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DIFFERENTIAL VARIATION IN THE MEAN ISOTOPIC SIGNATURES OF SPIDER HUNTING STRATEGIES INFLUENCED BY LANDSCAPE FEATURES

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ABSTRACT

Spiders may play a crucial role as versatile predators within agroecosystems. Their diverse behavioral patterns, organized into different guilds, can significantly impact multitrophic interactions. Natural vegetation cover surrounding orchards can influence this predatory behavior, which in turn can impact the feeding patterns of different spider predatory guilds. This study aims to examine the differences among spider guilds actively foraging on apple orchards with different levels of surrounding natural vegetation density (SNVD). To achieve this, natural carbon and nitrogen isotope enrichment was used to assess the variations in isotopic signatures among spider guilds across a gradient of surrounding natural vegetation cover, categorized into three levels (low, medium, and high density), as an indicator of landscape complexity. The mean carbon and nitrogen isotopic signatures exhibited greater variability in diurnal aerial ambushers and orb-weaving spiders, particularly in landscapes with high complexity. Interestingly, similar variability was observed in samples from orchards surrounded primarily by agricultural land (with low SNVD). No significant differences in spider abundance were found across guilds or SNVD categories in

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apple orchards, suggesting that the spiders guilds identified in these orchards are not influenced by landscape categories. We further describe the guilds identified, which could potentially contribute to the biological control of pests in apple orchards.

Key words. Isotopic signature, agroecology, natural enemies, Araneae, guild.

INTRODUCTION

Apple orchards in Chile are an important component of the agricultural landscape in the central valley, which is the primary area for agricultural production in the country (CIREN-ODEPA 2023; Peñalver-Cruz et al., 2019). These agricultural landscapes are composed of a mosaic of managed, introduced, and native vegetation and can be described as a set of agricultural patches within a complex gradient of natural and semi-natural vegetation, exhibiting different composition and configurational complexity (Zhao et al., 2016). Local factors such as surrounding natural vegetation cover, adjacent habitats to agricultural patches, and farm management practices influence the arthropod community (Happe, 2019; Karp et al., 2018). Spiders, as generalist predators forming an abundant and species-rich community in agricultural patches (Bogya et al., 1999), are influenced by landscape composition and management features, including multi-trophic interactions (Marc et al., 1999; Nyffeler, 1999; Vasconcellos-Neto et al., 2017). In fact, several studies have demonstrated that landscape features, such as adjacent natural vegetation or semi-natural woody patches, have an impact on spider abundance (Elliott et al., 2002; Schmidt and Tscharntke, 2005; Bianchi et al., 2006; Miliczky and Horton, 2007; Mestre et al., 2018; Peñalver-Cruz et al., 2019). Therefore, the objective of this study was to examine the differences among spider guilds actively foraging in apple orchards with different levels of surrounding natural vegetation density (SNVD). To achieve this, isotopic signatures of spiders were used.

Spiders have developed various hunting strategies to adapt to prey diversity and variation in prey availability, both spatially and temporally (Uetz et al., 1999). Therefore, understanding their role in agricultural landscapes requires an examination of how spider trophic structure is organized and how spiders respond to landscape complexity. Most spider species feed on a diverse range of prey, consuming herbivores (e.g. Hemiptera), detritivores (e.g. Collembola), and other predators (e.g. Araneae) in both agricultural (Nyffeler and Sunderland, 2003) and natural habitats (Birkhofer and Wolters, 2012), which can influence pest availability. Given the great variety of prey they consume and the trophic position of these prey items, spiders' isotopic signatures should reflect these differences (Collier et al., 2002). Trophic interactions can be analyzed using natural nitrogen and carbon isotope enrichment (expressed as $\delta^{15}N$ and $\delta^{13}C$, respectively), which provides insights into primary food source and relative position within a food web (Boecklen et al., 2011). This technique has been widely employed to study trophic relationships in arthropod food webs both in natural (Collier et al., 2002; Kupfer et al., 2006) and agricultural ecosystems (McNabb et al. 2001; Wise et al. 2006; Mestre et al., 2018). The enrichment of ^{15}N can be interpreted as the trophic position of an individual (Gannes et al., 1997; Post, 2002); nitrogen isotopes experience metabolic fractionation as these move up the food chain, from plants to herbivores to prey, and finally to predators. Consequently, the $\delta^{15}N$ of a predator will be higher than that of its prey (Fry, 2006). Therefore, super predators exhibit higher $\delta^{15}N$ values than simple predators, and intraguild predators (IGP) are expected to have higher $\delta^{15}N$ than predators that are exclusively prey to these species. On the other hand, $\delta^{13}C$ reflects the isotopic signature of the food source, while the carbon isotopic ratio is used to trace the energy flow through food webs or to identify primary food sources. Isotopic signatures of these elements are transferred from the base to the top of the food web, allowing the relative contribution of isotopically distinct basal resources to be determined at higher trophic levels, and thus this variation must be accounted for by considering both the sample size and variability within the consumer population (Traugott et al., 2007). However, similar to $\delta^{15}N$, $\delta^{13}C$ generally tends to increase in a stepwise pattern with successive trophic levels (Post, 2002).

We hypothesize that guilds of spiders foraging on apple orchards surrounded by high SNVD will exhibit higher $\delta^{15}N$ mean isotopic signatures and greater variability in $\delta^{13}C$ compared to the same guilds foraging on apple orchards surrounded by low SNVD. Additionally, we expect guilds such as diurnal aerial ambushers and-orb weavers to display higher isotopic signatures, as these guilds are known to engage in greater intraguild predation by consuming both herbivorous prey and other predators (Wise et al., 2006; Michalko et al., 2022). Given their diverse prey selection, these guilds could be an important role as biological control agents in apple orchards. To test this hypothesis, we analyzed the natural carbon and nitrogen enrichment isotopic signatures (Stable Isotope Analysis (SIA)) of spiders actively foraging on various substrates (rock, leaf litter, soil, vegetation, trees) at the border of nine apple orchards in central Mediterranean Chile, which were inserted in a landscape composition gradient.

MATERIALS AND METHODS

The study was conducted in apple orchards situated in the agricultural landscape from the Mediterranean zone of central Chile, from O'Higgins to Maule regions (34° to 36°S), during the summer and spring of the Southern Hemisphere in 2021 and 2022 (Fig. 1).

Landscape composition. Three non-overlapping 15 x 15 km study landscapes were selected, including a complete gradient of landscape complexity based on the percentage of surrounding natural and semi-natural vegetation of apple orchards. Landscape N°1 corresponds to agricultural orchards established in the province of San Fernando district (34°35′02″S 70°59′21″O); Landscape N°2 to orchards located in Romeral district (34°58′00″S 71°08′00″O); Landscape N°3 to orchards located in Molina district (35°06′47″S 71°18′20″O). First, a total of 23 apple orchards, representing the complete gradient of surrounding natural vegetation cover, were selected. The vegetation consists of sclerophyllous forests in the coastal mountain range and the foothills of the Andes (Romero, unpublished). To measure spider abundance, 9 of the 23 orchards were selected to carry out an SIA from spiders. The proportional area of different land-uses was calculated within a 1 km-wide buffer polygon surrounding each orchard. The percentage of SNVD was determined as the sum of the following covers: natural forest, natural shrubs and water bodies since many natural and naturalized plants are associated to these (Lavandero et al., 2025). Spatial information on land-use at the country level was extracted from Zhao et al. (2016). Subsequently, each buffer was assigned to one of three categories depending on the percentage of SNVD: Low (0 – 35%), Medium (36 – 70%), and High (71 – 100%).

Sampling and identification of guilds. Specimen collection was carried out at each of the nine orchards selected, with a sampling effort of 45 min per person, randomly sampling various substrates (rock, leaf litter, soil, vegetation, trees) along a 50-meter long and 4-meter wide transect (total area of 200 m^2) starting from the border of each selected orchard. Each individual spider specimen was collected using sterile

Fig. 1. Study sites corresponding to nine apple orchards where spiders were collected for stable isotope analyses. Sample collection was conducted between the VI and VII regions of Chile in December 2022.

gloves to avoid contamination and placed in individual plastic tubes (0.5 mL). The specimens were immediately placed on ice to lower their metabolism and prevent regurgitation. The samples were then transported to the laboratory, where they were stored at -80 °C and subsequently lyophilized in preparation for SIA.

To categorize the abundance, spiders were captured in December 2021 and December 2022 and identified at the family level (Table 1). Categorization was conducted according to Bizuet-Flores et al. (2015) and Dias et al. (2009), who used foraging strategies to predict arthropod prey group as shared resources exerting different predatory pressures, resulting in eight guilds in our study. To compare their isotopic signatures ($\delta^{15}N$ and $\delta^{13}C$) between spider guilds, diurnal aerial ambushers, diurnal space web–weavers, nocturnal aerial runners and orb-weavers were selected, as these guilds had sufficient sample sizes for isotopic signature comparison (>5).

Stable Isotope Analysis. Specimens' whole bodies were individually crushed following the method of deHart et al. (2017) and homogenized with a glass mortar. To obtain $\delta^{15}N$ and $\delta^{13}C$ values, 0.4 ±0.5 mg of material was subsampled into individual tin capsules (5x9 mm) using a microscale with clean micro spatulas and forceps. Each capsule was folded, sealed and stored in a desiccator cabinet to ensure sample stability during transport and subsequent shipment to Plateau d'Isotopie de Normandie (PLATIN'), Caen University, France. There, the samples were prepared for isotopic analysis in natural abundance variations of ^{13}C and ^{15}N.

Freeze–dried, powdered, and homogenized samples were analyzed using an elemental analyzer EA3000 (EuroVector) coupled to a IsoPrime mass spectrometer (Elementar) for particulate organic carbon and particulate nitrogen in order to calculate their C/N atomic ratio (Cat/Nat). The calibration was performed using an international isotopic standard (IAEA, Vienna, Austria): atmospheric air for nitrogen ($^{15}N/^{14}N = 0.0036735$) and V-PDB (Pee Dee Belenite) for carbon ($^{13}C/^{12}C = 0.0112372$). The resultant gas of the elemental analyses was introduced into

Table 1. Number of spider individuals and their taxonomic identification in accordance with Aguilera and Casanueva, 2005), and guild assignment in accordance with Bizuet-Flores et al. (2015) and Dias et al. (2009) from orchards in Chile, with three different levels of surrounding natural vegetation density (SNVD) used for the isotopic analysis.

	Surrounding Natural Vegetation Densities			
Spider families per guild	**Low**	**Medium**	**High**	**Total**
Aerial hunters				
Anyphaenidae	1	1	3	5
Diurnal aerial ambushers				
Thomisidae	2	12	11	25
Diurnal space web-weavers				
Linyphiidae	3	8	6	17
Theridiidae	1	1	2	4
Ground runners				
Corinnidae	1			1
Gnaphosidae			1	1
Lycosidae			1	1
Zodariidae		1		1
Nocturnal aerial ambushers				
Agelenidae		1		1
Nocturnal aerial runners				
Salticidae	3	7	8	18
Orb-weaver				
Araneidae	3	4	7	14
Uloboridae	1			1
Sensing web weavers				
Oecobiidae	1		1	2
Total	16	35	40	91

an isotope ratio mass spectrometer (IRMS) to determine carbon and nitrogen isotopes. Stable isotopic deviation was expressed as the relative per thousand (‰) differences between the samples and the conventional standards, V-PDB for carbon and atmospheric N_2 for nitrogen, according to the following equation:

$$\delta(‰) = \left[\left(\frac{Rsample}{Rstandard}\right) - 1\right] x1000$$

Where δ is ^{13}C or ^{15}N abundance and *R* is the ^{13}C:^{12}C or ^{15}N:^{14}N ratio. The internal standard was BN 2022 (d^{15}N: 2.27 ± 0.23‰ and d^{13}C: -29,40 ± 0.61‰). The precision for the analyses was ±0.05‰ for carbon and ±0.19‰ for nitrogen, based on the typical standards for isotope analyses conducted at PLATIN' for arthropods. Following Mestre et al. (2018), to analyze the mean isotopic signatures within the spider guilds used for SIA, 79 specimens were collected with nitrile gloves to avoid cross-contamination, and placed on dry ice for transport to the biological control laboratory of the Universidad de Talca. The number of samples was determined based on financial constraints associated with the cost of SIA.

Statistical Analysis. All analyses were carried out using R version 4.2.1. (R Core Team, 2021). Leven's and Shapiro-Wilk tests were applied to determine whether the variances were homoscedastic and to verify the normality of the data, respectively, using the Rcmdr package (Fox et al., 2024). The δ^{15}N values were log-transformed, as they were not normal. To test differences in abundances between SNVD and guilds, generalized linear models with negative binomial distribution were used, with SNVD as the explanatory variable. Differences in mean isotopic signatures in δ^{15}N and δ^{13}C were assessed using generalized linear models with a Poisson distribution, with guilds and landscape category as explanatory variables. Subsequently, overdispersion in the models was assessed, and an ANOVA test was performed to determine statistical differences between the factors in the models.

RESULTS

No significant differences in spider abundance were found between the different SNVD categories (GLM: x^2= 3.9636; *d.f*= 2; p=0.137820), nor was there an interaction between SNVD categories and the main identified guilds (Table 1) (GLM: x^2= 0.4.1207; *d.f*= 11; p=0.966252). Regarding δ^{13}C, there were no significant differences in the mean isotopic signatures between guilds (GLM: x^2= 3.5118; *d.f*= 3; p=0.31923), SNVD categories (GLM: x^2= 2.8500; *d.f*= 2; p=0.24050), or their interaction (GLM: x^2= 11.9129; *d.f*= 6; p=0.06394). δ^{15}N showed no significant differences in mean isotopic signatures between guilds (GLM: x^2= 2.3808; *d.f*= 3; p=0.4972), SNVD categories (GLM: x^2= 2.0480; *d.f*= 2; p=0.3592), or their interaction (GLM: x^2= 2.2232; *d.f*= 6; p=0.8981).

Mean isotopic signatures for spider guilds according to landscape complexity

Although not statistically significant, the mean isotopic signatures for spider guilds showed slight variations across the SNVD categories (Fig. 2). For δ^{13}C, the mean ± SD of diurnal aerial ambushers slightly changed in medium and high SNVD (-25.067 ± 2.485; 25.994 ± 2.290, respectively), but it decreased to -21.090±7.613 in low SNVD. Regarding δ^{15}N, the mean ± SD remained nearly the same in low and high SNVD, with values δ^{15}N 5.157 ± 2.235 and 5.093 ± 2.724, respectively (Table 2). However, in medium SNVD, δ^{15}N decreased to 3.956 ± 2.506.

Diurnal space web-weavers showed minimal variation in their mean isotopic signature for δ^{13}C between low and high SNVD categories (Table 2), with a slight decrease observed in the medium SNVD category (mean ± SD = -24.006 ± 4.379), although this change was not statistically significant. For δ^{15}N, a decreasing trend was observed as SNVD increased, with values of 5.161 ± 1.243; 4.531 ± 2.337; and 3.820±2.113 for low, medium, and high SNVD (Table 2), though these differences were not statistically significant.

Nocturnal aerial runners exhibited an increase in their mean isotopic signature for δ^{13}C as SNVD increased (Table 2), with the greatest differences observed between low and high SNVD (-22.938 ± 3.901; -27.262 ± 0.965, respectively; Table 2). However, for δ^{15}N, no significant changes were observed across the SNVD gradient (Table 2). The δ^{15}N values were 3.282 ± 0.760; 3.2103 ± 0.655; and 3.733 ± 1.905 for low, medium and high SNVD, respectively. None of the isotopic signatures from this guild across the SNVD showed statistically significant differences.

The mean isotopic signatures for δ^{13}C in the orb-weaver guild varied across the gradient (Table 2), but without statistically significant differences. The highest δ^{13}C value was observed for medium SNVD (mean ± SD = -26.065 ± 0.317), and the lowest for high SNVD (mean ± SD = -22.842 ± 4.483). Regarding δ^{15}N, the lowest mean isotopic signature (Table 2) was found in low SNVD (mean ± SD = 4.271 ± 2.855), while the lowest values corresponded to medium SNVD (mean ± SD = 2.542 ± 1.9191).

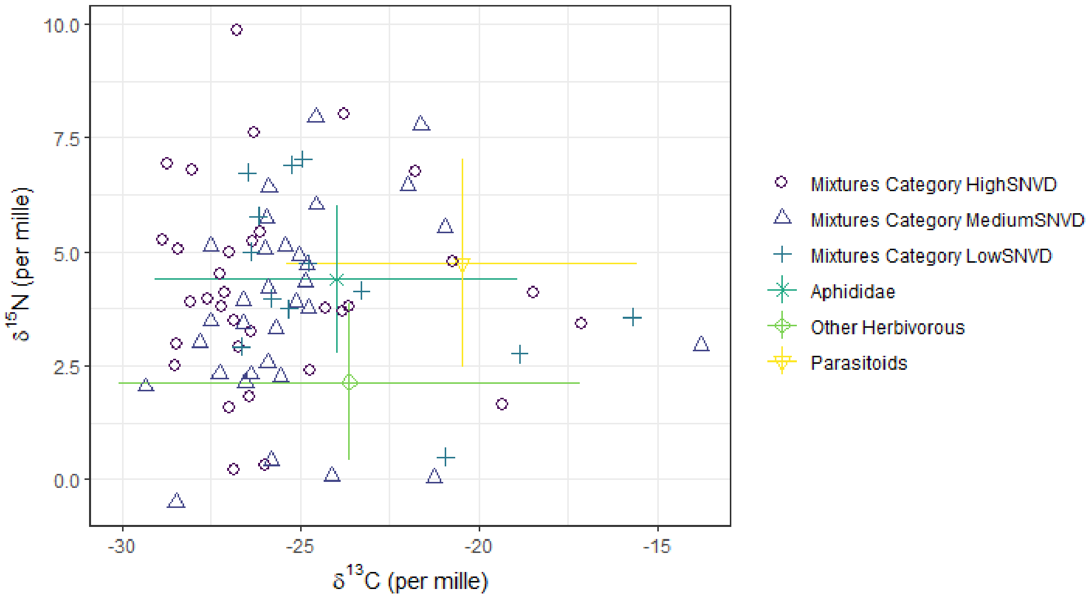

Fig. 2. Isotopic signatures biplot showing spider guilds (mixtures) and possible feeding items (sources) in apple orchards with three different surrounding natural vegetation densities. Means ±δ SE are shown for δ 15N and δ 13C (± 95% CI).

Table 2. Mean isotopic signatures for each spider guild in apple orchards with three different levels of surrounding natural vegetation density (SNVD). Means ±δ SE are shown for δ 15N and δ 13C (± 95% CI).

Low SNVD	Mean 15N±sd 15N	Mean D13C±sd D13C
Diurnal Aerial Ambushers	5.15724374±2.23591923	-21.09057±7.61353197
Diurnal Space web-weavers	5.16143386±1.24346119	-25.549991±0.6905814
Nocturnal Aerial Runners	3.2821515±0.76077461	-22.938616±3.90140249
Orb-weavers	4.27122112±2.85525394	-24.339375±2.33134822
Medium SNVD		
Diurnal Aerial Ambushers	3.95686744±2.50677343	-25.067286±2.48589749
Diurnal Space web-weavers	4.53147902±2.33754513	-24.006664±4.37936153
Nocturnal Aerial Runners	3.21039567±0.65591517	-26.068531±1.0623946
Orb-weavers	2.54295933±1.91910817	-26.065552±0.31747369
High SNVD		
Diurnal Aerial Ambushers	5.09315304±2.72475262	-25.994814±2.29042709
Diurnal Space web-weavers	3.82021586±2.11339149	-25.817191±2.46094663
Nocturnal Aerial Runners	3.73335099±1.90566305	-27.262061±0.96522015
Orb-weavers	3.77178245±1.13014512	-22.842143±4.48312198

DISCUSSION

No differences in spider abundance were observed among the apple orchards evaluated in the central valley of Chile under different landscape composition, suggesting that the spiders guilds present are not influenced by this landscape variable. However, the number of spider guilds within the apple orchards increased from 6 to 7 as SNVD increased from low to medium, maintaining the same number in high SNVD (7 guilds). Likewise, no statistical differences were observed in terms of abundance per guild in apple orchards. This agrees with Orellana et al. (2012), who found no significant differences in spider abundance between *Prunus* *dulcis* orchards and natural vegetation borders in Chile. This may be because spider populations in perennial crops are less mobile (Entling et al., 2011) and thus less responsive to the composition of the surrounding landscape. Additionally, perennial crops support a greater stability of in-field vegetation, which contributes to increased structural and compositional complexity (Lefebvre et al., 2016).

Changes in the mean isotopic signatures of spider guilds were not significant according to landscape complexity, with no clear association to specific SNVD categories. Previous studies using stable isotopes (Morente and Ruano, 2022) have shown that assemblages of spider (Araneidae - Thomisidae) species with different hunting strategies (Table 1), such as orb-weavers and diurnal aerial ambushers (Araneidae and Thomisidae, respectively), may exert higher predatory pressure on certain agricultural pests. In the present study, there were changes in mean isotopic signatures for the orb-weaver guild, with higher $\delta^{13}C$ in apple orchards within landscapes with medium SNVD, and higher $\delta^{15}N$ in low SNVD. These findings suggest that these spiders might be preying on other natural enemies, as mentioned by Mestre et al. (2013). We suggest that spiders that have higher $\delta^{15}N$ than their typical herbivorous prey are key candidates for being considered IGP and could play a key role in structuring the arthropod community, as reported by Mestre et al. (2013). These guilds could influence the delivery of ecosystem services, particularly pest control in agricultural systems by affecting other natural enemies that might be potentially more important for the target pest control. For example, orb-weavers may prey on a wide variety of arthropods, with a high preference for insects (Nyffeler and Benz, 1989), making them important natural enemies. Some authors suggest that active hunting spiders are more effective natural enemies for pest control than orb-weavers (Marc et al., 1999; Nyffeler, 1999), as some families such as Thomisidae (diurnal aerial ambusher) have a broader trophic niche (Michalko and Pekár, 2016). However, a broader trophic niche may negatively impact the control of other important natural enemies. When spiders prey on these natural enemies, they may reduce their consumptive and non - consumptive effect on pests (Schmidt-Entling and Siegenthaler, 2009; Michalko et al., 2019a). In fact, IGP are very common among active hunting spiders (Hodge, 1999; Birkhofer and Wolters, 2012; Mestre et al., 2013) and spiders can constitute up to a quarter or a third of the diet of hunting spiders (Michalko and Pekár, 2016). Generalist spider species lack specialized adaptations to overcome intraguild prey (Pekár and Toft, 2015), and other spiders could represent a low-ranking dietary item for these generalists. The intensity of IGP tends to decrease when alternative innocuous and more palatable prey are available (Michalko and Pekár, 2015; Petráková et al., 2016).

Despite the various factors that can influence the context in which IGP affect pest suppression efficiency between predators, if masopredator mortality is buffered by immigration, the effect of IGP on pest suppression would be minimal (Michalko et al., 2019b). Preying on multiple trophic levels allow spiders to optimize their nutritional demands, thereby improving their nutritional balance (Matsumura et al., 2004; Mayntz and Toft, 2006; Wilder et al., 2013). In addition, IGP can help overcome periods of prey shortage, preventing starvation and maintaining high abundances in the agroecosystem (Toft and Wise, 1999; Mayntz and Toft, 2006).

The lack of information on isotopic variation in spiders makes it difficult to interpret our results and discuss their implications. The data obtained are not sufficient to confirm an effect of the natural vegetation cover on mean isotopic variations. However, our findings contribute to the understanding of the potential role of spiders in agroecosystems and suggest that, regardless of the landscape variable considered here, spiders could potentially complement the biological control of pests in apple orchards.

CONCLUSIONS

Based on the above, we can conclude that, although we did not find sufficient evidence to accept our hypothesis, the isotopic variability of spider guilds in apple trees in central Chile could change with local management. Future experiments that consider local habitat (e.g., plant architecture, phenology, etc.) are needed to better understand the role of spiders as natural enemies.

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Author Contributions

Conceptualization, Enrique Maldonado-Santos, Blas Lavandero; methodology, Enrique Maldonado-Santos, Blas Lavandero, Bruno Jaloux, Darko D. Cotoras, Juan L. Celis Diez, Emmanuelle Travaillé; data collection, Enrique Maldonado formal analysis, Enrique Maldonado-Santos, Emmanuelle Travaillé; writing—original draft preparation Enrique Maldonado-Santos; writing—review and editing, Enrique Maldonado-Santos, Blas Lavandero, Bruno Jaloux, Darko D. Cotoras, Juan L. Celis-Diez; funding acquisition, Juan L. Celis-Diez, Blas Lavandero.

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