.

# Materials and Methods

## DNA extraction and ISSR analysis

Leaves of *Bursera linanoe* were collected from four populations in South-Central Mexico: *Atenango del Río*, *Guerrero* (*n*=36), *Tlalquiltenango*, *Morelos* (*n*=21), *Santa María Tecomavaca*, *Oaxaca* (*n*=21), and *San Juan Bautista Cuicatlán*, *Oaxaca* (*n*=14). Genomic DNA was extracted using a modified version of the CTAB (cetyltrimethylammonium bromide) protocol (Doyle & Doyle, 1987; Saghai-Maroof et al., 1984), previously optimized for the species. The conditions for amplification, visualization, and band coding followed the protocols described by Coppi et al. (2010), Cruz-Larios et al. (2024) and Dos Santos-Araújo et al. (2016). The data obtained were used to analyze population structure and genetic connectivity.

## Data analysis and population structure

The ISSR (Inter-Simple Sequence Repeats) profiles were coded as binary dominant markers. The genetic structure was assessed using hierarchical AMOVA; the proportion of genetic variation between groups (*FCT*), the proportion of genetic variation between populations within groups (*FSC*), and the total genetic differentiation between populations (*FST*) were estimated, with permutation tests to determine significance. Genetic differentiation was explored using Principal component analysis (PCA)

implemented in Adegenet (R Core Team, 2024), based on a genetic covariance matrix calculated from the loci shared between pairs of individuals.

Distance-based isolation was assessed using the Mantel test (Mantel, 1967) between the genetic distance and the geographic distance matrices. The spatial genetic structure was analyzed using the TESS3R software package, which considered *K* values ranging from 1 to 10, with 20 replicates for each *K* value (Caye et al., 2016). The optimal number of genetic groups was determined using the method of Evanno et al. (2005). Subsequently, ancestry coefficients were calculated for each individual and plotted to visualize the patterns of genetic structure, admixture, and population differentiation between the study sites. Recent gene flow was estimated using the divMigrate function of the diveRsity package version 4.6.0 (Keenan et al., 2013), and the most significant migration relationships between populations were represented by a connectivity network.

## Landscape resistance modeling

A landscape resilience model was constructed using the V series land use and vegetation layer and the Mexican continuous digital elevation model, both developed by the National Institute of Statistics, Geography, and Informatics of Mexico (Instituto Nacional de Estadística, Geografía e Informática [INEGI], 2015). The vegetation cover and altitude were reclassified into resistance categories based on movement difficulty and the known altitudinal distribution of the species (Supplementary material: Table S1 and Table S2). Both layers were integrated into a single raster, with each cell assigned the maximum resistance value. Based on the coordinates of the populations, Euclidean and path-length distances were calculated as cumulative costs.

The relationship between genetic differentiation and spatial variables was assessed using maximum likelihood mixed models of population pairs (MLPE; Van Strien et al., 2012). The models were fitted using lme4 (Bates et al., 2015) and compared using *AICc* with MuMIn (Barton, 2026). Also estimated was the Conditional coefficient of determination (Nakagawa & Schielzeth, 2013), using the r.squaredGLMM function.

## Modeling the potential distribution of dispersers

Studies conducted on species of the genus *Bursera* in the *Balsas* river basin have documented that various birds of the family Tyrannidae—particularly those of the genera *Myiarchus*, *Tyrannus*, and *Myiodynastes*—actively participate in the removal and dispersal of fruits (Almazán-Núñez et al., 2016; Rodríguez-Godínez et al., 2022). Based on this background information, the potential for spatial association between *Bursera linanoe* and the Tyrannidae species recorded in Mexico was evaluated using the SPECIES platform of the National Commission for the Knowledge and Use of Biodiversity (*Comisión Nacional para el Conocimiento y Uso de la Biodiversidad*, *Conabio*) (Stephens et al., 2019). The analysis was based on the spatial overlap between occurrence records and the overlap between potential distributions. Given the nature of the approach used, the associations identified were interpreted as hypotheses of potential ecological interactions rather than as direct evidence of effective dispersal or functional connectivity (Supplementary material: Figure S1).

The potential distribution of *B. linanoe* was estimated using records from the Global Biodiversity Information Facility (GBIF, 2021) and field observations (Cruz-Larios, 2022); to this end, the protocol described by Escalona-Prado (2025) was followed for a total of 176 occurrence points (Supplementary material: Figure S2). The significance of the correlation was assessed using the $\varepsilon$ parameter and the percentage

of occurrence by decile. Potential dispersal species were modeled alongside *B. linanoe* in Wallace (Kass et al., 2018, 2023), using 19 bioclimatic variables from WorldClim (Fick & Hijmans, 2017) at 2.5 arc min resolution, with 5-km spatial filtering. Various combinations of response functions and regularization multipliers were considered, and the model with the lowest Akaike information criterion (*AIC*) was selected.

The results were converted to presence/absence using the $10^{th}$ percentile from the training set (Sage et al., 2017). The maps were generated in QGIS v3.36.1 (QGIS Development Team, 2024), and the overlapping areas were calculated using raster map algebra (Hijmans et al., 2026). It was assumed that greater spatial overlap between the potential distribution of *B. linanoe* and that of frugivorous species increases the likelihood of ecological encounters and dispersal events.

# Results

## Population structure

The analyses revealed marked variations in genetic structure between the *Bursera linanoe* populations (Table 1). The average *FST* value of 0.3059 ($p<0.0001$) indicates a high genetic differentiation, exceeding the threshold of 0.25 considered by Wright (1978) as evidence of a very high differentiation between populations. An AMOVA consistently showed the largest proportion of genetic variation to be between populations within groups (*FSC*=0.28-0.31), while the variance between broad groups (*FCT*) was low or negative in most of the schemes evaluated, suggesting little regional genetic structure. The only exception was the pattern that distinguished *San Juan Bautista Cuicatlán* (*Oaxaca* 2) from the rest of the towns, in which a significant difference between groups was detected (*FCT*=0.079; $p<0.0001$).

**Table 1.** Results of a hierarchical AMOVA in four populations of *Bursera linanoe* (La Llave) Rzed., Calderón & Medina under different clustering schemes.

| | **Groups** | | | |
|---|---|---|---|---|
| | **(*Guerrero*, *Morelos*, *Oaxaca* 1) *vs.* (*Oaxaca* 2)** | **(*Guerrero*, *Morelos*) *vs.* (*Oaxaca* 1 y 2)** | **(*Guerrero*, *Oaxaca* 1) *vs.* (*Morelos*, *Oaxaca* 2)** | ***Guerrero vs.* (*Morelos*, *Oaxaca* 1, *Oaxaca* 2)** |
| *FSC* | 0.28449 | 0.30869 | 0.30965 | 0.30663 |
| *FST* | 0.34134 | 0.30453 | 0.30402 | 0.30563 |
| *FCT* | 0.07945 | -0.00600 | -0.00816 | -0.00143 |

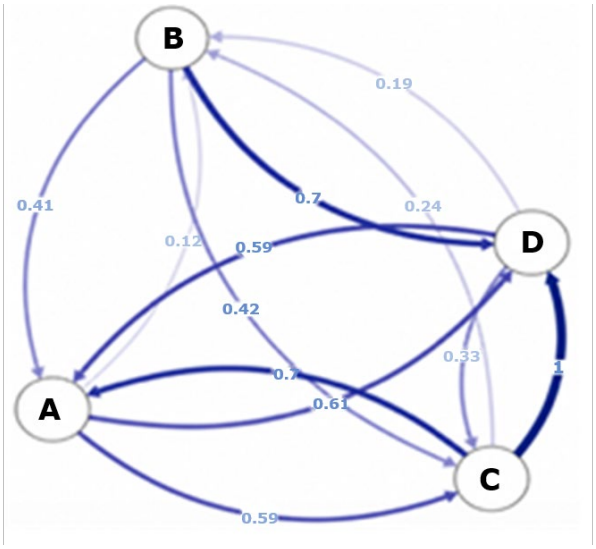
*FSC* = Proportion of genetic variation between populations within groups; *FST* = Total genetic differentiation between populations; *FCT* = Proportion of genetic variation between groups.

In consonance with the above, a Principal component analysis (Supplementary material: Figure S3) showed a partial clustering of individuals based on their population of origin, while the distance-based isolation test (Supplementary material: Figure S4) revealed a significant positive correlation between geographic distance and genetic differentiation.

The estimate of the optimal number of groups (*K*) reached its maximum at *K*=3 (*ΔK*=3.9612) and *K*=4 (*ΔK*=2.4891), indicating the presence of three or four major genetic clusters among the 92 individuals analyzed. These results were consistent with the patterns detected by AMOVA and PCA, which revealed moderate genetic differentiation and spatial structuring of the populations. Furthermore, the analyses conducted using TESS3R revealed consistent clustering patterns; three main geographic clusters were identified, corresponding to *Morelos*, *Guerrero*, and *Oaxaca* (Supplementary material: Figure S3 to Figure S6).

The relative migration network between the four *Bursera linanoe* populations showed contrasting patterns of genetic connectivity (Figure 1). The highest values of bidirectional migration were observed between *Guerrero* and *Morelos* (estimated relative migration values: *Nm*=0.7) and between *Guerrero* and *Oaxaca* 1 (*Nm*=0.6-0.7), suggesting a relatively high level of gene flow between these populations. In

addition, a significant flow was detected from the *Oaxaca* 1 and *Oaxaca* 2 populations (*Nm*=1.0), which proved to be the strongest connection in the network. In contrast, the weakest connections involved mainly *Oaxaca* 2 and *Morelos*, with *Nm* values below 0.2 in certain flow directions.




The nodes correspond to the sampling sites: A = *Guerrero*, B = *Morelos*, C = *Oaxaca* 1, D = *Oaxaca* 2.

**Figure 1.** Relative migration network between four populations of *Bursera linanoe* (La Llave) Rzed., Calderón & Medina based on *Nm* values.

Taken together, these results suggest that *Guerrero* and *Oaxaca* 1 act as relatively well-connected nodes within the network, while *Oaxaca* 2 exhibits a connectivity that is more dependent on flows from neighboring populations.

The high *FST* values observed between populations indicate reduced gene flow and considerable genetic differentiation at the regional scale. This pattern is consistent with the estimated relative migration values (*Nm*), which showed a heterogeneous connectivity between localities, with some connections that were strong while others were considerably restricted. In particular, populations with lower *Nm* values tended

to show greater genetic differentiation. Furthermore, the low or negative *FCT* values obtained in most clustering schemes indicated that genetic variation was distributed primarily between populations rather than across broad regions.

## Modeling the landscape of resistance

A comparison of mixed-population models (MLPE) determined that Euclidean geographic distance and landscape resistance distance provided similar statistical support for explaining genetic differentiation between populations (Table 2).

**Table 2.** Comparison of landscape genetics models based on maximum likelihood mixed-effects models of population effects.

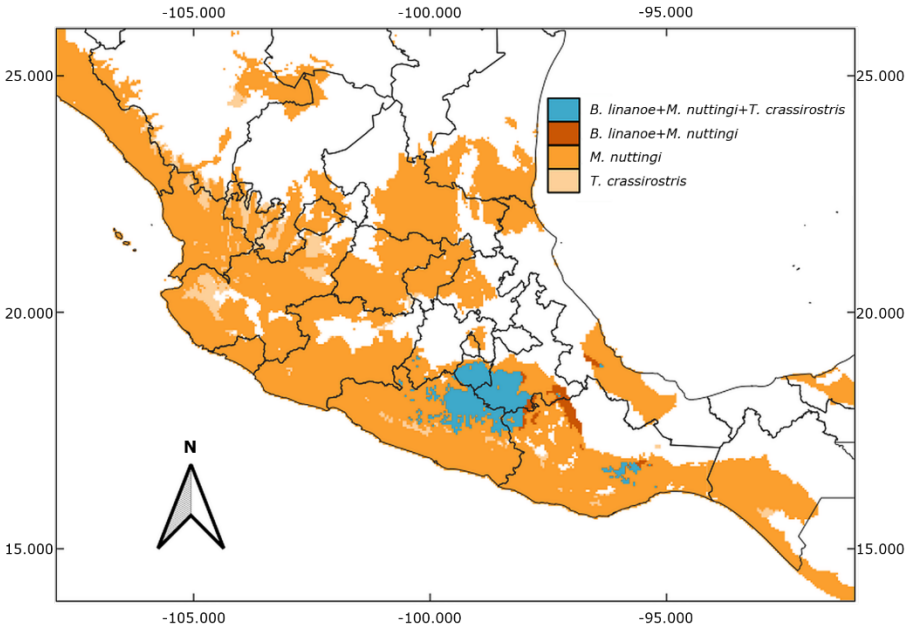
| Landscape variable | *K* | *AICc* | *ΔAICc* | Conditional $R^2$ | $w_i$ |
|---|---|---|---|---|---|
| Endurance distance | 2 | -12.135 | 0.018 | 0.013 | 0.50 |
| Geographical distance | 2 | -12.117 | 0.000 | 0.011 | 0.50 |

*K* = Number of parameters; *AICc* = Akaike information criterion; *ΔAICc* = Difference of *AICc*; $R^2$ = Conditional coefficient of determination; $w_i$ = Akaike weight.

The *AICc* values were virtually equivalent (*ΔAICc*<0.1), which indicated that the models based on geographic distance and resistance distance provided identical empirical support to account for the observed genetic differentiation. These results suggest that gene flow patterns are not explained solely by geographic distance or landscape configuration, but rather by the interaction between the two factors.

## Modeling the potential distribution of dispersers

The highest potential interactions were recorded in *Myiarchus nuttingi* Ridgway ($\varepsilon$=8.37; incidence/decile=57.47 %), *Tyrannus crassirostris* Swainson ($\varepsilon$=8.16; 47.83 %), and *Tyrannus melancholicus* Vieillot ($\varepsilon$=6.99; 21.67 %). However, *T. melancholicus* was excluded because it had only 14 entries in Mexico (out of 104 in GBIF, 2024a). The species *M. nuttingi* (GBIF, 2024b) and *T. crassirostris* (GBIF, 2024c) were included in the potential distribution models, built using 176 records for *Bursera linanoe*, 215 for *M. nuttingi*, and 146 for *T. crassirostris* (Supplementary material: Table S3). Both species have broader ranges than *B. linanoe* and coexist in the region where *B. linanoe* is most widespread (Figure 2).




The colors indicate the ranges of each species and areas of overlap.

**Figure 2.** Geographic distribution of *Myiarchus nuttingi* Ridgway and *Tyrannus crassirostris* Swainson and their overlap with *Bursera linanoe* (La Llave) Rzed., Calderón & Medina in Mexico.

# Discussion

## Genetic clustering and spatial distribution

Genetic structure analysis revealed a spatial pattern consistent with Bursera linanoe, with clusters corresponding to its geographic origin. The *K*-estimation identified three major genetic units, grouped in Morelos, Guerrero, and Oaxaca. Because the AMOVA, PCA, and TESS3R analyses primarily supported the separation between these geographic regions, *K*=3 was considered the most parsimonious approach for interpreting the genetic structure at the regional level. This pattern suggests limitations on gene flow associated with habitat fragmentation and geographic barriers, conforming with distance-based isolation and with findings in species with restricted dispersal (Hamrick et al., 1993). Furthermore, populations within the *Balsas* river basin share more alleles than those separated by orographic barriers, which demonstrates the effect of the landscape on the genetic connectivity. The TESS3R results were consistent in identifying similar patterns of genetic clustering and shared ancestry among the analyzed populations.

The observed genetic structure could also reflect historical processes, in addition to contemporary dispersal mechanisms. The Pleistocene Arc hypothesis proposes greater connectivity between dry tropical forests during the Last Glacial Maximum (Thomas et al., 2017), which may have facilitated historical episodes of genetic exchange between populations that are currently isolated. The *Cuicatlán* region of *Oaxaca*, considered a climate refuge (Gámez et al., 2014), is thought to have served as a reservoir of genetic diversity during past climate fluctuations that contribute to current patterns of differentiation.

Finally, differences in genetic diversity between localities highlight the need to implement tailored conservation strategies that treat each population as a complementary gene pool. However, these explanations should be considered indirect historical inferences, since they were not explicitly evaluated in this study.

The differences in genetic diversity observed between localities suggest that the populations have experienced different demographic histories and levels of connectivity. Populations with lower gene flow may be more susceptible to the effects of genetic drift, the loss of rare alleles, and increased genetic differentiation; whereas those with greater connectivity are more likely to maintain variation through gene flow.

## Gene flow and connectivity between populations

An analysis of the genetic migration network revealed a heterogeneous spatial connectivity between the four populations of *B. linanoe*. The central populations showed consistent two-way gene flow, suggesting the existence of functional corridors that facilitate gene flow between nearby localities, consistently with what has been documented for species in the dry tropics (Arias et al., 2012). In contrast, an asymmetric gene flow toward the peripheral population of *San Juan Bautista Cuicatlán* (*Oaxaca* 2) was detected, with a predominant contribution from *Santa María Tecomavaca* (*Oaxaca* 1) and little gene flow in the opposite direction. This pattern is consistent with source-pool dynamics in marginalized populations (Gilroy & Edwards, 2017). Local ecological conditions—characterized by greater aridity, fragmentation, and calcareous soils—could limit the species' establishment and reduce its regional genetic contribution.

Likewise, the landscape structure and changes in land use influence the connectivity by affecting the movement of dispersers and pollinators (Sotelo-Caro et al., 2023). In this context, only *Myiarchus nuttingi* extends its range to the easternmost part of *B. linanoe*'s range, suggesting a potential role in the biological connectivity between

populations. The interaction between the biotic dispersal and the landscape structure presumably determines the current gene flow pattern.

## Landscape resilience

The similarity in statistical support between models based on geographic distance and landscape resistance suggests that the latter modulates, but does not determine, gene flow patterns; this may be due to the ability of biotic dispersers to traverse contrasting land cover types without a marked loss of functional connectivity, as has been documented in tropical species (Schroeder et al., 2014). However, this study includes only four populations, which limits the number of paired comparisons and reduces the statistical power of the landscape genetics models. It has been noted that at least 8-10 populations are required to detect spatial effects with greater robustness (Oyler-McCance et al., 2013); therefore, the absence of clear differences between models should be interpreted with caution.

Taken together, the results suggest that, in addition to distance and landscape configuration, ecological factors such as dispersal mechanisms and biotic interactions may play a decisive role in the genetic structuring of *B. linanoe*.

## The role of biotic dispersers in connectivity

A key component is the role of fruit-eating birds in the connectivity of *B. linanoe*. The co-occurrence analysis identified species with a high spatial affinity (Reyes-Ortiz et al., 2022) whose ranges overlap with those of the focal species and extend to peripheral populations. In particular, *Myiarchus nuttingi* extends to the easternmost part of the range, suggesting a role as a connectivity vector. This is consistent with studies that identify *Myiarchus* and other tyrantlets as primary dispersers of *Bursera* (Ortiz-Pulido & Rico-Gray, 2006). In the case of *B. longipes* (Rose) Standl., *Myiarchus* and *Tyrannus* species disperse viable seeds, which facilitates their dispersal and establishment (Almazán-Núñez et al., 2016; Guzmán-Pozos et al., 2018).

The decline in fruit-eating bird populations would reduce genetic connectivity among *Bursera linanoe* populations and limit natural regeneration processes, highlighting the importance of incorporating ecological interactions and functional processes into conservation strategies (Howe, 2016).

## Implications for conservation

The patterns of genetic structure, the differential gene flow, and the dependence on dispersers have direct implications for the conservation of *Bursera linanoe*. The presence of genetic clusters indicates that the populations in *Morelos*, *Guerrero*, and *Oaxaca* constitute distinct units; therefore, reforestation using material from different sources should be avoided (Bucharova et al., 2017). It is recommended to establish regional management units that will preserve the genetic integrity and prevent the loss of local adaptations (Boshier et al., 2015), prioritizing *in situ* conservation.

Management actions could include conserving remnant vegetation, establishing living fences (rows of native trees and shrubs along agricultural boundaries that function as biological corridors), planting native species, and coordinating across regions to maintain landscape connectivity.

*B. linanoe*'s dependence on fruit-eating birds highlights the need for an ecosystem-based approach that integrates both tree populations and the habitat and mobility of their dispersers, particularly *Myiarchus nuttingi* and *Tyrannus crassirostris*. Maintaining these interactions is essential for genetic connectivity and natural regeneration, and should prioritize approaches that take into account such ecological processes as seed dispersal, the movement of fruit-eating birds, and the maintenance of the functional connectivity between habitat fragments (Valiente-Banuet et al., 2015).

# Conclusions

The integration of molecular data, spatial modeling, and ecological information reveals a complex pattern of genetic differentiation and connectivity in *Bursera linanoe.* The analyses show moderate to high genetic differentiation between populations, despite their relative geographic proximity, suggesting the combined influence of historical processes, landscape characteristics, and contemporary constraints on gene flow. With regard to the genetic structure, three main clusters associated with the regions of *Morelos*, *Guerrero*, and *Oaxaca* have been identified, indicating limited connectivity between regions and a consistent spatial organization of genetic variation. Besides, an asymmetric gene flow has been detected, with bidirectional connectivity between central populations and a predominant flow toward *San Juan Bautista Cuicatlán*, *Oaxaca*, suggesting source-pool dynamics.

Landscape genetics models indicate that the geographic distance and the landscape resistance have similar explanatory power for the observed patterns of genetic differentiation. Taken together, these results support the hypothesis that the genetic structure of *B. linanoe* arises from the interaction of multiple ecological and historical factors, rather than from a single dominant mechanism.

From a conservation perspective, the high level of genetic diversity maintained within populations and the differentiation observed between regions highlight the importance of conserving both local diversity pools and the processes that promote functional connectivity. Protecting the remnant vegetation, restoring biological corridors, and conserving dispersal agents would help maintain the species' long-term evolutionary viability.

Finally, these results should be supplemented with studies that directly validate the role of dispersers in maintaining genetic connectivity, including recording seed dispersal events, wildlife movements, and their effective contribution to the gene flow. Likewise, it will be important to assess the potential biases associated with the occurrence records utilized in the distribution models and to analyze their relationship with the observed connectivity patterns. Inclusion of the populations from the state of *Puebla* is a priority for future research, as this geographical location—midway between the Central and Southern regions of the distribution range of *Bursera linanoe*—could promote regional genetic connectivity. Assessing the genetic diversity, population structure, and gene flow patterns of this species endemic to Mexico will help determine its contribution to maintaining landscape connectivity and strengthen strategies for its conservation.

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## Conflict of interest

The authors declare that they have no conflict of interest.

## Contributions by author

Iris J. Cruz-Larios: genetic and spatial analyses, interpretation of the results, preparation of figures, and drafting of the manuscript; Alejandra C. Moreno-Letelier: research design and direction, methodological support, interpretation of the results, and critical revision of the manuscript.

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