Journal of Medicinal Natural Products

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Review

The Potential of *Origanum vulgare* L. in Food Preservation: A Review of Bioactivities, Mechanisms, and Modern Applications

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Received: 23 October 2025; Revised: 19 November 2025; Accepted: 27 November 2025; Published: 1 December 2025

Abstract: The consumer awareness regarding the risks associated with synthetic preservatives has significantly boosted the demand for natural and safe alternatives. *Origanum vulgare* L. (oregano) demonstrates high potential as a natural preservative due to its powerful bioactive compounds, such as carvacrol, thymol, and rosmarinic acid. The scientific evidence on the potential application of *O. vulgare* as a multifunctional preservative in the food industry forms the focus of this review. The essential oil and extracts of this plant, rich in phenolic compounds exhibit a broad spectrum of antimicrobial properties. The preservative spectrum includes antibacterial activity against spoilage and pathogenic bacteria, antifungal activity against storage molds, such as *Aspergillus* and *Penicillium*, anti-yeast activity, and insecticidal effects against major stored-product pests. The mechanisms of action involve microbial cell membrane disruption, oxidative stress induction, and interference with metabolic processes. Furthermore, the antioxidant properties of *O. vulgare* contribute to protecting the chemical quality of food by inhibiting lipid peroxidation. However, the challenges of high volatility and low water solubility restrict direct application. Nanotechnology, particularly nanoencapsulation, improves the stability and efficacy of this natural preservative. Consequently, *O. vulgare* represents a sustainable alternative to synthetic preservatives with a promising outlook for next-generation food preservation technologies. This review highlights the potential of *O. vulgare* in food preservation through bioactivities, mechanisms, and modern applications

Keywords: preserved foods; food spoilage; post harvest decay; rosmarinic acid; oregano; mycotoxins

1. Introduction

The primary objective of food preservation is to prevent spoilage caused by both microbial proliferation and chemical degradation. Traditional methodologies (such as salting and drying) were largely effective against microbial activity but offered limited protection against lipid peroxidation and the onset of rancidity. The development of chemical preservatives fundamentally altered food stabilization strategies by targeting these distinct spoilage pathways. These agents are classified based on their mechanism of action into three principal categories. Antimicrobial agents such as organic acids, and nitrites impede microbial proliferation. Primary antioxidants such as butylated hydroxyanisole, and butylated hydroxytoluene interrupt the free-radical chain reactions of lipid peroxidation. Sequestrants or synergists such as ethylenediaminetetraacetic acid, and citric acid that chelate pro-oxidant metal ions which catalyze oxidation [1]. Although the use of chemical preservatives has been in the spotlight for years, current scientific evidence indicates that chemical food additives, including artificial colorants, benzoate preservatives, sweeteners, and emulsifiers, are associated with an increased risk of neuropsychiatric disorders, cardiovascular diseases, metabolic syndrome, as well as potential genotoxic and carcinogenic effects [2].

The increasing consumer awareness of these risks has boosted demand for natural preservatives as a safe substitute for extending the shelf life of food. These compounds are divided into three main groups based on their origin. The first group, plant-based compounds, includes secondary plant metabolites such as phenolic compounds and essential oils (EOs). The second group, animal-based compounds, are antimicrobial compounds obtained from sources such as eggs (lysozyme), milk (lactoferrin and lactoperoxidase), and the exoskeletons of crustaceans (chitosan), and the third group, microbial-based compounds, includes metabolites resulting from fermentation by microorganisms (mainly lactic acid bacteria), such as bacteriocins (nisin), organic acids, and hydrogen peroxide [3]. Among these, the use of plant-based preservatives has been of great interest [4–6].

Origanum vulgare L., commonly known as oregano, is one of the most important medicinal and aromatic plants in the Lamiaceae family. As the most diverse species in the *Origanum* genus, it is native to the Mediterranean and Eurasian regions and, due to its high economic importance, is widely cultivated worldwide in addition to growing wild. The main phytochemical constituents of this plant include two major groups, EOs, and phenolic compounds. Although other active compounds such as terpenoids, tannins, and sterols have also been identified [7]. The most significant compounds identified in *O. vulgare* are the highly active phenols, thymol and carvacrol, alongside terpenes such as γ-terpinene, *p*-cymene, sabinene, and β-caryophyllene, which are characteristic of its essential oil (EO). Additionally, rosmarinic acid is recognized as the predominant phenolic acid, while flavonoids like luteolin-*O*-glucuronide and luteolin-7-*O*-glucoside are other key constituents of the plant [8,9]. Figure 1 illustrates the chemical structures of the key bioactive compounds identified in *O. vulgare*.

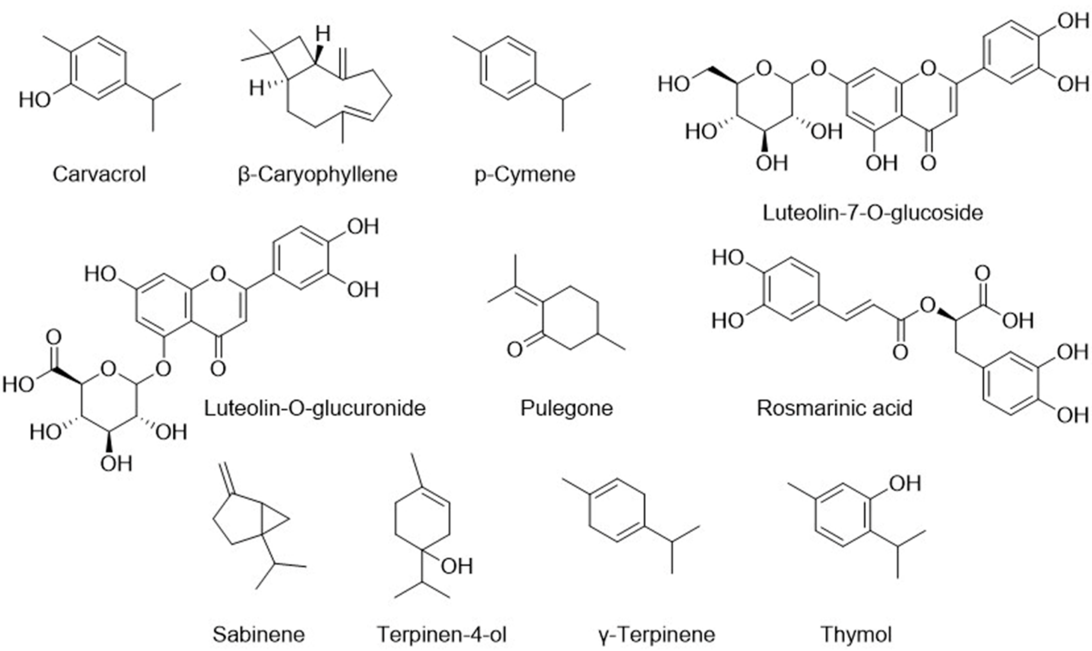

Figure 1. Chemical structures of the key bioactive compounds identified in *O. vulgare.*

O. vulgare is distinguished from other culinary herbs by the simultaneous abundance of carvacrol, thymol, and rosmarinic acid, a unique phytochemical profile that underpins its broad antimicrobial, antioxidant, and insecticidal activities [7–9]. his distinctive composition, together with extensive evidence of efficacy in diverse food systems, justifies a focused review on this species rather than a generalized survey of plant-sourced preservatives. *O. vulgare* exhibits a wide range of biological effects, most notably antimicrobial (antibacterial, antifungal, and antiviral), antioxidant, anti-inflammatory, and anticancer properties [7–10]. The plant also demonstrates significant protective effects against damage induced by chemotherapy, including hepatoprotective [11], lung protection [12], and genoprotective actions on healthy cells [13,14]. Furthermore, by enhancing the activity of drugs like cisplatin, its extract shows potential as a natural complementary therapy for managing cancer and inflammation [15]. *O. vulgare*, with its distinctive phytochemical profile and broad biological activities, is a promising candidate for natural food preservation, requiring detailed examination of mechanisms, applications, and future potential.

2. Traditional Uses

The use of medicinal and aromatic plants in traditional medicine has a rich history. Among these, species of the genus Origanum, particularly *O. vulgare*, have held a prominent position in various cultures worldwide due to their diverse therapeutic properties [16]. The use of *O. vulgare* dates back to the ancient Greek and Roman empires, where leaves were applied topically to treat skin wounds, alleviate muscle aches, and serve as a general antiseptic [17]. This traditional knowledge has persisted to the present day, with different parts of the plant being utilized in various regions to treat a wide range of ailments.

In the Mediterranean region, particularly in Greece, the use of *O. vulgare* is deeply rooted. An ethnobotanical study in the local markets of Peloponnese revealed that the aerial parts of this plant (locally known as "Rigani") are widely used as an infusion, decoction, or inhalation to treat respiratory issues such as cough, bronchitis, the common cold, influenza, and asthma. It has also been employed to manage digestive disorders like diarrhea, flatulence, and stomachache, and used topically as a mouthwash for canker sores and toothache, and as an antiseptic skin wash [18]. In Turkey, the *Origanum* genus is considered one of the most frequently used botanicals for treating influenza. Herbal teas prepared from the aerial parts of three *O. vulgare* subspecies (subsp. *gracile*, subsp. *hirtum*, and subsp. *viridulum*) are commonly used for this purpose [19].

This pattern is mirrored in North Africa. In Morocco, *O. vulgare* is recognized as a plant of high local importance for treating influenza, with a fidelity level for this application reaching 51.78% among local women [20]. Furthermore, a recent cross-sectional study in a Moroccan hospital indicated that three native *Origanum* species were the most consumed medicinal plants among patients (54.7%). Their leaves and aerial parts were predominantly used as an infusion, decoction, or inhalation to treat influenza and cough [21].

The scope of this plant's traditional application extends to other continents. In Uzbekistan, local healers use a decoction of the plant's aerial parts to improve digestion and as an expectorant, diaphoretic, toothache reliever, and a sedative for the nervous system [22]. In the Philippines, *O. vulgare* is the second most utilized plant among local farmers (67% of participants), who use a decoction of its leaves both orally and in aromatic herbal baths to alleviate symptoms of asthma, cough, and the common cold [23].

Similar therapeutic applications have been extensively documented for *Origanum majorana* (syn. *O. vulgare*) as well. This species is also used in the traditional medicine of Mediterranean countries to treat respiratory diseases such as influenza, cough, and the common cold, as well as for its sedative and gastrointestinal antispasmodic effects [24]. This overlap highlights the medicinal importance of the entire *Origanum* genus, and particularly *O. vulgare*, across diverse cultures.

3. Antibacterial Activity

O. vulgare, particularly its EO and extracts, has been extensively studied as a potent antimicrobial agent due to its content of bioactive compounds. Research indicates that its efficacy is dependent on factors such as chemical composition (chemotype), the concentration used, the target microorganism, and the complexity of the food matrix.

3.1. In Vitro Efficacy

Numerous studies have confirmed the high antimicrobial potential of oregano EO under controlled laboratory conditions. In a study conducted by Torabian Kakhki et al. (2020), oregano EO with a balanced chemotype of thymol (35.18%) and carvacrol (34.00%) demonstrated significant activity against both Gram-positive and Gram-negative bacteria. Among these, the Gram-negative bacterium *Shewanella putrefaciens* showed the highest sensitivity to the EO, exhibiting an inhibition zone of 22.00 mm. The minimum inhibitory concentration (MIC) and minimum bactericidal concentration values for this bacterium were both reported as 0.64 mg/mL, indicating a strong bactericidal effect. The time-kill assay further confirmed the rapid action of this EO, as 80% of the *S. putrefaciens* population was eliminated in just 4 h [25].

Similarly, György et al. (2023), using the agar diffusion method, demonstrated the powerful inhibitory activity of oregano EO against a wide range of bacteria, including various species of *Pseudomonas*, *Enterobacter*, *Bacillus*, and *Proteus*. The strongest effect in this study was observed against *Pseudomonas baetica* and *Pseudomonas aeruginosa* [26]. Furthermore, Khalifa (2022) reported that oregano EO, at a MIC of 0.23 mg/mL, effectively inhibited the growth of *Serratia liquefaciens*, which had been identified as a spoilage agent in apples [27]. Collectively, these results highlight the intrinsic potential of oregano EO as a broad-spectrum antibacterial agent, particularly against Gram-negative pathogens.

3.2. Application in Food Systems

The effectiveness of oregano has also been investigated in real food models, with results varying depending on the product type and storage conditions.

3.2.1. Plant Products and Vegetables

The practical application of oregano EO in controlling post-harvest spoilage agents has been validated. Apples inoculated with *S. liquefaciens* and treated with oregano EO at the MIC showed no signs of rot after 8 days of storage in an *in vivo* test [27]. Additionally, vegetables including tomatoes, cucumbers, carrots, and hot peppers coated with an edible film containing oregano EO had significantly lower aerobic mesophilic bacterial counts after 11 days compared with control group [26].

3.2.2. Seafood Products

Contrary to most studies focusing on EOs, Sterniša et al. (2020) investigated the activity of an ethanolic extract from oregano inflorescences, rich in rosmarinic acid, against fish spoilage bacteria. This extract inhibited the growth of Pseudomonas and Shewanella strains with MIC values of 1.56 or 3.13 mg/mL. The direct application of this extract onto fish meat also reduced the population of H_2S-producing bacteria after 9 days of refrigerated storage, indicating the potential of non-volatile phenolic compounds in controlling spoilage [28]. The efficacy of oregano EO is strongly influenced by chemotype and preparation method [25–27], while the activity of ethanolic extracts depends on polyphenol content, particularly rosmarinic acid [28].

3.2.3. Dairy Products

In fresh Minas Frescal cheese, a combination of oregano (0.07 µL/g) and rosemary (2.65 µL/g) EOs exerted a very strong inhibitory effect on the pathogen *Escherichia coli* O157:H7, drastically reducing its population over 15 days of storage. Although this combination also had an inhibitory effect on the probiotic bacterium *Lactobacillus acidophilus*, its population remained at a functional level [29]. In another study, Kunová et al. (2023) compared the effect of dried oregano powder (1%) with its EO (1%) in sheep cheese. Surprisingly, the results showed that the dried herb was even more effective than its EO in reducing the total bacterial count and inhibiting coliforms, positioning it as a cheap and efficient alternative [30].

3.2.4. Meat Products

The results in this category have been variable. Belichovska et al. (2025) found that an herbal mixture containing oregano effectively reduced the total bacterial count, and particularly the Enterobacteriaceae family, in the meat product cevapcici after 7 days [31]. In contrast, Vergara et al. (2020), in a study on lamb burgers, observed no significant difference in the total microbial and Pseudomonas counts between samples treated with different forms of oregano and the control group. Unexpectedly, all forms of oregano failed to inhibit the growth of Enterobacteriaceae and even showed a higher population than the control group. However, in the same study, oregano oleoresin significantly inhibited the growth of lactic acid bacteria [32].

3.3. Studies with Contradictory Results and the Importance of Concentration, Appropriate Form, and Other Factors

Some research has reported no or limited effects of oregano, highlighting the importance of factors like concentration and the food matrix. For instance, Fusaro et al. (2022) showed that the addition of a combination of oregano and rosemary EOs at a low concentration (0.05 mL/kg) to beef burgers stored under a modified atmosphere had no statistically significant effect on inhibiting the growth of any of the microbial groups studied. The researchers attributed this to the low concentration of the EO and its potential interaction with food components [33]. Similarly, Mironescu and Georgescu (2021) reported that a thymol-rich oregano EO (55.25%) at a dose of 0.5 µL showed no visible inhibitory effect on the growth of *Bacillus cereus* and *Salmonella anatum*. This lack of activity was attributed to the low concentration of the EO in the test [34]. The concentration data (MIC, MBC, LD_{50}, IC_{50}) are consistently reported across antibacterial [25–34], antifungal [35–53], anti-yeast [34,54–58], and anti-insect sections [59–65], highlighting the importance of dose in determining reproducible activity.

The available evidence clearly demonstrates that *O. vulgare* and its products possess strong antibacterial potential against spoilage and pathogenic bacteria. However, translation of this potential from *in vitro* conditions to complex food systems requires careful optimization. It seems factors such as selecting the appropriate form (EO, extract, dried herb), effective dose, food matrix, interactions must be considered. The chemical chemotype including the ratio of thymol to carvacrol or presence of rosmarinic acid, is critical for reproducible results.

4. Antifungal Activity

O. vulgare, particularly its EO, shows broad-spectrum antifungal potential. Numerous studies have demonstrated activities against food spoilage molds and plant pathogens. This activity is mainly attributed to phenolic compounds, namely carvacrol and thymol. Research has shown that the efficacy of this EO depends on the chemotype, concentration, fungal species, and application method, whether direct contact or vapor phase.

4.1. Activity against Important Pathogenic and Spoilage Fungi

Oregano EO has demonstrated significant inhibitory activity against the most important fungi responsible for spoilage in agricultural products and foodstuffs:

Penicillium species: These molds are among the main causes of food spoilage. In a study on ten different *Penicillium* species, oregano EO of the carvacrol chemotype (43.26%) showed relatively weak inhibitory activity at low concentrations. The EO was completely ineffective against *P. polonicum* [35]. However, other studies have confirmed its high potency; a carvacrol-rich EO (82.42%) was able to inhibit the growth of *P. commune* and *P. crustosum* strains isolated from cheese at very low concentrations (MIC: 0.08–0.63 mg/mL) [36]. Furthermore, a thymol-rich EO (81.29%) showed significant inhibitory activity (up to 90.02%) against *P. expansum* [37].These results indicate a strong dependence of the effect on the EO's chemotype and the fungal species.

Aspergillus species: Oregano EO and carvacrol effectively inhibit the growth of hazardous molds of this genus. In one study, the vapor phase of the EO showed very high activity against *A. flavus* and *P. commune* [38]. Carvacrol alone is also capable of completely preventing the proliferation of *A. flavus* in wheat grains [39]. In addition to growth inhibition, the EO and carvacrol can also inhibit the production of the mycotoxin fumonisin B2 by *A. niger* [40].

Botrytis cinerea (Grey mold): This fungus is one of the most significant post-harvest pathogens. Numerous studies have demonstrated the efficacy of oregano EO and the pure compounds carvacrol and thymol against it. These compounds are capable of completely inhibiting spore germination and mycelial growth [41–43]. The application of the EO's vapor phase on grapes and cherry tomatoes prevented fruit rot by 73% and 96.39%, respectively [43,44]. Interestingly, the pure compounds thymol and carvacrol, at half the concentration of the complete EO, achieved 100% inhibition [43].

Fusarium species: This genus includes species resistant to chemical fungicides. Oregano EO showed a stable and strong effect on *F. oxysporum* in Minas cheese, completely inhibiting its spore germination over 30 days [45]. In another study, this EO was able to completely inhibit (100%) the mycelial growth of pesticide-resistant *Fusarium* species [46].

Other fungi: The antifungal activity of oregano EO has also been proven against other species such as *Cladosporium cladosporioides* [47], *Monilinia* species [48], and fungi causing spoilage in tropical fruits, like *Lasiodiplodia theobromae* and *Alternaria alternata* [49].

4.2. Comparison of Vapor Phase vs. Direct Contact Efficacy

One of the key and recurring findings in research is the significantly higher efficacy of oregano EO's vapor phase compared to direct contact [38,39,43,49]. The volatile organic compounds present in the EO can inhibit fungal growth without the need for physical contact. For example, the EC_{50} value of the EO for inhibiting *B. cinerea* in the vapor phase was approximately three times lower than in direct contact (16.44 vs. 52.92 mg/L). This pattern was also observed for the pure compounds carvacrol and thymol, with even more dramatic reductions in EC_{50} [43]. Similarly, the MIC for the fungi *A. alternata* and *Fusarium solani* was sharply reduced in the vapor phase [49]. This characteristic highlights the high potential of this EO for use in fumigation systems and active packaging to protect post-harvest products [38,44,48,50].

4.3. Practical Applications and Limitations

The antifungal potential of oregano EO has been confirmed in various practical applications. Oregano EO added to cheese to control spoilage molds [36]. A separate study confirmed similar activity in cheese [45]. In tomato sauce, it prevented the growth of *P. purpurogenum* [51]. Ethanolic extracts inhibited mold growth in alfalfa [52] corn silage treated with oregano extracts reduced mycotoxins such as zearalenone and deoxynivalenol (DON) [53]. EO fumigation controlled grey mold on grapes [44], inhibited spoilage in tomatoes [43], and protected stored wheat against fungi and the production of the mycotoxin DON [50].

However, certain limitations must also be considered. Oregano EO vapors exhibit a significant phytotoxic effect, inhibiting the germination of wheat [50] and quinoa seeds germination, making them unsuitable for planting [46]. Also, in some applications, such as cheese, the inhibitory effect may be temporary and diminish over time [45]. Furthermore, the impact of the extracts on different types of mycotoxins can be variable; it may decrease the concentration of some, have no effect on others, and even increase some others [52,53]. Finally, most studies report fungistatic activity, indicating growth inhibition without fungal death. Overall, these findings confirm that the antifungal efficacy of *O. vulgare* depends on both chemotype and effective dose. MIC and inhibition values reported across fungal studies [35–37] demonstrate that reproducible inhibition is achieved only at sufficient concentrations, while low doses fail to suppress growth. Differences in thymol and carvacrol ratios further explain variability in outcomes.

5. Anti-Yeast Activity

The anti-yeast potential of *O. vulgare* against various yeast species, particularly those implicated in food spoilage or clinical infections, has been investigated in various studies. The plant's activity is significantly dependent on the EO chemotype and the extraction method.

In one study, extracts of *O. vulgare* prepared using supercritical fluid extraction (SFE) demonstrated inhibitory activity against the yeast *Candida albicans* (ATCC 60193). Among the different conditions tested, the extract obtained at a pressure of 250 bar and a temperature of 40 °C was the most effective [54]. In another investigation aimed at optimizing extraction, aqueous maceration and SFE methods were compared. The results indicated that the SFE extract, prepared at 25 MPa and 40 °C, exhibited the most potent activity against *C. albicans* (ATCC 60193) with a MIC of 0.311 mg/mL. This value was markedly superior to the MIC of the optimized aqueous extract (0.872 mg/mL) [55]. The same yeast species (*C. albicans* ATCC 10231) was tested against a carvacrol-rich (81.20%) EO in a different study. The results showed that the MIC for this EO was 0.62% (v/v), but since the minimum fungicidal concentration was higher than 5%, its effect was described as primarily fungistatic [56].

In a separate study, the efficacy of oregano EO was evaluated against several strains from the *Candida* and *Pichia* genera. The EO used inhibited the growth of all tested *Candida* strains (*C. albicans*, *Candida glabrata*, *Candida krusei*) at a concentration of 375 µg/mL. Notably, the EO had a more potent effect on the *Pichia* species, inhibiting the growth of *Pichia membranifaciens* and *Pichia pijperi* at half the concentration, 187.5 µg/mL [57].

Activity against the important spoilage yeast, *Saccharomyces cerevisiae*, has also received attention. The EO of *O. vulgare* subsp. *hirtum*, rich in thymol (48.12%) and carvacrol (27.19%), successfully inhibited the growth of this yeast, with its MIC and minimum lethal concentration values determined to be 1647 and 6590 mg/L, respectively. The practical application of this EO was also validated in tomato juice, where a concentration of 350 ppm significantly controlled the growth of *S. cerevisiae* at both room and refrigerated temperatures [58]. However, in another study using a low dose (0.5 µL) of an EO with a thymol-rich chemotype (55.25%), no measurable inhibitory effect against *S. cerevisiae* was observed, a result that the researchers attributed to an insufficient concentration of the EO [34]. Overall, these findings confirm that the anti-yeast activity of *O. vulgare* depends on both chemotype and effective dose. MIC and lethal concentration values reported across yeast studies [34,54–58], demonstrate that reproducible inhibition is achieved only at sufficient concentrations, while low doses fail to suppress growth. Differences in thymol and carvacrol ratios further explain variability in outcomes.

6. Anti-Insect Activity

The use of natural compounds as alternatives to synthetic insecticides in the management of stored-product pests has garnered increasing attention due to environmental and health concerns. Among these, *O. vulgare* has demonstrated significant potential for controlling stored-product pests owing to its diverse active compounds. The activity of this plant has been investigated in various forms (EO, dried plant powder) and through different modes of action (contact, fumigant, repellent, and antifeedant) against major pests such as *Tribolium* and *Sitophilus* species.

6.1. Contact and Fumigant Toxicity

The EO of *O. vulgare* and its subspecies, particularly carvacrol and thymol-rich chemotypes, possess potent contact and fumigant toxicity. In a study on four Origanum species, the EO of *O. vulgare* var. *verticium*, containing 35.0% carvacrol, exhibited the strongest contact toxicity against *Rhyzopertha dominica* with an LD_{50} value of 0.046 µL/insect, and against *Sitophilus oryzae* and *Sitophilus granarius* with LD_{50} values of 0.061 and 0.066 µL/insect, respectively, after 24 h [59]. Another study on *S. granarius* using an EO of a different chemotype (rich in carvacrol, 25.4%, and thymol, 7.51%) also confirmed its high contact toxicity, with LD_{50} and LD_{90} values calculated at 3.05 and 10.02 µg/insect, respectively, after 48 h [60].

The fumigant toxicity of oregano EO is also highly significant. In the study by Alkan, the *O. vulgare* var. verticium EO exhibited the highest toxicity against *S. oryzae*, with LC_{50} and LC_{90} values of 0.0104 and 0.0262 µL/mL air, respectively [59]. Fumigant efficacy against different life stages of the pest has also been proven; the EO of an Egyptian chemotype, predominantly containing pulegone (77.45%), demonstrated the most potent toxicity among ten tested EOs against both larvae and adults of *Tribolium confusum*. The LC_{50} of this EO against adults was 1.26 µL/L air after 7 days, and against larvae, it was 22.81 µL/L air. The EO also exhibited significant ovicidal activity with an LC_{50} of 5.84 µL/L air [61].

6.2. Behavioral Effects (Repellency and Antifeedant)

In addition to its direct lethal effects, *O. vulgare* can also influence pest behavior. An EO rich in carvacrol (56.62%) showed effective repellent properties against adults of *Tribolium castaneum* (80.00 ± 10.00% repellency after 120 h) and larvae of *Plodia interpunctella* (77.12 ± 10.80% repellency after 72 h). However, the same EO acted as an attractant for *T. castaneum* larvae [62]. In another study, a carvacrol-rich (81.4%) EO had strong repellent properties (70 ± 10.5% after 24 h) against *T. confusum* and, more importantly, exhibited a very powerful antifeedant effect, which led to weight loss in the treated insects [63]. Behavioral and physiological effects were also observed in *S. granarius*, where, in addition to its repellent properties, the EO caused a reduction in the insects' respiration rate, indicating physiological stress [60].

6.3. Application Methods and Novel Formulations

To enhance efficacy and practical application, various forms of oregano have been tested. In one study, a 3% dose of dried *O. vulgare* leaf powder resulted in a corrected mortality (%) of 55.0 ± 13.2%. Furthermore, in the repellency assay, the oregano powder performed exceptionally well, recording a repellency index of 0.7 ± 0.2 [64]. Another application method involved coating wheat grains with a microemulsion of *O. vulgare* ssp. *hirtum* EO (rich in carvacrol, 95.3%). At a concentration of 1000 ppm, this method was particularly effective against *T. castaneum* larvae, causing 87.8% mortality after 14 days. Interestingly, this treatment was also highly toxic to adults of *Trogoderma granarium*, eliminating 82.2% of them after 7 days. However, the EO showed low toxicity against *T. granarium* larvae [65]. These results underscore the importance of considering the pest species and its developmental stage in pest management programs. Overall, these diverse biological activities (antibacterial, antifungal, anti-yeast, and anti-insect) establish the broad-spectrum preservative potential of *O. vulgare*. Figure 2 depicts an overview of the broad-spectrum biological activities of *O. vulgare* as a natural preservative.

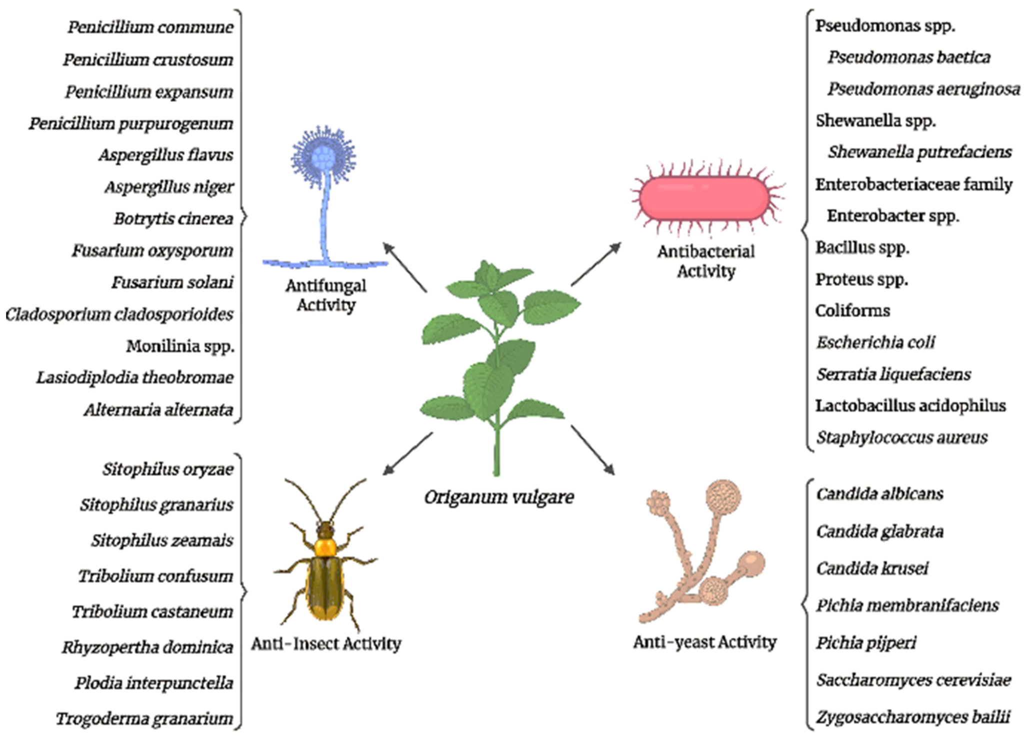

Figure 2. Overview of the broad-spectrum biological activities of *O. vulgare* as a natural preservative.

Furthermore, these findings confirm that the anti-insect activity of O. vulgare depends on both chemotype and effective dose. LD_{50}, LD_{90}, and LC_{50} values reported across insect studies [59–65] demonstrate that reproducible toxicity and repellency are achieved only at sufficient concentrations, while low doses fail to suppress pest populations. These shifts in thymol, carvacrol, and pulegone composition help explain the variability in insecticidal efficacy.

7. Preservative Effects and Related Mechanisms

As previously discussed, *O. vulgare* EO inhibits the growth of microorganisms through a multi-target strategy. This includes cell membrane disruption, interference with central metabolism, induction of oxidative stress, and inhibition of vital pathways. At the same time, with strong antioxidant properties and the ability to modulate host physiology, it protects the food matrix from spoilage, establishing it as a powerful and multifunctional natural preservative. Moreover, the preservative efficacy of *O. vulgare* depends on both chemotype and effective dose. MIC, LC_{50}, and antioxidant values reported across preservative studies [66–68] show that reproducible protection is achieved only at sufficient concentrations, while low doses fail to prevent microbial growth or oxidative damage. These shifts in thymol, carvacrol, and related phenolic composition help explain the variability in preservative outcomes. Figure 3 presents the multifaceted mechanisms of action of *O. vulgare* in food preservation.

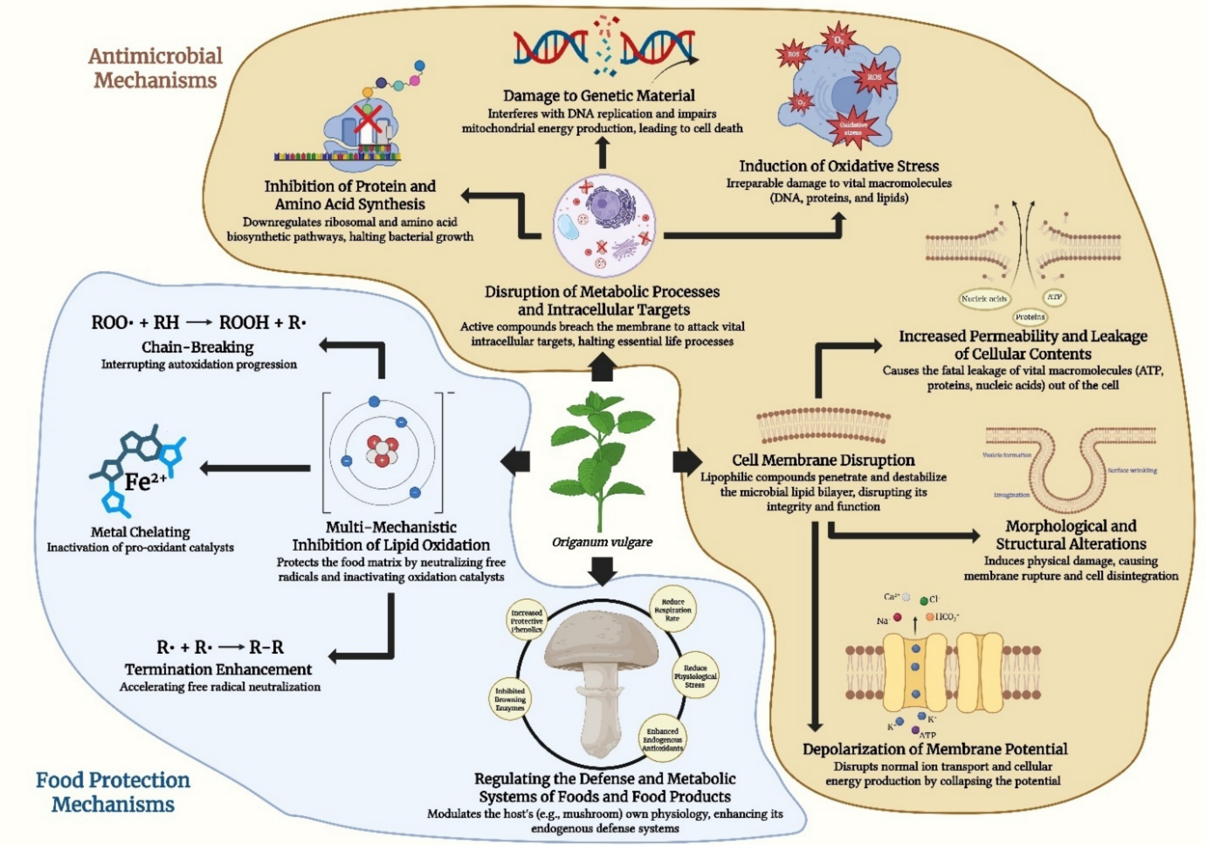

Figure 3. The multifaceted mechanisms of action of *O. vulgare* in food preservation.

7.1. Primary Mechanism: Cell Membrane Disruption

The primary target of the active compounds in oregano EO is the cell membrane of microorganisms. Due to their lipophilic nature, these compounds readily penetrate the lipid bilayer of bacteria, fungi, and protozoa, severely disrupting its integrity and function [66,67]. This destructive process occurs through several simultaneous pathways. Oregano EO significantly increases membrane permeability [68]. This leads to the extensive leakage of critical intracellular macromolecules such as nucleic acids, proteins, and ATP out of the cell [68–71]. For instance, in the treatment of *E. coli* O157:H7 with this EO, the concentrations of extracellular nucleic acids and proteins increased 9.75-fold and 6.42-fold, respectively [68]. The EO causes the depolarization of the cell membrane potential, which impairs its normal function in ion transport and energy production [68].

Morphological and structural alterations accompany these effects, as microscopic observations reveal cell surface wrinkling, invagination, vesicle formation, and ultimately complete membrane rupture and disintegration of the cellular structure [67–71]. These damages have been clearly observed in a wide range of microorganisms, including *S. aureus* [67], *E. coli* [68], *A. flavus* [39], and even the parasite *Leishmania infantum* [72]. This mechanism of membrane disruption can be intensified by other methods. For example, combining the EO with ultrasound significantly enhances the physical destruction of the membrane [71], while its combination with ε-polylysine inflicts more severe damage to the bacterial membrane [70].

7.2. Disruption of Metabolic Processes and Intracellular Targets

After breaching the membrane's defensive barrier, the compounds of oregano EO attack vital intracellular targets. Proteomic studies on *S. aureus* show that carvacrol-rich EO downregulates the expression of key proteins in ribosomal pathways and amino acid biosynthesis (valine, leucine, isoleucine, phenylalanine), thereby halting bacterial growth and proliferation [67]. Oregano EO causes a significant increase in the production of reactive oxygen species (ROS) within the microbial cell [39,72]. This oxidative stress inflicts irreparable damage to vital macromolecules such as DNA, proteins, and lipids [69,71,73].

In the fungus *A. flavus*, carvacrol leads to ROS accumulation and disrupts antioxidant defense systems [39]. Similarly, in the parasite *Leishmania*, increased ROS production is one of the primary pathways leading to cell death [72]. This effect can be strongly potentiated by combining the EO with ultrasound [71] or light [73]. EO also penetrates the cell and damages genetic material [74], disrupting DNA replication, impairing mitochondrial function, and inhibiting key intracellular enzymes. This interference with the energy cycle ultimately leads to cell death via apoptosis or autophagy [39,70–72].

7.3. Antioxidant Mechanisms in Food Protection

In addition to its antimicrobial properties, oregano EO is a potent antioxidant that prevents lipid oxidation and food spoilage [73,75]. Phenolic compounds such as carvacrol and terpinen-4-ol interrupt autoxidation chain reactions, preventing their progression[75], and their efficacy in inhibiting lipid peroxidation has been reported to exceed that of the synthetic antioxidant butylated hydroxytoluene [76]. Non-phenolic terpenes such as gamma-terpinene contribute to oxidative stability by accelerating the termination reactions of free radicals [75]. Carvacrol can form stable complexes with metal ions such as iron (II). This action prevents metal ions from acting as catalysts in oxidation reactions [73,76].

7.4. Indirect Mechanisms: Modulation of Host Physiology and Defense System

In some applications, such as active packaging, oregano EO contributes to shelf-life extension not by directly acting on microbes, but by regulating the defense and metabolic systems of the food product itself. In a study on the button mushroom (*Agaricus bisporus*), an active film containing oregano EO reduced the respiration rate and physiological stress in the mushroom tissue, increased the activity of the mushroom's endogenous antioxidant enzymes (superoxide dismutase and catalase), inhibited the enzymes responsible for browning (polyphenol oxidase and peroxidase), and, by regulating the phenylpropanoid pathway, contributed to the accumulation of protective phenolic compounds in the mushroom tissue [77].

These indirect preservative effects are strongly influenced by concentration, with reproducible physiological modulation observed only at sufficient doses, while sub-lethal levels fail to achieve stability. In addition, residues after EO extraction retain nonvolatile phenolics with preservative activity, enhancing sustainability of the industrial chain [52,53].

In summary, oregano EO effectively inhibits the growth of microorganisms through a multi-target strategy, including cell membrane disruption, interference with central metabolism, induction of oxidative stress, and inhibition of vital pathways. Concurrently, with its strong antioxidant properties and its ability to modulate host physiology, it protects the food matrix from spoilage, establishing it as a powerful and multifunctional natural preservative.

8. Nanotechnology and Future Perspective

The application of nanotechnology has emerged as a highly effective strategy to overcome the inherent limitations of oregano EO such as high volatility and low water solubility, thereby enhancing its preservative potential in food systems. Nanoencapsulation techniques, including the fabrication of nano-emulsions and polymeric nanoparticles, have been shown to significantly improve the stability, water dispersibility, and controlled release of oregano EO's active compounds [10,78–80]. For instance, chitosan-based coatings containing oregano EO nano-formulations have effectively delayed microbial growth and lipid oxidation in turkey meat, consequently extending its shelf life while maintaining high sensory acceptability [81]. Similarly, oregano EO-loaded nano-emulsions have demonstrated potent antifungal activity against spoilage fungi like Penicillium sp. and Fusarium sp. in cheese [82], and anti-yeast activity against *Zygosaccharomyces bailii* in salad dressings, often proving more effective than the non-encapsulated oil [80]. Advanced fabrication methods such as electro-spraying have enabled the production of thermally stable chitosan and polyvinyl alcohol-chitosan nanoparticles with high encapsulation efficiency (up to 79.6%) and a sustained-release profile, which significantly increases the antifungal efficacy against post-harvest pathogens like *A. alternata* and *A. niger* [10,78]. Furthermore, polymeric nanoparticles of oregano EO have shown enhanced insecticidal effects against stored-product pests, coupled with a favorable safety profile, indicating their potential as a safe and potent delivery system in the food industry [83].

The well-documented, broad-spectrum antimicrobial and antioxidant properties of *O. vulgare* are primarily attributed to cell membrane disruption and induction of oxidative stress [66–68]. Nanotechnology presents a clear path forward for its practical application as a food preservative. The challenges associated with the direct use of oregano EO, such as its interaction with the food matrix and the need for effective concentrations, can be effectively mitigated through nano-delivery systems that ensure higher efficacy at lower doses [80].

Future research should focus on optimizing these nano-formulations for specific food matrices to maximize their activity while minimizing sensory impacts. The development of scalable and cost-effective production methods is imperative for the transition of these technologies from the laboratory to an industrial scale. Although initial studies indicate a good safety profile [83]. Smart active packaging systems represent a promising frontier. In these systems, nano-encapsulated oregano EO is released in response to environmental triggers such as pH changes or the presence of specific microorganisms. Such intelligent systems would allow for a targeted and more efficient use of this potent natural preservative, paving the way for a new generation of safe and sustainable food preservation technologies.

9. Conclusions

This review demonstrates that *O. vulgare*, particularly its oregano EO and extracts, holds significant potential as a multifunctional natural preservative in the food industry. Its potent bioactive compounds, especially carvacrol and thymol, underpin broad antimicrobial activity against bacteria, fungi, yeasts, and stored-product pests. The mechanisms involve disruption of microbial cell membranes, interference with metabolic processes such as protein synthesis, and induction of oxidative stress. At the same time, strong antioxidant properties protect the food matrix by inhibiting lipid peroxidation and chelating metal ions. This review also emphasizes the challenges of practical application, including chemotype variation, concentration requirements, and interactions with food components. Modern technologies, particularly nanotechnology, provide solutions by enhancing stability, water dispersibility, and controlled release of oregano EO. Nano-formulations improve efficacy at lower doses and extend activity in real food systems. This review concludes that integrating traditional knowledge with scientific innovation, focusing on smart nano-formulations, comprehensive safety assessments, and optimization for specific food matrices, can pave the way for replacing synthetic preservatives. Oregano EO emerges as a sustainable and powerful cornerstone for the next generation of food preservation technologies.

Author Contributions: M.H.H.: Writing—original draft, software-structure drawing, review and final editing. L.N.: Validation, review and final editing. E.H.: Conceptualization, review and final editing. S.D.S.: review and final editing. All authors have read and agreed to the published version of the manuscript.

Funding: Lutfun Nahar gratefully acknowledges the support from the European Regional Development Project ENOCH #CZ.02.1.01/0.0/0.0/ 16_019/0000868, and the Czech Science Foundation Project #23-05474S.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Conflicts of Interest: Given the role as Editor-in-Chief, Lutfun Nahar had no involvement in the peer review of this paper and had no access to information regarding its peer-review process. Full responsibility for the editorial process of this paper was delegated to another editor of the journal.

Use of AI and AI-Assisted Technologies: No AI tools were utilized for this paper.

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