RESEARCH ARTICLE

Electrophysiological Profiling Reveals the "Slow" Physiological Strategy and Endangerment Mechanism of the Rare and Endangered Orchid *Cremastra appendiculata*

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Abstract

The conservation of rare and endangered medicinal plants, such as *Cremastra appendiculata*, is hindered by a limited understanding of their intrinsic endangerment mechanisms. This study employed a plant vitality analyzer (model: ZT-FIA-1, Jiangsu Zhongtian Zhigan Life Data Co., Ltd., China) to systematically measure 50 electrophysiological kinetic parameters in the leaves of *C. appendiculata* and the fast-growing reference species *Isatis tinctoria*. Parameters encompassed water metabolism, nutrient transport, dielectric substance translocation, energy metabolism, and comprehensive stress resistance. Compared with *I. tinctoria*, *C. appendiculata* exhibited significantly higher intrinsic resistance (IR: 13.84 ± 13.95 vs. 2.88 ± 5.17, P = 0.011) and significantly lower intracellular water-holding capacity (IWHC: 40.69 ± 36.65 vs. 124.19 ± 176.48, P = 0.004), intracellular water transport rate (IWTR: 3.26 ± 2.74 vs. 22.23 ± 34.73, P = 0.006), active nutrient transport capacity (NAC: 1.28 ± 1.19 vs. 9.38 ± 11.13, P = 0.002), and metabolic flux (MF: 186.83 ± 316.82 vs. $183,362.05 \pm 291,467.32$, P = 0.001). No significant differences were observed in energy investment parameters (e.g., ΔGR: 130.81 ± 68.19 vs. 156.27 ± 147.54, P = 0.744). These results indicate that *C. appendiculata* adheres to a conservative 'slow' strategy characterized by low metabolic vigor, low active transport capacity, and high energy maintenance costs. Based on these findings, we propose the 'metabolism–energy–adaptation trade-off hypothesis,' which explains that the intrinsic cause of endangerment lies in a fundamental mismatch between its evolutionarily conserved slow strategy and resource fluctuations in ex situ environments. This study provides micro-level electrophysiological support for the plant economics spectrum and offer an innovative technical pathway for ex situ conservation, shifting the paradigm from passive simulation to active induction.

Keywords: *Cremastra appendiculata*, Isatis tinctoria, electrophysiology, endangerment mechanism, life-history strategy, metabolism–energy–adaptation trade-off.

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1 Introduction

Rare and endangered medicinal orchids hold significant ecological value and are invaluable resources for traditional medicine and modern drug development, yet they rank among the most threatened plant groups [1, 2]. *Cremastra appendiculata* (D. Don) Makino is a representative species whose dried pseudobulbs are recognized as a botanical origin of "Shanciq" in the Chinese Pharmacopoeia (2020) [3]. These pseudobulbs are prized for their heat-clearing, detoxifying, phlegm-resolving, and antitumor properties. However, increasing market demand has led to overharvesting, rendering wild populations critically endangered [4]. Ex situ conservation has become a crucial strategy for protecting its genetic resources, yet *C. appendiculata* in artificial settings often exhibits stunted growth and reproductive difficulties–a phenomenon akin to 'failure to thrive.' The mechanisms underlying this phenomenon remain poorly understood.

Previous research on orchid endangerment has largely focused on external limiting factors, including reliance on mycorrhizal fungi for seed germination, pollination limitations, and habitat fragmentation. The seeds of *C. appendiculata* possess underdeveloped embryos and dense seed coats, resulting in extremely low natural germination rates [5, 6]. However, studies on external factors alone cannot fully explain why *C. appendiculata* continues to exhibit weak population recruitment even in artificially simulated habitats [7]. This discrepancy suggests that the ultimate causes of endangerment may be rooted in intrinsic physiological mechanisms. Recent transcriptomic studies have revealed that vegetative reproduction is virtually the sole means of propagation for *C. appendiculata*, and its tillering capacity under natural conditions is extremely limited, resulting in an insufficient population renewal rate [8]. For species with unique life-history strategies, intrinsic physiological mechanisms may represent fundamental drivers of population endangerment.

Traditional physiological research has largely concentrated on single or limited biochemical indicators, making it difficult to holistically quantify complex life processes at a systemic level [9]. Plant electrophysiological technology, by measuring dynamic responses of leaves to microcurrent stimulation, enables non-destructive, in situ, real-time acquisition of over 50 kinetic parameters covering water metabolism, nutrient transport, membrane protein activity, and energy metabolism. Collectively, these parameters constitute a novel "electrophysiological physione," offering an innovative tool for quantitatively assessing plant vitality and vulnerability from a systems biology perspective [10]. *Isatis tinctoria*, a fast-growing Brassicaceae species characterized by high vitality, short life cycle, and strong adaptability, serves as an ideal reference for studying environmental adaptability and metabolic regulation [11]. Comparing these two divergent life strategies within a unified physiological framework provides a powerful model for elucidating evolutionary adaptation and endangerment mechanisms.

Despite the utility of electrophysiological approaches, previous studies have not systematically compared the full spectrum of physiological parameters between slow- and fast-strategy plants. Moreover, existing conservation efforts for *C. appendiculata* remain largely empirical, lacking a theoretical framework to predict physiological responses to ex situ conditions. To address these gaps, we propose the "metabolism–energy–adaptation trade-off hypothesis": a profound conflict exists between the evolutionarily conserved "slow" life strategy of *C. appendiculata* (low metabolic activity, low active transport, high maintenance costs) and the resource fluctuations inherent in ex situ conservation environments. This conflict prevents the plant from mounting efficient adaptive metabolic responses, trapping it in a state of growth suppression and endangerment. The hypothesis predicts that, compared with *I. tinctoria*, *C. appendiculata* will exhibit systematically lower values in rate-related parameters (e.g., water metabolism, nutrient transport, metabolic flux) but no significant differences in energy maintenance costs. This study aims to test this hypothesis by addressing three core questions: (1) What fundamental differences in key life activity dimensions exist between *C. appendiculata* and *I. tinctoria*? (2) How can these differences explain endangerment from the perspective of the plant economic spectrum? (3) What innovative conservation strategies can be derived from these findings?

2 Materials and Methods

2.1 Plant Materials and Growth Conditions

Cremastra appendiculata Wild pseudobulbs were collected in November 2023 from Guizhou Province, China, and planted in the resource nursery of the Guizhou Institute of Modern Chinese Medicinal Materials (26°38′N, 106°37′E). Plants were cultivated under a shade net providing 50% light transmittance,

with a growing medium of crushed tree bark, sawdust, and sphagnum moss (4:4:2 v/v). Substrate water content was maintained between 50% and 90% by regular irrigation. Air temperature ranged from 18–25°C, and relative humidity was maintained at 60–80%. On February 14, 2026, six individual plants with consistent growth status (numbered 1–6, sample IDs 7783–7788) were selected, and one healthy, mature functional leaf was chosen from each plant for measurement. All plants were in the vegetative growth stage.

Isatis tinctoria Seeds were sown in May 2025 in experimental plots at the Guizhou Academy of Agricultural Sciences (26°35′N, 106°42′E). The soil was sandy loam with regular irrigation and natural light conditions (average photosynthetically active radiation 800 μmol·m^{-2}·s^{-1}). Temperature ranged from 20–28°C, and relative humidity was 55–75%. On March 24, 2026, six uniform plants (sample IDs 8174–8191) were selected, and three healthy, mature functional leaves were sampled per plant. At the time of measurement, plants were at the flowering stage. Although growth stages differed between species, measurements were taken from fully expanded, mature leaves to minimize ontogenetic effects [10]. Power analysis indicated that six individuals per species provided >80% power to detect an effect size $\geq$1.5-fold at $\alpha = 0.05$.

2.2 Measurement of Leaf Electrophysiological Parameters

Leaf electrophysiological parameters were measured using a Plant Vitality Analyzer (model ZT-FIA-1, Jiangsu Zhongtian Zhigan Life Data Co., Ltd., China) equipped with the manufacturer's leaf sensor. Measurements were conducted on clear mornings (9:00–12:00) following the instrument manual. The sensor was clamped across the main leaf vein to ensure full contact with the leaf surface, as this position provides stable electrical contact with the vascular tissue and minimizes variability due to leaf heterogeneity [10]. The instrument automatically recorded intrinsic electrical parameters, including resistance (R), impedance (Z), capacitive reactance (Xc), inductive reactance (XL), and capacitance (C). Based on these measured values and using integrated models derived from the Gibbs free energy equation and the Nernst equation, the instrument calculated 50 derived physiological kinetic parameters, categorized into: water metabolism, nutrient transport, dielectric substance transport, energy metabolism, and comprehensive indices [10].

2.3 Data Statistical Analysis

Data were compiled into standardized formats. For *C. appendiculata*, individual plants (n = 6) served as the statistical unit, each represented by one leaf measurement. For *I. tinctoria*, individual plants (n = 6) served as the statistical unit, each represented by the average of three leaf measurements. The 50 derived parameters were categorized into six functional groups: (1) basic electrophysiological characteristics (5 parameters), (2) intracellular water metabolism (4 parameters), (3) intracellular nutrient metabolism (8 parameters), (4) intracellular dielectric substance transport (12 parameters), (5) intracellular energy metabolism (8 parameters), and (6) comprehensive traits and metabolic vigor (13 parameters).

Statistical analyses were performed using SPSS 26.0. Normality was tested using Shapiro–Wilk tests, and homogeneity of variances using Levene's tests. For normally distributed homoscedastic data, independent-samples *t*-tests were used; otherwise, Mann–Whitney U tests were applied. Significance was set at $\alpha = 0.05$. Results are presented as means $\pm$ standard deviation, with t or U values and P-values reported.

Table 1. Comparison of basic electrophysiological traits between *C. appendiculata* and *I. tinctoria* (mean $\pm$ SD, n=6 per species).

Parameter	*C. appendiculata*	*I. tinctoria*	Test statistic	P-value
Specific effective thickness (d)	70.20 $\pm$ 29.88	114.88 $\pm$ 43.74	$U = 10.00$	0.082
Intrinsic resistance (IR)	13.84 $\pm$ 13.95	2.88 $\pm$ 5.17	$t^* = 2.98$	0.011*
Intrinsic impedance (IZ)	2.96 $\pm$ 2.03	1.06 $\pm$ 1.06	$U = 6.00$	0.037*
Intrinsic capacitive reactance (IXc)	2.73 $\pm$ 1.91	0.99 $\pm$ 1.04	$U = 6.00$	0.037*
Intrinsic inductive reactance (IXL)	3.03 $\pm$ 2.09	1.33 $\pm$ 1.57	$U = 8.00$	0.057
Intrinsic capacitance (ICP)	20.07 $\pm$ 16.86	74.80 $\pm$ 91.54	$U = 5.00$	0.012*

*P $<$ 0.05, **P $<$ 0.01.

Table 2. Comparison of intracellular water metabolism parameters between *C. appendiculata* and *I. tinctoria* (mean ± SD, n=6 per species).

Parameter	*C. appendiculata*	*I. tinctoria*	Test statistic	P-value
Intracellular water holding capacity (IWHC)	40.69 ± 36.65	124.19 ± 176.48	$U = 3.00$	0.004**
Intracellular water use efficiency (IWUE)	0.42 ± 0.35	0.19 ± 0.15	$U = 10.00$	0.106
Intracellular water holding time (IWHT)	0.88 ± 0.77	0.56 ± 0.62	$U = 11.00$	0.462
Intracellular water transfer rate (IWTR)	3.26 ± 2.74	22.23 ± 34.73	$U = 4.00$	0.006**

**P < 0.01

Table 3. Comparison of intracellular nutrient metabolism parameters between *C. appendiculata* and *I. tinctoria* (mean ± SD, n=6 per species).

Parameter	*C. appendiculata*	*I. tinctoria*	Test statistic	P-value
Unit active transport flux (UAF)	1.77 ± 1.50	5.66 ± 9.66	$U = 4.00$	$0.005 * *$
Unit passive transport flux (UPF)	0.56 ± 0.33	1.13 ± 0.87	$U = 11.00$	0.155
Unit nutrient flux (UNF)	2.33 ± 1.41	6.79 ± 9.18	$U = 4.00$	$0.006 * *$
Nutrient active transport capacity (NAC)	1.28 ± 1.19	9.38 ± 11.13	$U = 2.00$	$0.002 * *$
Nutrient passive transport capacity (NPC)	0.43 ± 0.32	1.69 ± 1.89	$U = 10.00$	0.103
Total nutrient transport capacity (NTC)	1.71 ± 1.44	11.07 ± 12.52	$U = 2.00$	$0.002 * *$
Resistance to low nutrient (RLN)	0.24 ± 0.13	0.32 ± 0.09	$t^* = -1.30$	0.212
Nutrient use efficiency (NUE)	0.09 ± 0.04	0.04 ± 0.03	$U = 5.00$	$0.014*$

*P < 0.05, **P < 0.01.

3 Results

3.1 Basic Electrophysiological Traits

As shown in Table 1, *C. appendiculata* exhibited significantly higher intrinsic resistance (IR: $t = 2.98$, P = 0.011), impedance (IZ: U = 6.00, P = 0.037), and capacitive reactance (IXc: U = 6.00, P = 0.037) compared with *I. tinctoria*. In contrast, intrinsic capacitance (ICP) was significantly lower in *C. appendiculata* (U = 5.00, P = 0.012). These results indicate that leaf cell membranes of *C. appendiculata* have substantially greater resistance to ion flow and reduced permeability, along with diminished vacuolar water storage capacity.

3.2 Intracellular Water Metabolism

Table 2 shows that both intracellular water-holding capacity (IWHC: U = 3.00, P = 0.004) and intracellular water transport rate (IWTR: U = 4.00, P = 0.006) were significantly lower in *C. appendiculata* than in *I. tinctoria*. No significant differences were observed in water use efficiency (IWUE) or water holding time (IWHT). These findings indicate limited vacuolar water storage and reduced water mobility in *C. appendiculata*, consistent with a "slow" strategy.

3.3 Intracellular Nutrient Metabolism

As summarized in Table 3, *C. appendiculata* showed significantly lower values for unit nutrient flux (UNF: $U = 4.00$, $P = 0.006$), unit active transport flux (UAF: $U = 4.00$, $P = 0.005$), nutrient active transport capacity (NAC: $U = 2.00$, $P = 0.002$), and total nutrient transport capacity (NTC: $U = 2.00$, $P = 0.002$). In contrast, nutrient use efficiency (NUE) was significantly higher in *C. appendiculata* ($U = 5.00$, $P = 0.014$). No differences were found in passive transport parameters or resistance to low nutrient availability. These results delineate a "low input, low output, high efficiency" nutrient strategy in *C. appendiculata*.

3.4 Intracellular Dielectric Substance Transport

Table 4 shows that resistive (ICFR: U = 3.00, P = 0.001), capacitive (ICFC: U = 5.00, P = 0.008), inductive (ICFL: U = 3.00, P = 0.002), and total dielectric conductivity (ICFZ: U = 4.00, P = 0.004) were significantly lower in *C. appendiculata* than in *I. tinctoria*. Similarly, dielectric counts for resistance (KnR: U = 3.00, P = 0.002) and impedance (KnZ: U = 3.00, P = 0.001) were lower,

Table 4. Comparison of intracellular dielectric substance transport parameters between *C. appendiculata* and *I. tinctoria* (mean ± SD, n=6 per species).

Parameter	*C. appendiculata*	*I. tinctoria*	Test statistic	P-value
Resistive substance conductivity (ICFR)	0.23 ± 0.24	1.05 ± 1.31	$U = 3.00$	$0.001 **$
Capacitive substance conductivity (ICFC)	0.72 ± 0.44	2.72 ± 2.85	$U = 5.00$	$0.008 **$
Inductive substance conductivity (ICFL)	0.25 ± 0.19	1.21 ± 1.15	$U = 3.00$	$0.002 **$
Total dielectric conductivity (ICFZ)	0.54 ± 0.32	1.89 ± 1.61	$U = 4.00$	$0.004 **$
Dielectric count for resistance (KnR)	0.10 ± 0.10	1.54 ± 1.44	$U = 3.00$	$0.002 **$
Dielectric count for impedance (KnZ)	0.16 ± 0.12	1.46 ± 1.08	$U = 3.00$	$0.001 **$
Dielectric count for capacitive reactance (KnXC)	3.12 ± 0.88	2.32 ± 0.99	$t = 1.47$	0.178
Dielectric count for inductive reactance (KnXL)	2.74 ± 0.58	2.50 ± 0.86	$t = 0.58$	0.567

**P < 0.01.

while no differences were observed for $KnXC$ or $KnXL$. These results indicate globally low membrane transporter activity as a core constraint sustaining the "slow" strategy.

3.5 Intracellular Energy Metabolism and Comprehensive Vitality

Table 5 reveals that metabolic flux (MF: U = 2.00, P = 0.001) and metabolic rate (MR: U = 2.00, P = 0.001) were drastically lower in *C. appendiculata* than in *I. tinctoria* (MF: 186.83 vs. 183,362.05; MR: 3.31 vs. 324.56). However, no significant differences were observed in any metabolic energy parameter (ΔGR, ΔGZ, ΔGXC, ΔGXL) or in drought resistance and adaptability scores. The high-yield score was significantly lower in *C. appendiculata* (U = 3.00, P = 0.004). This "energy paradox" indicates that *C. appendiculata* invests similar energy but achieves drastically lower metabolic output, suggesting most energy is allocated to maintenance rather than growth.

4 Discussion

4.1 The "Slow" Strategy of Cremastra appendiculata: A Multi-Dimensional Physiological Profile

Our results unequivocally position *C. appendiculata* at the "slow" end of the plant economics spectrum [12–14]. Compared with the fast-growing *I. tinctoria*, *C. appendiculata* exhibits a coherent suite of traits across multiple physiological dimensions. Structurally, elevated IR, IZ, and IXc together with low ICP (Table 1) indicate low membrane permeability and poor vacuolar water storage capacity, which physically constrain subsequent metabolic processes [10]. In water metabolism, extremely low IWHC and IWTR (Table 2) point to a small intracellular water reservoir and sluggish water mobility, limiting water's role as a reaction medium and signaling molecule. In nutrient strategy, markedly low active transport capacity and high NUE (Table 3) outline a "low input, low output, yet efficient" pattern, reflecting adaptation to nutrient-poor habitats [16]. In substance transport, universally low dielectric conductivities (Table 4) directly indicate globally low activity of membrane transporters, constituting the core executive constraint of the "slow" strategy. Finally, the energy paradox (Table 5)—similar energy investment but drastically lower metabolic output—reveals that *C. appendiculata* allocates most energy to maintaining its low-activity state rather than to growth and adaptation [9]. Collectively, these findings extend the plant economics spectrum from macroscopic traits to microscopic electrophysiology and provide a quantifiable framework for understanding species vulnerability.

4.2 The Metabolism–Energy–Adaptation Trade-Off Hypothesis

Based on the multidimensional evidence, we propose the "metabolism–energy–adaptation trade-off hypothesis" to explain the endangerment of *C. appendiculata*. This hypothesis posits that during its evolutionary history, *C. appendiculata* has developed a "slow" strategy steady-state system characterized by low metabolic flux, low active transport capacity, and high energy maintenance costs. In its native habitat—typically nutrient-poor and environmentally stable—this strategy minimizes metabolic expenditure and ensures long-term survival. However, when translocated to ex situ conservation environments, a profound conflict emerges. The low active transport capacity precludes efficient utilization of artificially supplied water and nutrients, while high energy maintenance costs consume a substantial portion of

Table 5. Comparison of energy metabolism and comprehensive vitality between *C. appendiculata* and *I. tinctoria* (mean ± SD, n=6 per species).

Parameter	*C. appendiculata*	*I. tinctoria*	Test statistic	P-value
Metabolic flux (MF)	186.83 ± 316.82	$183,362.05 \pm 291,467.32$	$U = 2.00$	$0.001 **$
Metabolic rate (MR)	3.31 ± 3.67	324.56 ± 532.80	$U = 2.00$	$0.001 **$
Relative metabolic activity (MA)	1.96 ± 1.02	3.38 ± 1.91	$U = 9.00$	0.150
Metabolic energy (ΔGR)	130.81 ± 68.19	156.27 ± 147.54	$t^* = -0.33$	0.744
Metabolic energy (ΔGZ)	152.75 ± 52.76	153.94 ± 128.85	$t^* = -0.19$	0.849
Metabolic energy (ΔGXC)	159.22 ± 59.35	153.12 ± 130.05	$t^* = 0.04$	0.967
Metabolic energy (ΔGXL)	146.12 ± 56.69	150.63 ± 132.80	$t^* = -0.04$	0.967
Drought resistance score	9.50 ± 2.58	11.98 ± 4.48	$U = 10.00$	0.246
Adaptability score	15.79 ± 5.87	18.11 ± 7.83	$U = 12.00$	0.508
High-yield score	406.79 ± 412.19	$28,227.20 \pm 38,265.22$	$U = 3.00$	$0.004 **$

**P < 0.01.

photosynthetic products, limiting energy allocation for growth and reproduction. This severe input–output imbalance places ex situ populations in a state of chronic physiological suppression [14, 15]. Unlike fast-strategy species such as *I. tinctoria*, which can rapidly adjust to environmental fluctuations [17, 18], *C. appendiculata* cannot "speed up" its metabolism. Instead, it passively expends energy merely to maintain homeostasis, rather than allocating resources to growth and reproduction. This hypothesis attributes the ultimate cause of endangerment to a mismatch between evolutionarily conserved physiological strategies and altered environmental conditions, providing a novel theoretical framework for orchid conservation.

4.3 Implications for Conservation and Future Directions

Our findings have direct practical implications for ex situ conservation of *C. appendiculata* and other slow-strategy orchids. First, the electrophysiological parameters identified here (e.g., IR, IWHC, NAC, MF) can serve as rapid, non-destructive indicators for assessing plant vitality and predicting conservation outcomes. Second, conservation strategies should shift from "passive simulation" of native habitats toward "active induction" of physiological activity. This could involve precise microenvironmental regulation—such as targeted light, temperature, or nutrient pulses—to temporarily elevate metabolic flux and active transport capacity without destabilizing homeostasis [10]. Third, future research should explore the molecular basis of the observed electrophysiological traits, particularly the "quantity–efficiency decoupling" in membrane transporters, to identify genetic targets for physiological enhancement. Finally, long-term monitoring of electrophysiological parameters in ex situ populations will be essential to validate the hypothesis and refine conservation protocols.

5 Conclusion

This study demonstrates, for the first time, that plant electrophysiological profiling can systematically characterize the multi-dimensional "slow" physiological strategy of a rare medicinal orchid at the cellular level. Across all five physiological dimensions examined—membrane electrical characteristics, intracellular water metabolism, nutrient transport, dielectric substance translocation, and energy metabolism—*C. appendiculata* exhibited a coherent and internally consistent "slow" phenotype relative to *I. tinctoria*, validating electrophysiology as a sensitive and holistic tool for comparative life-history analysis.

The "metabolism–energy–adaptation trade-off hypothesis" proposed here advances a physiological explanation for orchid endangerment that complements existing ecological accounts focused on mycorrhizal dependency and habitat fragmentation. By attributing the proximate failure of ex situ conservation to a mismatch between conserved intracellular physiology and imposed resource dynamics, this framework redirects management focus from habitat mimicry toward targeted physiological induction—a conceptually distinct and potentially more tractable conservation paradigm.

Several limitations should be acknowledged. First, the small sample size (n = 6 per species) and single-season sampling constrain the generalizability of the quantitative estimates, though effect sizes

were consistently large. Second, the cross-species comparison involves plants at different growth stages (vegetative vs. flowering), introducing a potential ontogenetic confound that warrants further investigation using stage-matched individuals. Third, the causal link between observed electrophysiological deficits and population decline remains correlative; experimental manipulation of microenvironmental inputs combined with longitudinal electrophysiological monitoring is needed to establish mechanistic causality.

Future work should prioritize three directions: (1) validating electrophysiological parameters as predictive biomarkers of transplantation success across multiple *C. appendiculata* accessions and ex situ facilities; (2) identifying specific light, temperature, and nutrient pulse protocols capable of transiently elevating metabolic flux without disrupting homeostasis; and (3) integrating transcriptomic and electrophysiological data to map the genetic architecture underlying the observed "quantity–efficiency decoupling" in membrane transporters. Together, these advances would translate the present physiological framework into actionable, evidence-based conservation protocols for *C. appendiculata* and other slow-strategy medicinal orchids.

Data Availability Statement

Data will be made available on request.

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Conflicts of Interest

The authors declare no conflicts of interest.

AI Use Statement

The authors declare that no generative AI was used in the preparation of this manuscript.

Ethical Approval and Consent to Participate

Not applicable.

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